THE MORPHOLOGY, REPRODUCTIVE BIOLOGY AND HABITAT UTILISATION OF THE EXOTIC INVASIVE LIZARD, THE BROWN ANOLE (*ANOLIS SAGREI*), IN TAIWAN

by

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(Date submitted)

DECLARATION

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I declare that **THE MORPHOLOGY, REPRODUCTIVE BIOLOGY AND HABITAT UTILISATION OF THE EXOTIC INVASIVE LIZARD, THE BROWN ANOLE (*ANOLIS SAGREI*), IN TAIWAN** is my own work and that all the sources that I have used or quoted have been indicated and acknowledged by means of complete references.

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Summary

Surveys and vegetation analyses were used to determine the known distribution and the characteristics of the habitat utilised by *Anolis sagrei* in Taiwan. Sampled lizards were used for morphological comparisons, and to investigate the reproductive biology of this species in Taiwan.

The results of this study indicate that the distribution of *A. sagrei* in Taiwan is extensive (≥237 ha) in Chiayi City and County (southwestern study site) and scattered (≥8 ha) in Hualien City and County (eastern study site). These lizards were mostly found in open sunny degraded man-made habitats.

Although some variations were noted in the comparisons between the *A. sagrei* collected from the two study sites, it was concluded that the two populations likely have the same founder population.

The reproductive biology study indicated that photoperiod and the associated temperatures determine the reproductive cycles in *A. sagrei*. It also demonstrated that reproduction in this species is energetically demanding.

Key Terms

abdominal fat weight cycle; *Anolis sagrei*; brown anole; habitat preference; human commensal; income breeder; invasive species; liver weight cycle; lizard; photoperiod; reproductive biology

TABLE OF CONTENTS

APPENDICES

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Tables

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Appendices

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CHAPTER 1 – INTRODUCTION

1.1. BACKGROUND TO THE STUDY

Lizards first appeared about 150 to 200 million years ago, during the late Jurrasic period (Mattison, 1997; Evans, 2003; Pianka and Vitt, 2003). Today, modern lizards (order: Squamata; suborder: Sauria) constitute the largest clade (> 4 500 species) of living reptiles, and occur in almost all parts of the world, except the poles and a few oceanic islands (Mattison, 1997; Zug *et al*., 2001). Based on their distribution, lizard families are broadly categorized into one of the following categories (Mattison, 1997; Pianka and Vitt, 2003):

- Families that have a distribution that is almost worldwide.
- Families that have a wide distribution in a particular region of the world.
- Families that have a restricted distribution, or relic populations in parts of the world.

Throughout the geographic range of lizards, they occur in a wide variety of habitats, ranging from deserts to tropical forests, and within specific habitats, different lizard species often utilise different habitat niches (Pianka and Vitt, 2003). Some lizards, such as the giant girdled lizard (*Cordylus giganteus*) and the Peter's ground agama (*Agama armata*), are terrestrial, and are usually restricted to living on the soil surface (Branch, 1998). A few species, such as the greater legless skinks (*Acontias* spp.) and blind legless skinks (*Typhlosaurus* spp.), are fossorial and are usually found under stones or logs, in loose soil or leaf litter (Branch, 1998). Others, such as the dwarf chameleons (*Bradypodiun* spp.), are arboreal and are rarely found on the ground (Branch, 1998).

Many species, such as the brown basilisk (*Basiliscus vittatus*) and the bearded dragon (*Pogona barbata*), are semi-arboreal and can often be found on the ground or perching on tree trunks and other objects (Cogger, 2000; Lee, 2000). Although no lizard species is known to be truly aquatic, some species, such as the Nile monitor (*Varanus niloticus*), are semi-aquatic, and use lakes and rivers for foraging and to escape from potential predators (Branch, 1998; Spawls *et al*., 2002). Even though some species such as the mangrove skink (*Emoia atrocostata*), live among rocks and crevices of the littoral zone of some coastal areas (Cogger, 2000), the Galápagos marine iguana (*Amblyrhynchus cristatus*), is the only species known to make use of a marine environment for feeding (Trillmich and Trillmich, 1986; Pianka and Vitt, 2003).

Since lizards inhabit and utilise a variety of habitats and niches, it is not surprising that there is much variation in their diets. With the exception of a few lizard species, such as the Galápagos land iguana (*Conolophus subcristatus*) and the Solomon Islands skink (*Corucia zebrata*), which are herbivorous (Cooper, 2000; Costantini *et al*., 2005), the majority of lizards are carnivorous, and even among herbivorous species, most will occasionally prey on some arthropods and other invertebrates, especially as juveniles (Pianka and Vitt, 2003). Some large lizard species, such as the banded Gila monster (*Heloderma suspectum cinctum*), prey on vertebrates such as small rodents and birds (Beck, 1990), while the Komodo dragon (*Varanus komodoensis*), the largest living lizard species, is capable of preying on large prey such as pigs and water buffalo (*Bubalus bubalis*) (Pianka and Vitt, 2003). Lizard species such as the thorny devil (*Moloch horridus*), which specialises in feeding on ants (Pianka and Pianka, 1970), and Burton's legless lizard (*Lialis burtonis*), which only preys on other lizards (Wall and Shine, 2013), are highly specialized in their diets and will only prey on specific prey types, while other species such as blue-tongued skinks (*Tiliqua scincoides*) have a catholic diet and will feed on whatever suitable food sources are available (Koenig *et al*., 2001). Often, lizards that live in or around human households will learn to utilise food that they would not encounter in the wild. For example, Poulin *et al*. (1995) reported on Pacific house geckos (*Hemidactylus frenatus*) drinking sugar water from hummingbird birdfeeders, whilst striped skinks (*Trachylepis punctatissima*) have been recorded feeding in an urban setting on various unnatural food sources, such as bits of bread, cake, ice cream, jelly (Fig. 1.1), mince, popcorn, potato chips and spaghetti (Norval and Norval, 2007).

Figure 1.1. A striped skink (*Trachylepis punctatissima*) feeding on raspberry jelly that was dropped on a paved area in an urban garden in Johannesburg, South Africa.

Due to this large variation in the diet of lizards as a group, it is not possible to provide an accurate description of their diets. However, various lizard species tend to make use of one of two foraging strategies, each with food that has certain characteristics (Huey and Pianka, 1981; Pianka and Vitt, 2003):

- Widely foraging – these are active lizards that tend to prey more on food items that are sedentary, unpredictably distributed, clumped, and/or are large and hidden.
- Sit-and-wait (ambush) – these are usually sedentary lizards, which tend to prey on more active food items that are mobile, on the surface, and visually conspicuous.

The evolutionary adaptations of lizards to particular habitats and niches not only lead to variations in their diets and foraging modes, but also in other natural history aspects such as reproduction. Reproduction in lizards begins with mate attraction and courting through various types of signals, which can be visual, chemical, acoustic and/or tactile (Pianka and Vitt, 2003). The function of these signals during mate attraction and courting is for species identification and mate selection (Pianka and Vitt, 2003). Although most lizards are polygamous, some long-lived species are monogamous (at least for a given breeding season), and in some species such as the Australian sleepy lizard (*Tiliqua rugosa*), partnerships of the same individuals may reform for consecutive years (Bull and Pamula, 1998; Bull, 2000; Pianka and Vitt, 2003).

Mate attraction is usually followed by mating, during which a male lizard twists his tail beneath that of the female, inserting one of his everted hemipenes into the female's cloaca and transfers sperm directly into it (Mattison, 1997). Male lizards often use their jaws to grasp the female during mating, and copulation may take place several times over a few days or several weeks (Mattison, 1997). Fertilization does not always take place immediately, and the females of some species, such as *H. frenatus*, have the ability to store sperm for up to several months (Cuellar, 1966; Murphy-Walker and Haley, 1996; Mattison, 1997). Such oviductal sperm storage enables females to produce consecutive fertile clutches or litters after isolation from males (Murphy-Walker and Haley, 1996), and can even permit females that mate with multiple males to produce genetically diverse offspring (Calsbeek *et al*., 2007).

Mating and egg fertilization do not take place in all lizard species. Some lizard species, such as the mourning gecko (*Lepidodactylus lugubris*), are the result of hybridisation between congeneric bisexual species (Darevsky *et al*., 1985; Yamashiro *et al*., 2000; Zug *et al*., 2001). The resulting hybrids are all-female obligate parthenogenetic species (Röll and von Düring, 2008), and although in species such as the New Mexico whiptail lizard (*Aspidoscelis neomexicana*), some females engage in pseudocopulation (one female behaves like a male and attempts to mate with another female) (Zug *et al*., 2001), no true copulation takes place. Therefore, with the exception of rare instances of mutation in obligate parthenogenic species, offspring are genetically identical diploid clones of the mother (Röll and von Düring, 2008). When a parthenogenic female backcrosses with a male of one of the parental or of another related species, it results in triploid clones, some of which are sterile males (Darevsky *et al*., 1985; Zug *et al*., 2001; Röll and von Düring, 2008). Since each female of an obligate parthenogenic species produces almost exclusively females, the population growth of such species can be very large (Zug *et al*., 2001).

Another form of asexual reproduction can be observed in some varanids. In the absence of males for extended periods of time, the females of the Argus monitor (*Varanus panoptes*), *V. komodoensis*, and ornate Nile monitor (*Varanus ornatus*) have the ability to be facultative parthenogenic (Lenk *et al*., 2005; Watts *et al*., 2006; Hennessy, 2010). However, since the sex determination in monitor lizards involves a ZZ/ZW mechanism, during asexual reproduction (i.e. facultative parthenogenic reproduction) the homozygous offspring will be either WW, which is not a viable combination, or are all ZZ males (Röll and von Düring, 2008). Facultative parthenogenic reproduction has only been recorded in females kept isolated in captivity for extended periods of time, and has not been recorded in wild populations (Röll and von Düring, 2008). In addition to that, since only some of the offspring are viable, and are males, this form of reproduction does not replace sexual reproduction, and thus can be expected to play an unimportant role in the species concerned (Röll and von Düring, 2008).

Like most other reptiles, the majority of lizard species are oviparous (Mattison, 1997; Zug *et al*., 2001; Pianka and Vitt, 2003), but about 20% are viviparous. In oviparous species, the ovum is fertilized in the upper portion of the oviduct and then as it progresses down the oviduct, it is subsequently coated with albumin, and finally a thin layer of protein fibers (the egg shell) (Zug *et al*., 2001). In some species, such as the Stejneger's grass lizard (*Takydromus stejnegeri*), the eggs are deposited in a suitable nesting site soon after being formed (Lin *et al*., 2004), while other species, such as some populations of the common lizard (*Zootoca vivipara*; formerly *Lacerta vivipara*), retain their eggs in the oviduct, allowing embryonic development to be more advanced, before oviposition

(Heulin *et al.*, 2002). This intrauterine retention and incubation of eggs is what is believed to have eventually led to the evolution of live-bearing in some reptile species, i.e. a complete development of embryos within the mother, and the neonates being delivered live without an eggshell encasing them (Shine and Bull, 1979).

Formerly, the term "ovoviviparous" was used for live-bearing lizard species in which the embryonic development relied exclusively on the supplied yolk, and "viviparous" for species in which the embryo relied on non-yolk nutrition from the mother (Blackburn, 1982). Currently, the majority of people working on these species refer to all live-bearing species as viviparous since the distinction between ovoviviparity and viviparity in reptiles is artificial and impractical (Blackburn, 1982). Viviparity in lizards has enabled some species, such as *Z. vivipara*, to colonize cooler temperate zone habitats, which would otherwise have been unsuitable due to the environmental conditions that would prevent embryonic development in eggs produced by oviparous species (Blackburn, 1982; Surget-Groba *et al*., 2001; Zug *et al*., 2001; Pianka and Vitt, 2003).

Among lizard species, there is considerable variation in the reproductive period (breeding season), which can be induced and regulated by direct factors such as temperature, photoperiod and/or rainfall, and by indirect factors such as food availability (Mattison, 1997; Pianka and Vitt, 2003). In some tropical species, reproduction can take place throughout the year, while reproduction in temperate zone species is usually restricted to a few months of the year during which the requirements for reproduction are met (Tinkle, 1969; Pianka and Vitt, 2003).

There is also variation among lizard species in the number of eggs per clutch or neonates per litter produced. For example, all members of the genus *Anolis*, produce a single egg (Andrews and Rand, 1974), whilst species, such as *V. niloticus*, may produce clutches consisting of up to 60 eggs (Branch, 1998; Spawls *et al*. 2002). Such variation in the number of potential offspring per reproductive bout is not limited to only oviparous species, and viviparous species also exhibit a large variation in the number of neonates produced per litter. For example, *T. rugosa* produces only one to three neonates per litter (Bull, 1987), whereas the related species, *T. scincoides* can produce up to 18 neonates per litter (Shea, 1981). In species, such as the flap-necked chameleon (*Chamaeleo dilepis*) and Cape grass lizard (*Cordylus anguinus*), the number of eggs per clutch or neonates per litter depends on the body size of the female, with larger females being able to produce more offspring per breeding period (Du Toit *et al*., 2003; Pianka and Vitt, 2003; Reaney *et al*., 2012).

In some other oviparous species, such as the side-blotched lizard (*Uta stansburiana*), and viviparous species, such as the southern water skink (*Eulamprus tympanum*), clutches or litters can consist of either a few large eggs or neonates, or many smaller eggs or neonates, depending on the available energy and prey (Nussbaum, 1981; Doughty and Shine, 1998; Warner *et al*., 2007). When prey is plentiful, females produce many, but smaller offspring (*r*-selection), however, if resources are limited, females produce fewer, but larger and more competitive offspring (*K*-selection) (Pianka and Vitt, 2003).

Clutches or litters not only vary in size, but also in the frequency in which they are produced. Although many lizards, such as the Cape flat lizard (*Platysaurus capensis* *minor*), have cyclic breeding seasons and only produce one or two clutches or litters per breeding season (Van Wyk and Mouton, 1996), some species, such as the northern grass lizard (*Takydromus septentrionalis*) are able to produce multiple clutches depending on the abundance of prey, and under conditions of excess food can produce numerous clutches in a relatively short period of time (Luo *et al*., 2010).

In the jacky dragon (*Amphibolurus muricatus*), a common south-eastern Australian species with a cyclic breeding season, it was found that both stored energy and recently acquired nutrients were utilised to fuel reproduction (Warner *et al*., 2008). This energetics strategy is very likely used by many lizard species, but not all. In the side-blotched lizard (*Uta stansburiana*), a cyclic breeding species from the Pacific coast of North America, the initial clutch is produced using stored energy (capital breeding; i.e. it utilises energy that was acquired and stored prior to the reproductive period for reproduction), and recently acquired energy is used to produce the second clutch (income breeding; it utilises energy acquired during the reproductive period for reproduction) (Hahn and Tinkle, 1965). Some other species, such as the collared lizard (*Crotaphytus collaris*), are completely capital breeders, and the amount of stored energy influences the clutch frequency (Telemeco and Baird, 2011). In some tropical species, such as the geckos *Cosymbotus platyurus*, *H. frenatus*, and *Peropus mutilatus*, there are no reproductive seasons and the lizards can reproduce throughout the year (Church, 1962). These species also has no fat bodies present throughout the year (Church, 1962), indicating that they are solely income breeders. It is thus apparent that in lizards, as in other animals, the energy acquired by foraging is allocated towards growth, maintenance, storage and reproduction, but among species, as in the other aspects of their natural history, there are variations in their allocation patterns.

Lizards and other squamates exhibit male heterogamety (XY and XXY) and female heterogamety (ZW), and although the sex of offspring is determined genetically in many species, in some species there seems to be a lack of sex chromosomes (Viets *et al*., 1994; Zug *et al*., 2001; Pianka and Vitt, 2003; Sarre *et al*., 2004). The result is that in many such species (from the families Agamidae, Eublepharidae, Iguanidae, and Lacertidae), the incubation temperature during the second trimester of the embryonic development determines the sex of the offspring (Bull, 1980; Viets *et al*., 1994; Zug *et al*., 2001; Pianka and Vitt, 2003; Sarre *et al*., 2004). Temperature-dependent sex determination is not only limited to oviparous species, and has even been recorded in the spotted skink (*Niveoscincus ocellatus*; family Scincidae), a viviparous species from Tasmania (Wapstra *et al*., 2004). Among species in which there is temperature-dependent sex determination, the temperature range within which development takes place and sex is determined is generally relatively small (*ca*. 25 - 35 ºC) (Zug *et al*., 2001). In most of the species in which the sex-determination pattern has been extensively examined, low and high incubation temperatures usually produce females, and at intermediate temperatures most of the offspring are males (Viets *et al*., 1994; Pianka and Vitt, 2003). For example, in the leopard gecko (*Eublepharis macularius*), hatchlings are predominately females if the eggs are incubated at cool (24 – 28 ºC) and high (32 – 35 ºC) incubation temperatures, but are mainly males at intermediate (32 – 32.5 ºC) incubation temperatures (Viets *et al*., 1993). In other species, such as the common agama (*Agama agama*) at low temperatures, most offspring are reportedly females, whereas males usually result from high temperatures (Viets *et al*., 1994; Zug *et al*., 2001).

Nest site choices are not only important for species with temperature-dependent sex determination. As in any oviparous reptiles, there is an acceptable temperature range wherein successful embryonic development can take place (Birchard, 2004), so an oviparous female lizard has to select a nest site that falls within a particular temperature range. Many geckos, such as the Cape dwarf gecko (*Lygodactylus capensis*), produce eggs that have calcified shells, which are resistant to dehydration, so eggs can be laid under loose bark or in cracks in rocks with the right temperatures (Branch, 1998; Pianka and Vitt, 2003). However, most oviparous lizards produce eggs with a leathery shell that permits the absorbtion of water (Pianka and Vitt, 2003). In these species the female must select a nest site that meets the thermal and hydric environment requirements of the particular species (Overall, 1994). As can be expected, there are considerable variations in the nest sites selected by various species. In *V. niloticus*, for example, the female excavates a hole in a termite nest that is still occupied by the termites, and lays her eggs within it (Branch, 1998; Spawls *et al*., 2002). The termites then repair the nest, and as a result the eggs of the lizard are enclosed within the nest where they are incubated by the constant temperature and humidity within the nest (Branch, 1998; Spawls *et al*., 2002). Some lizards, such as the long-tailed skink (*Eutropis longicaudata*), lay their eggs under large rocks (Huang and Pike, 2011), whilst others, like the blue-tailed tree lizard (*Holaspis guentheri*), simply deposit their eggs under loose bark or in leaf litter (Branch, 1998). However, like the ground agama (*Agama aculeata*), most lizards deposit their eggs in carefully constructed nest holes in the ground, which are then buried (Branch, 1998; Pianka and Vitt, 2003).

Most lizards are secondary consumers in ecosystems, i.e. they are both predators and prey (Mattison, 1997; Pianka and Vitt, 2003). Lizards are preyed upon by a variety of mammals, birds, snakes, other larger lizards, some amphibians, and even some large arthropods, and therefore have evolved various defensive mechanisms for escaping predation (Mattison, 1997; Pianka and Vitt, 2003). Some species, such as the dwarf chameleon (*Bradypodion transvaalense*), rely on their cryptic coloration to prevent them from being detected by predators (Stuart-Fox *et al.*, 2006), and will rarely resort to fleeing to escape capture. Most lizard species will flee, and the fleeing behavior is often influenced by the lifestyle of the species. Terrestrial species usually flee to the nearest shelter, which can be a burrow, rock or other object under which it can hide (Pianka and Vitt, 2003). Arboreal species usually flee to a higher part of the tree or shrub it is in. Some arboreal species, such as the southern tree agama (*Acanthocerus atricollis*), may even move around the trunk of a tree in such a manner that it places the tree trunk between itself and the potential predator (Branch, 1998), a behavior referred to as squirreling (Regalado, 1998). Species that are usually associated with rivers, such as most members of the genus *Neusticurus*, may dive into the water to escape from predators (Pianka and Vitt, 2003). Some species display at potential predators, i.e. an honest signal to predators that they were detected by the lizard and that the lizard is in a physical condition that would enable it to run fast enough and/or far enough to avoid capture. Such displays can include dewlap and push-up displays as done by the Puerto Rican crested anole (*Anolis cristatellus*) (Leal, 1999), tail displays such as those of the zebra-tailed lizard (*Callisaurus draconoides*) (Hasson *et al*., 1989), or arm-waving displays as done by the Bonaire whiptail lizard (*Cnemidophorus murinus*) (Cooper *et al*., 2004). The sub-adults of some species, such as the Bushveld lizard (*Heliobolus lugubris*, formerly *Eremias lugubris*), mimic noxious invertebrates (in the case of *H. lugubris*, a ground beetle, *Anthia* sp.; Huey and Pianka, 1977) in both coloration and locomotion, to avoid predation, while some other species, such as the scaly-foot (*Delma fraseri*) from Australia, mimic venomous snakes (in the case of *D. fraseri*, a the eastern brown snake, *Pseudonaja* [*Demansia*] *textiles*; Johnson, 1975) (Mattison, 1997; Zug *et al*., 2001). Larger species, such as the frillneck lizard (*Chlamydosaurus kingii*), employs bluff to intimidate potential predators (Shine, 1990), while some, like *V. niloticus*, may actually retaliate if cornered by a predator (Branch, 1998; Spawls *et al*., 2002). Some horned lizards (*Phrynosoma* spp.) may resort to ocular-sinus blood-squirting, while some members of the gecko genus *Diplodactylus* spray a sticky unpalatable liquid from their tail, to deter predators (Rosenburg and Russell, 1980; Sherbrooke and Middendorf, 2001; Zug *et al*., 2001).

When grasped by predators, individuals from most lizard species will struggle and many will retaliate in order to escape. During attacks by predators, the armadillo girdled lizard (*Cordylus cataphractus*) bites its own tail, forming a circle with its body, and thus becomes a prey item that is difficult to subdue and/or too large to ingest (Branch, 1998; Mouton *et al*., 1999). Many species also make use of tail loss (caudal autotomy) to escape from predators, and the juveniles of numerous species have brightly colored tails to draw the attention of predators towards the less important tail and away from the more vital parts of the body (Arnold, 1984; Bateman and Fleming, 2009).

Tail autotomy is a common defensive mechanism in lizards as a response to attempted predation (Vitt *et al*., 1977; Arnold, 1984; Bateman and Fleming, 2009). However, since the tails of lizards may be utilised in predator distraction and escape, sexual displays, defense, balance, fat storage, locomotor stabilization, and/or climbing (Vitt *et al*., 1977), the loss of a tail could result in relatively short term (in species that are capable of regenerating the lost tail) or permanent (in species that are incapable of regenerating the lost tail) costs (Arnold, 1984; McConnachie and Whiting, 2003; Bateman and Fleming, 2009). Since the metabolic costs of regenerating a lost portion of the tail will bring an additional energetic burden to the lizard (McConnachie and Whiting, 2003; Naya *et al*., 2007), it can be expected that the animal would have to meet these energetic demands by increased foraging and/or by directing energy away from growth, maintenance and reproduction (Arnold, 1988). In some lizards, when enough food is available, the associated costs, such as reduced body growth rate, during tail regeneration can be minimized (Ballinger and Tinkle, 1979).

Tail loss frequency has been employed to estimate estimate predation intensity on lizard populations (Schoener, 1979; Schoener and Schoener, 1982b; Pianka and Vitt, 2003). This method has weaknesses and limitations, because efficient predators will capture the lizard and thus not leave a broken tail (Jaksić and Busack, 1984; Medel *et al*., 1988; Pianka and Vitt, 2003). Tail loss frequency and regeneration therefore rather indicates lizard escape ability and predator inefficiency (Jaksić and Busack, 1984; Pianka and Vitt, 2003). In addition to that, it must also be taken into consideration that tail autotomy is not always due to attempted predation events, and can also be due to aggressive interactions between rivals (Arnold, 1984; Pianka and Vitt, 2003). As a result tail loss frequency data should be interpreted with caution.

Due to their association with humans, some small lizard species, such as the tropical gecko (*Hemidactylus mabouia*), are accidentally introduced into new localities by human activities (Meshaka *et al*., 2004). Other species, such as the black spinytail iguana (*Ctenosaura similis*), are intentially imported into some countries as pets (Meshaka *et al*., 2004). When introduced species escape and establish viable populations in the wild, are able to disperse without significant human assistance, and have a large impact on the new environments, they are considered to be invasive species (Davis and Thompson, 2000). Since lizards do not cause damages to agricultural products, the impacts of invasive lizards are primarily ecological. Through predation, invasive lizards can have an impact on prey populations, and can displace native lizard species as a result of competition. An example of how an invasive lizard can impact native species is the green anole (*Anolis carolinensis*) in the Ogasawara Islands of Japan, where the lizard is believed to be partly responsible for the decline of the five endemic odonates (*Boninagrion ezoin*, *Hemicordulia ogasawarensis*, *Indolestes boninensis*, *Rhinocypha ogasawarensis* and *Boninthemis Insularis*) and the Ogasawara snake-eyed skink (*Cryptoblepharus nigropunctatus*) as a result of competition and/or predation (Yoshimura and Okochi, 2005; Toda *et al*., 2010).

Of the 42 lizard species that have been recorded in Taiwan (Table 1.1), 17 are endemic, 20 are indigenous, and five are exotic invasive species. Even though *A. carolinensis*, and the tokay gecko (*Gekko gecko*), are both exotic species and have been recorded in the wild in Taiwan (Norval *et al*., 2011c; Norval *et al*., 2012c), there is currently no indication that viable populations exist in the wild, and are therefore not included in the current list of herpetofauna of Taiwan.

1.2. STUDY SPECIES

The genus *Anolis* is currently classified as belonging to the family, Dactyloidae, but was formerly placed under Iguanidae or Polychrotidae (Schulte *et al*., 2003; Townsend *et al*., 2011). It is one of the largest lizard genera, and contains over 300 species, which occur naturally throughout the warmer regions of the Americas (Sanger *et al*., 2008). The brown anole, (*Anolis sagrei*) Dumeril and Bibron 1837, is also sometimes called the Cuban anole (Meshaka *et al*., 2004). Although it has been proposed to reclassify *Anolis sagrei* as *Norops sagrei* (Guyer and Savage, 1986; Nicholson *et al*., 2012) the reclassification remains controversial (Cannatella, and de Queiroz, 1989; Poe, 2013), and consequently, herein the more widely accepted nomenclature, *Anolis sagrei*, is used.

Anolis sagrei is believed to have originated in Cuba, and subsequently colonised the neighbouring islands of Archipiélago de los Colorados, Archipiélago de los Canarreos, Archipiélago de Sabana-Camagüey, Archipiélago de los Jardines de la Reina, and Isla de la Juventud (Williams, 1969; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999). Through riding on floating vegetation (rafting; Williams, 1969), and even possibly

Table 1.1. A list of the lizard species known to occur in Taiwan and the surrounding offshore islets within the territorial waters of Taiwan.

Family	Species	Status
Agamidae	*Japalura brevipes*	Endemic
	Japalura luei	Endemic
	Japalura makii	Endemic
	Japalura polygonata xanthostoma	Endemic
	Japalura swinhonis	Endemic
	Physignathus cocincinus	Introduced
Anguidae	*Dopasia harti*	Indigenous *
Dactyloidae	*Anolis sagrei*	Introduced
Gekkonidae	*Gehyra mutilata*	Indigenous
	Gekko hokouensis	Indigenous
	Gekko kikuchii	Endemic *
	Gekko monarchus	Introduced
	Hemidactylus bowringii	Indigenous
	Hemidactylus frenatus	Indigenous ?
	Hemidactylus stejnegeri	Indigenous
	Hemiphyllodactylus typus typus	Indigenous ?
	Lepidactylus lugubris	Introduced
	Lepidodactylus yami	Endemic *
Iguanidae	*Iguana iguana*	Introduced
Lacertidae	*Takydromus formosanus*	Endemic
	Takydromus hsuehshanesis	Endemic
	Takydromus kuehnei	Indigenous
	Takydromus luyeanus	Endemic
	Takydromus sauteri	Endemic
	Takydromus septentrionalis	Indigenous
	Takydromus stejnegeri	Endemic
	Takydromus viridipunctatus	Endemic
Scincidae	*Ateuchosaurus chinensis*	Indigenous *
	Emoia atrocostata	Indigenous
	Eutropis cumingi	Indigenous *
	Eutropis longicaudata	Indigenous
	Eutropis multicarinata	Indigenous *
	Eutropis multifasciata	Introduced
	Plestiodon chinensis formosensis	Endemic
	Plestiodon chinensis leucostictus	Endemic *
	Plestiodon elegans	Indigenous
	Scincella boettgeri	Indigenous
	Scincella formosensis	Endemic
	Scincella modesta	Indigenous
	Sphenomorphus incognitos	Indigenous
	Sphenomorphus indicus	Indigenous
	Sphenomorphus taiwanensis	Endemic **

Note: * – occurs on some of the surrounding offshore islets within the territorial waters of Taiwan but not on the main island.
** – a species complex that is currently being investigated and may possibly be divided into several species at a future stage.
? – a species of which the natural distribution is not clear, and which could be an invasive species in Taiwan.

free floatation (Schoener and Schoener, 1984), *A. sagrei* successfully dispersed further and managed to colonise the Bahamas, occurring on Cay Sal Bank, Great Bahama Bank, Crooked Bank, Little Bahama Bank, Rum Cay, Half Moon Cay, San Salvador, Little Cayman, and Cayman Brac (Williams, 1969; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999). *Anolis sagrei* also managed to colonise the Atlantic coast of México to Belize, including Isla Conzumel, Islas de la Bahía, and Swan Islands (Honduras) (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999).

Anolis sagrei is a very successful invasive species, and although not confirmed, it is suspected that *A. sagrei* was introduced into Jamaica by anthropogenic activities as opposed to getting there through natural dispersal mechanisms (J.B. Losos, *pers. com.*[1]). Introduced populations of *A. sagrei* have been recorded in parts of the Americas, as well as some localities in the Pacific region (Table 1.2). In Taiwan, *A. sagrei* is known to exist in two localities; Chisintang, Hualien County, eastern Taiwan (Chang, 2007), and Santzepu, Sheishan District, Chiayi County, southwestern Taiwan (Norval *et al*., 2002). Due to its small body size, which makes it easy to hide among objects, and its tendency to be anthropogenic-commensal, *A. sagrei* has a very high probability of colonizing new sites. For example, in addition to being dispersed along with nursery products (Kraus, 2009), these lizards have also been observed to disperse by riding on boats and recreation vehicles or on piles of firewood that are being transported (Campbell, 1996), and Norval and Mao (2007) demonstrated that *A. sagrei* can unintentionally be transported to new localities in bundles of bamboo. There is thus a very strong likelihood that the distribution of *A. sagrei* in Chisintang and Santzepu is more extensive than what is

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Table 1.2. Localities, outside the native range of *Anolis sagrei*, in which populations of these lizards have established.

Region	**Locality**	**Reference**
Cayman Islands	Grand Cayman	Minton and Minton, 1984; Franz *et al*., 1987
Grenada, West Indies	Saint George	Greene *et al*., 2002
Hawai'i (U.S.A.)	Hawai'i (island)	Krysko and Granatosky, 2010; Mautz and Shaffer, 2011
	Kaua'i	Kraus, 2003
	Maui	Kraus, 2006
	O'ahu	Kishinami and Kishinami, 1996; Kraus, 2002; Powell and Pansza, 2005
Jamaica	Manchester	Kolbe *et al*., 2004
	Portland	Kolbe *et al*., 2004
	St. Ann	Landwer *et al*., 1995
	St. Catherine	Kolbe *et al*., 2004
	West Moreland	Kolbe *et al*., 2004
México	Campeche	Calderon *et al*., 2003
	Veracruz	Zamora-Abrego *et al*., 2006
Singapore	Central Area	Tan and Lim, 2012
St. Martin	St. Maarten (Dutch Side)	Fläschendräger, 2010; Yokoyama, 2012
St. Vincent and the Grenadines	Saint Andrew	Henderson and Powell, 2005
	Saint George	Henderson and Powell, 2005
Taiwan	Chiayi County	Norval *et al*., 2002
	Hualien County	Chang, 2007
Turks and Caicos Islands	Providenciales Island	Burgess, 2012
United States of America	Alabama	Steffen and Birkhead, 2007
	Arkansas	McAllister *et al*., 2003
	Florida	Garman, 1887; Oliver, 1950; Duellman and Schwartz, 1958; Ruibal, 1964; King and Krakauer, 1966; Corwin *et al*., 1977; Meylan, 1977; Myers, 1978; Funk and Moll, 1979; Wygoda and Bain, 1980; Godley *et al*., 1981; Myers, 1981; Wilson and Porras, 1983; Winegarner *et al*., 1984; Steiner and McLamb, 1985; Cochran, 1990; Means, 1990; Stevenson and Crowe, 1992; Campbell and Hammontree, 1995a; Campbell, 1996; Means, 1996; Christman *et al*., 2000; Townsend and Lindsay, 2001; Townsend *et al*., 2002; Meshaka *et al*., 2004; Campbell, 2003; Bishop, 2005; Jackson, 2007; Means *et al*., 2008; Meshaka, 2011; Fulbright *et al*., 2013; Somma, 2013
	Georgia	Campbell and Hammontree, 1995b; Echternacht *et al*., 1995; Campbell, 1996; Parmley, 2002; Skelton and Parmley, 2005; Beaton, 2008; Jensen *et al*., 2011; Butler *et al*., 2012; Turnbough, 2012
	Louisiana	Thomas *et al*., 1990; Platt and Fontenot, 1994; Boundy, 2004; Wiley *et al*., 2007; Williams and Comeaux, 2008; Thawley, 2011; Boundy and Gregory, 2012
	South Carolina	Turnbough, 2006
	Texas	Krusling *et al*., 1995; McCoid, 2006; Wood, 2010; Reed and LaDuc, 2012; Rabe *et al*., 2012; Swanson *et al*., 2014

currently believed.

As a result of multiple introductions from various source populations most Florida, U.S.A., populations of *A. sagrei* have more genetic variation than native populations, in which genetic variations are geographically structured (Kolbe *et al*., 2004). In a genetic comparison study, involving *A. sagrei* specimens from the native and introduced range of this species, it was found that there is high genetic variation in the *A. sagrei* population in Santzepu, southwestern Taiwan and that this population is genetically similar to some populations in Florida (Kolbe *et al*., 2004). In addition to that, the nematode, *Cyrtosomum penneri*, which is known to infect many lizard species from several genera in North and Central America (Bursey *et al*., 2012), including *A. sagrei* in parts of Florida (Goldberg *et al*., 1994), has been recorded from *A. sagrei* specimens collected in Taiwan (Norval *et al*., 2011a; Norval *et al*., 2014b). These findings indicate that the population in Taiwan originated from Florida. The type locality (Santzepu, Sheishan District, Chiayi County) was described in the first report on *A. sagrei* in Taiwan (Norval *et al*., 2002), and to date, more than ten years later, no descriptions about the known distribution of this species in Taiwan has been made. Therefore, for future monitoring and study, a description of the known distribution of *A. sagrei* in Taiwan is essential.

Anolis sagrei is a relatively small species (males can reach a snout-vent length [SVL] of *ca*. 65 mm, and the females a SVL of *ca*. 48 mm), and is sexually dimorphic in coloration, scutellation and size (Lee, 1985; Lee, 1987; Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004). It has a slender lengthened body, and both sexes have a laterally compressed tail, which is almost twice as long as the SVL (Fig. 1.2 A and 1.3 A) (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). The limbs of both sexes are moderately long and slender, and the digits have *ca*. 14 to 36 expanded sub-digital lamellae (Fig. 1.2 B and 1.3 B) (Collette, 1961; Rodriguez Schettino, 1999; Lee, 2000; Norval *et al*., 2002). The head and neck are clearly distinguishable (Fig. 1.2 C and D and 1.3 C and D) (Rodriguez Schettino, 1999). The ear openings are small, circular and clearly visible (Fig. 1.2 E and 1.3 E), and both eyelids of each eye are moveable (Rodriguez Schettino, 1999). Both sexes have a functional dewlap, although that of the females only bears a trace of colour and is much smaller (Fig. 1.2 F and 1.3 F) (Rodriguez Schettino, 1999; Lee, 2000, Harrison and Poe, 2012). Nuchal, dorsal and/or caudal crests are also present in some *A. sagrei* males (Rodriguez Schettino, 1999; Lee, 2000), and are erected in escalated agonistic interactions between males (McMann and Paterson, 2012).

In *A. sagrei*, all the head scales (Fig. 1.2 C to E and 1.3 C to E) are keeled (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999) and the dorsal scales are circular, and larger keeled imbricate scales form a mid-dorsal longitudinal zone (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). The ventral scales are keeled, circular and imbricate, and larger than the dorsal scales (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). The scales on the digits are usually keeled or multicarinate (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999), but have been found to be smooth in some populations (Schwartz and Henderson, 1991). *Anolis sagrei* males have enlarged post-cloacal scales (Fig. 1.2 G) (Rodriguez Schettino, 1999).

Morphological comparisons, involving *A. sagrei* from peninsular Florida, the Florida Keys, the West Indies, and Central America, revealed interlocality and intralocality variations in Florida populations, even though all available evidence indicated that the colonization had largely originated from Cuba (Lee, 1985; Lee, 1987; Lee, 1992). In the initial description of *A. sagrei* from Taiwan, samples were taken from the southwestern population, and were morphologically compared with specimens from other parts of the world to confirm the identification of the species (Norval *et al*., 2002). Even though the eastern and southwestern populations are most probably from the same founder population, because it is very unlikely that *A. sagrei* was introduced from abroad into Taiwan in two localities, this still needs to be confirmed by morphological comparisons.

Because *A. sagrei* has the ability to change its dorsum colour and pattern, its coloration is quite variable (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). In all size classes the ground colour of both sexes, varies from yellowish-brown, tan, brown, dark brown, light grey, to almost black (Fig. 1.4 and 1.5) (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004), and in some rare cases individuals are russet in overall coloration (Rodriguez Schettino, 1999). The ventral and throat areas are a creamy white to beige, and in males the free edge of the dewlap, when not extended, forms a whitish streak along the centre of the throat (Conant and Collins, 1991). The coloration of

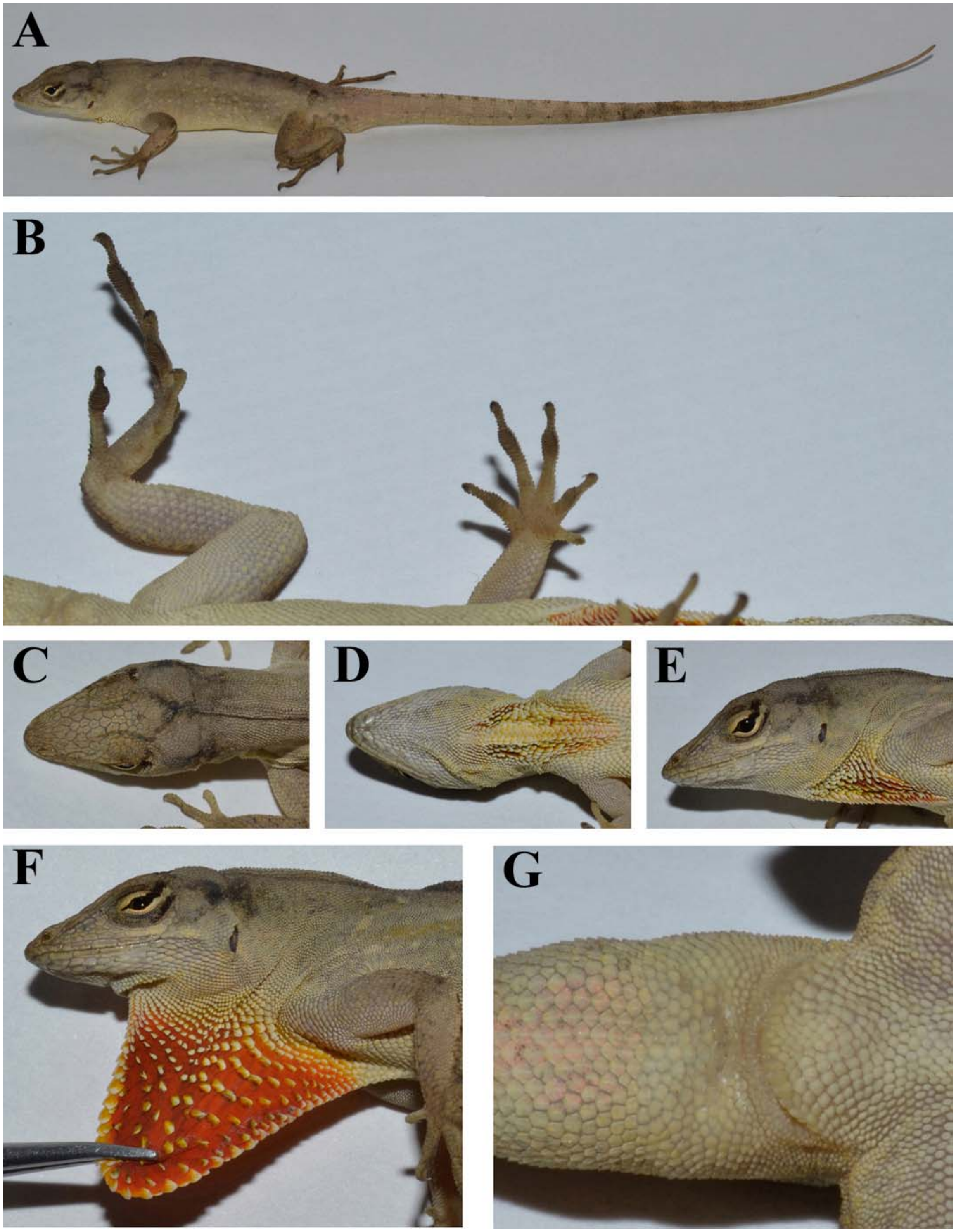

Figure 1.2. A lateral view of the body (A); the ventral view of the left forelimb and left hind limb (B); a dorsal (C), ventral (D) and lateral (E) view of the head; the dewlap (F); and the cloacal region of an *Anolis sagrei* male from Santzepu, Chiayi County, southwestern Taiwan.

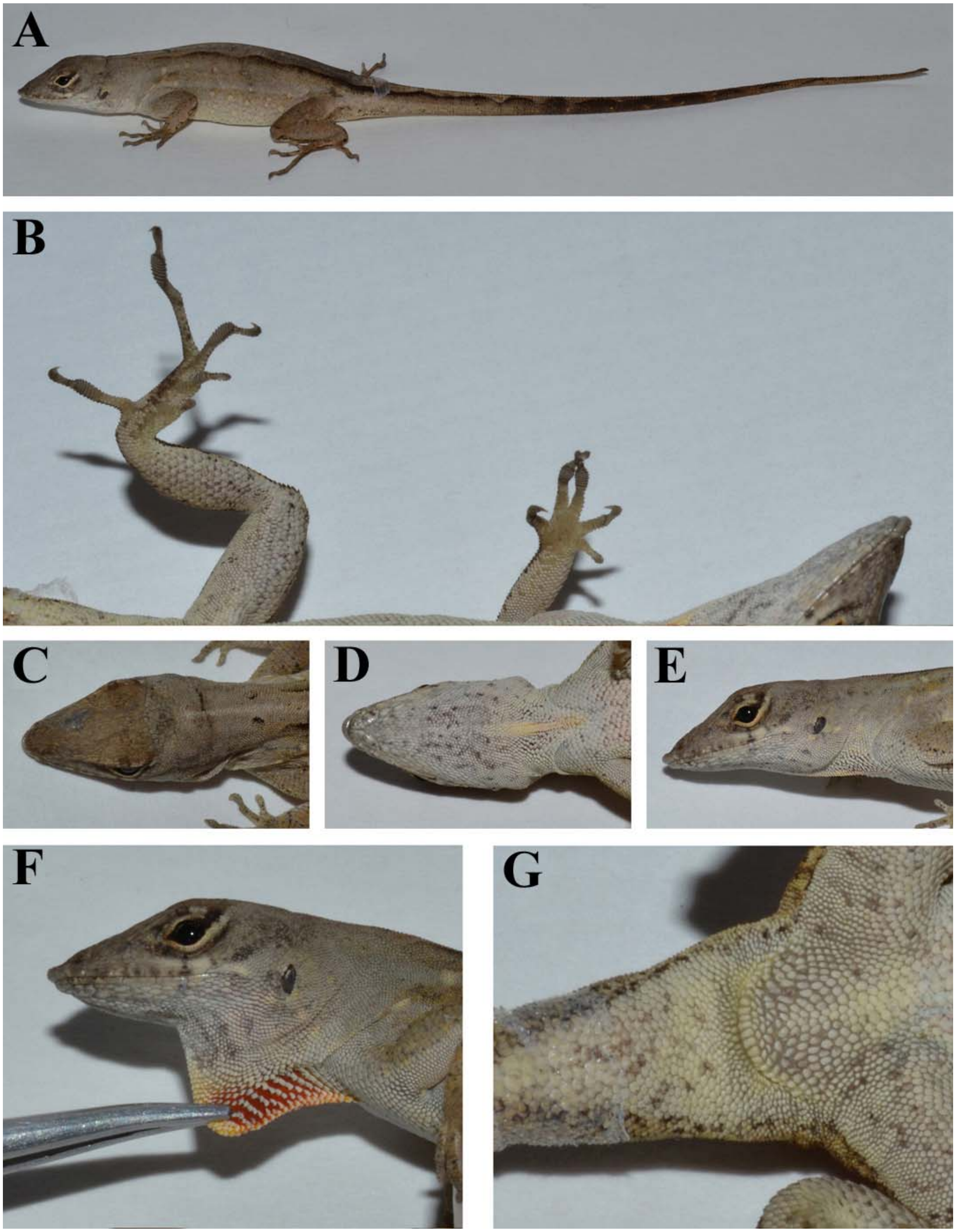

Figure 1.3. A lateral view of the body (A); the ventral view of the left forelimb and left hind limb (B); a dorsal (C), ventral (D) and lateral (E) view of the head; the dewlap (F); and the cloacal region of an *Anolis sagrei* female from Santzepu, Chiayi County, southwestern Taiwan.

the dewlap not only varies between populations, but also among individuals within the same population (Rodriguez Schettino, 1999), and ranges in colour from yellow-orange to orange-red, with a whitish to light yellow border (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004). The dewlap may have a uniform, blotched, or striped appearance (Schwartz and Henderson, 1991), and the scales of the dewlap are a creamy-white, or brown to black colour (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). The dorsal coloration patterns of both sexes consist of light brown, brown, black and/or yellow spots, bands (often ill-defined) and longitudinal lines on the body, limbs and tail (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000). The mid-dorsal coloration patterns of the males (Fig. 1.4) and females (Fig. 1.5) differ (Sanger *et al*., 2008). The males usually have a beige or light-brown line that extends along the spine, bordered on both sides by dark brown to black chevron-like markings, which are sometimes lighter edged (Norval *et al*., 2002). Yellow, beige, brown and black spots are usually present on the flanks, tail, limbs, and head (Norval *et al*., 2002). The females have a light, almost white, and clearly visible mid-dorsal line that usually extends from the back of the head along the spine to the tail (Conant and Collins, 1991; Rodriguez Schettino, 1999; Lee, 2000; Norval *et al*., 2002). The mid-dorsal line divides pale brown mid-dorsal rhombuses, which are bordered by yellow-edged dark triangular markings, which are often fused to form a black and brown zigzag pattern on both sides along the mid-dorsal line (Conant and Collins, 1991; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Norval *et al*., 2002).

Figure 1.4. Examples of some of the coloration patterns of *Anolis sagrei* males from Santzepu, Chiayi County, southwestern Taiwan.

Figure 1.5. Examples of some of the coloration patterns of *Anolis sagrei* females from Santzepu, Chiayi County, southwestern Taiwan.

Based on the structural niche they utilise, anoles are classified into various ecomorphs (Williams, 1972; Losos, 2009):

- Grass-bush species – species that can be found near the ground on the trunks of small trees, stems of grasses and other low vegetations such as small shrubs and bushes.
- Trunk-ground species – species that are usually found on the ground or tree trunks and other objects, usually within 1.5 m from the ground.
- Trunk species – species that are arboreal and are rarely found on surfaces other than broad tree trunks.
- Twig species – species that are arboreal and can primarily be found on twigs (narrow surfaces).
- Trunk-crown species – species that are primarily arboreal and can usually be found higher than 1.5 m from the ground, on the trunks, branches, twigs and leaves of trees.
- Crown-giant species – species that are arboreal and are usually found on the trunks and branches high in the crown of trees.

Anolis sagrei is a diurnal trunk-ground species that favours a variety of sunny habitat types and areas disturbed by humans (Schwartz and Henderson, 1991). These lizards usually perch conspicuously on objects (Lee, 2000), of various heights and diameters, with some niche partitioning among the sexes and age classes (Schoener, 1968). Adult males usually perch at higher positions and often make use of perches with a greater diameter, while females and juveniles are usually on the ground or a short distance above the ground on perches with a smaller diameter (Schoener, 1968; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999). *Anolis sagrei* is a habitat generalist, and in

Cuba, can be found at the edges and open areas in submontane rainforests, submontane mesophyllous evergreen forests, mesophyllous evergreen and semi-deciduous forests, pine forests, “mogote” vegetation complex, swamp forests, mangrove forests, coastal and sub-coastal microphyllous forests, semidesert thorny shrubwoods, and serpentine xeromorphic shrubwoods, but is absent in cloud forests and montane rainforests (Ruibal, 1964; Rodriguez Schettino, 1999). In other parts of its range it has also been noted that *A. sagrei* utilises open sunny habitats and are rarely found in deep woods or forests (Schwartz and Henderson, 1991). They are also well adapted to areas disturbed by humans (Ruibal, 1964; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004), which explains why these lizards tend to be very common in agricultural areas, parks, and gardens.

Anolis sagrei is a sit-and-wait (ambush) predator that preys on a variety of invertebrates, especially insects, although spiders, isopods, molluscs (Rodriguez Schettino, 1999; Lee, 2000; Norval *et al*., 2010), and occasionally fruit (Holbrook, 2012) and sap (Norval and Mao, 2013a), are also eaten. Since adult *A. sagrei* males are larger than the females, they are able to catch larger prey than females (Schoener, 1968; Rodriguez Schettino, 1999), and occasionally consume other smaller anoles, including young conspecifics (Campbell and Gerber, 1996; Campbell, 1999; Gerber, 1999; Lee, 2000; Nicholson *et al*., 2000; Norval, 2007; Krysko and Wasilewski, 2012; Reedy *et al*., 2013a).

Dietary studies of *A. sagrei* in southwestern Taiwan, have found that even though *A. sagrei* in Taiwan has a catholic diet (Table 1.3), as with conspecifics from other parts of the world, their main diet consists of large numbers of only a few prey types (Schoener, 1968; Norval *et al*., 2010). As found in a study in South Bimini (Schoener 1968), ants were by far the most common prey items of *A. sagrei* in southwestern Taiwan, followed by spiders, beetles, flies, and lepidopterans in that order of frequency (Huang *et al*., 2008a; Huang *et al*., 2008b; Norval *et al*., 2010; Norval *et al*., 2011d). Unlike in other studies in the Bahamas, in which it was found that *A. sagrei* preyed mainly on web spiders (Spiller and Schoener, 1988; Spiller and Schoener, 1990; Spiller and Schoener, 1997; Spiller and Schoener, 1998), the majority of the spiders fed on in southwestern Taiwan were ground-living species (Norval *et al*., 2007b; Huang *et al*., 2008a; Huang *et al*., 2008b). As for the most common prey items, ants, the majority belonged to species that are primarily terrestrial (Huang *et al*., 2008a; Huang *et al*., 2008b; Norval *et al*., 2011d). In the presence of terrestrial predators, *A. sagrei* tend to be more arboreal (Schoener and Schoener, 1978), so the results from the dietary studies in southwestern Taiwan suggest that *A. sagrei* is most likely more terrestrial in this locality.

Anolis sagrei is an aggressive competitor that has been shown to displace some other species of lizards from their habitats (Tokarz and Beck, 1987; Losos *et al*., 1993; Losos and Spiller, 1999), and through predation, have impacts on arthropod populations (Spiller and Schoener, 1994; Schoener and Spiller, 1996; Schoener *et al*., 2002). Similar results were also found in studies done in southwestern Taiwan, where it was found that through predation on certain species *A. sagrei* have impacts on both ant and spider communities by reducing the abundance of certain species (Huang *et al*., 2008a; Huang *et al*., 2008b). It was also found that in habitats devoid of ground cover, large *A. sagrei* males in Taiwan

Table 1.3. A summery of the results of studies pertaining to the diets of *Anolis sagrei*, *Eutropis longicaudata*, *Japalura swinhonis*, *Plestiodon elegans*, and *Sphenomorphus indicus*. The prey types were either expressed as a percentage of the total number of dietary items recorded (N %) and/or as a percentage of the number of lizards that preyed upon prey types, i.e. percentage of the frequency of occurrence (F %).

Class	**Order**	***Anolis sagrei***				***Eutropis longicaudata***		***Japalura swinhonis***			***Plestiodon elegans***		***Sphenomorphus indicus***	
		Schoener, 1968	**Huang *et al*. 2008b**	**Norval *et al*. (2010)**		**Huang, 2006**	**Norval *et al*., 2012c**	**Huang, 2007**	**Kuo *et al*., 2007**	**Norval *et al*., 2012d**	**Zhang and Ji, 2004**	**Norval *et al*., 2012c**	**Shieh *et al*., 1986**	**Norval *et al*., 2012c**
		N %	**N %**	**N %**	**F %**	**F %**	N %	**F %**	**F %**	**N %**	**N %**	**N %**	**N %**	**N %**
Insecta	Blattaria	-	0.72	0.5	2.59	-	-	-	-	0.3	1.51	-	3.28	-
	Coleoptera	7.24	5.99	6.94	22.51	20.46	14.28	5.0	28.57	1.96	18.73	-	6.56	-
	Collembola	-	0.17	0.34	1.39	-	-	-	-	-	-	-	2.19	-
	Dermaptera	0.05	0.04	0.24	1.2	-	-	-	-	0.08	4.01	-	4.37	-
	Diptera	20.60	3.65	7.86	20.12	0.8	-	-	-	0.6	2.84	-	-	-
	Hemiptera	0.5	4.76	4.26	19.92	15.15	21.44	-	21.43	0.68	1.0	-	6.01	-
	Homoptera	16.11	2.72	2.01	9.96	12.12	-	10.0	16.07	-	-	-	-	-
	Hymenoptera	26.75	49.51	49.93	51.79	2.27	28.57	80.0	87.5	90.71	7.19	-	6.01	12.5
	Isoptera	6.12	1.66	3.02	4.98	-	-	-	3.57	2.19	-	-	1.09	-
	Lepidoptera	3.5	20.72	6.1	27.89	3.03	14.29	-	53.57	1.59	17.89	-	12.57	12.5
	Mantodea	-	0.04	-	-	0.76	7.14	-	-	-	0.17	-	0.55	-
	Neuroptera	0.05	0.76	0.24	1.39	-	-	-	-	-	-	-	0.55	-
	Odonata	-	-	0.27	1.2	-	-	-	-	-	-	-	-	-
	Orthoptera	0.57	0.47	2.68	13.35	31.03	-	25.0	17.86	0.15	6.69	12.5	14.21	25.0
	Phasmatodea	-	-	-	-	-	-	-	-	0.08	-	-	-	-
	Plecoptera	-	-	0.24	1.39	-	-	-	-	-	-	-	-	-

Table 1.3. (*continued*)

Class	**Order**	***Anolis sagrei***				***Eutropis longicaudata***		***Japalura swinhonis***			***Plestiodon elegans***		***Sphenomorphus indicus***	
		N %	**N %**	**N %**	**F %**	**F %**	N %	**F %**	**F %**	**N %**	**N %**	**N %**	**N %**	**N %**
Insecta	Psocoptera	12.06	0.89	0.03	0.2	-	-	-	8.93	-	-	-	-	-
	Siphonaptera	-	-	-	-	-	-	-	-	-	-	-	0.55	-
	Thysanoptera	1.35	0.09	0.1	0.6	-	-	-	-	-	-	-	-	-
	Trichoptera	-	0.43	0.07	0.2	-	-	-	-	1.06	-	-	-	-
	Insect larva	-	-	-	-	3.0	-	15.0	-	-	-	-	-	-
Chilopoda	Geophilomorpha	-	-	-	-	-	-	-	-	-	2.34	-	-	-
	Scolopendromorpha	-	-	1.58	7.97	-	-	5.0	10.71	-	-	-	2.19	-
Diplopoda	Spirobolida	-	-	0.17	1.0	-	-	-	7.14	-	-	-	-	-
Arachnida	Acarina	1.07	-	0.03	0.2	-	-	-	-	-	-	-	0.55	-
	Aranea	1.42	7.39	9.99	33.07	0.8	-	10.0	44.64	0.3	12.38	75.0	17.49	-
	Pseudoscorpionida	-	-	-	-	2.27	-	-	-	-	-	-	-	-
Crustacea	Isopoda	-	-	0.91	3.19	-	-	-	12.5	0.08	11.87	12.5	10.38	37.5
Miscelaneous arthropods *		0.52	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda	Stylommatophora	-	-	1.07	5.98	-	-	-	10.71	-	2.17	-	4.37	-
Clitellata	Haplotaxida	-	-	-	-	-	7.14	-	-	-	4.52	-	0.55	12.5
Reptilia	Squamata	-	-	0.17	1.0	3.0	-	-	-	-	0.17	-	-	-
	Ova (Squamata)	-	-	-	-	1.52	7.14	-	-	-	0.33	-	-	-
Unknown		0.85	-	1.27	4.98	-	-	-	-	0.15	-	-	6.56	-
Plant material		1.22	-	-	-	5.3	-	-	-	0.08	6.19	-	-	-

Note: * - Chilopoda, Isopoda, and Pseudoscorpionida are more likely to be saurophagous (feeding on lizards) (Norval, 2007), most propably because in such habitats small lizards are more visible and have few places to use as shelter. In addition to that, in Taiwan *A. sagrei* is often sympatric with the native lizards *Eutropis longicaudata*, *Japalura swinhonis*, and *Plestiodon elegans*, and in some condition even with *Sphenomorphus indicus* (Norval, *pers. obs.*). Since many of the prey types reported from studies pertaining to the diets of these lizards were also recorded as prey types of *A. sagrei* (Table 1.3), it is likely that in the habitats in Taiwan where these lizards are sympatric, there is competition for at least some prey types.

Anolis sagrei males can become reproductively mature at a SVL of *ca*. 30 mm, and females at a SVL of *ca*. 34 mm (Lee *et al*., 1989; Norval *et al*., 2012b). At the onset of the reproductive period reproductively mature *A. sagrei* males and females establish their territories, which they then defend during the reproductive period (Evans, 1938; Schoener and Schoener, 1980a; Schoener and Schoener, 1982a; Scott, 1984; Les, 2013). The territories of *A. sagrei* males usually overlap with the territories of one or more females, which in turn have relatively overlapping territories themselves, and sometimes overlap the territories of more than a single male (Schoener and Schoener, 1980a; Schoener and Schoener, 1982a). *Anolis sagrei* is a promiscuous species and males tend to prefer courting and mating with unfamiliar females (Tokarz, 1992). The females select males that interact with them more actively (Flanagan and Bevier, 2014) and will mate with multiple males (Calsbeek *et al*., 2007). Because *A. sagrei* females are able to store sperm for more than two months, they are able to produce genetically diverse offspring (Fox, 1963; Sever and Hamlett, 2002; Calsbeek *et al*., 2007). *Anolis sagrei* females produce multiple clutches, each consisting of a single egg, which are produced at one to two week intervals, depending on the body size of the female and environmental factors such as food availability and the appropriate environment for oviposition (Brown and Sexton, 1973; Sanger *et al*., 2008; Cox and Calsbeek, 2010). The eggs are buried in the soil, often underneath objects such as pieces of wood or stones (Sanger *et al*., 2008; Norval *et al*., 2012b; Delaney *et al*., 2013), and *A. sagrei* females prefer to select nest sites with a relatively high humidity (Warner *et al*., 2012; Reedy *et al*., 2013b). Even though the embryos of *A. sagrei* can tolerate a broad range of environmental conditions (Warner *et al*., 2012), including being submerged for several hours (Losos *et al*., 2003; Norval and Mao, 2013b), the nest sites selected by a female have an influence on the fitness of her offspring. Compared with the hatchlings from eggs that are deposited in relatively dry nests (≤ 50 % moisture), hatchlings from eggs that are deposited in moist nests (*ca*. 75 % moisture) have greater hatching success, tend to be larger, and have overall increased survival rates (Reedy *et al*., 2013b).

The reproductive cycle (i.e. the period during which reproduction takes place) of *A. sagrei* has been studied in Belize (Sexton and Brown, 1977), Cuba (Rodriguez Schettino, 1999; Sanz Ochotorena and Uribe Aranzábal, 1999), Florida (Lee *et al*., 1989), Hawaii (Goldberg *et al*., 2002b), Jamaica (Licht and Gorman, 1970), and southwestern Taiwan (Norval *et al*., 2012b). In all these localities it was found that the reproductive period of this species is cyclic and long, and usually coincides with the rainy season. Still, even though Brown and Sexton (1973) demonstrated the importance of relative humidity for oviposition, most studies to date suggest that photoperiod and the associated temperatures are the cues that regulate the reproductive cycles of *A. sagrei* (Sexton and Brown, 1977; Lee *et al*., 1989; Goldberg *et al*., 2002b; Licht and Gorman, 1970).

The defence behaviour of *A. sagrei* involves various aspects. The coloration of these lizards is a form of camouflage under certain conditions (Schoener and Schoener, 1976). However, the most common defensive behaviour in this species is squirreling and fleeing, which may involve running and/or jumping to reach the nearest refuge (Regalado, 1998). Some individuals may also utilize pursuit-deterrent signals, involving head-bobbing, push-ups, and dewlap extension displays (Norval and Mao, 2013a). When grasped by a predator, *A. sagrei* may utilize bluff, caudal autotomy, retaliation, struggling and/or tonic immobility, combined with tail displays, to escape (Rodriguez Schettino, 1999; Norval and Mao, 2008; Levey, 2011).

Research on *A. sagrei* in Taiwan suggests that this species is becoming part of local ecosystems, not only as a predator, but also as a prey item. The long-tailed skink (*Eutropis longicaudata*, formerly *Mabuya longicaudata*; Mausfeld *et al*., 2002) (Norval *et al*., 2004), and the mountain wolf snake (*Lycodon ruhstrati ruhstrati*) (Fig. 1.6 A; Norval *et al*., 2007a; Norval and Mao, 2008) are the only reptiles observed preying on *A. sagrei* under natural conditions in Taiwan. It is also worth noting that on one occasion an observation was made of what is believed to have been a failed predation attempt on *A. sagrei* by an Asian king snake (*Dinodon rufozonatum rufozonatum*), making it another potential predator of *A. sagrei* (Norval and Mao, 2011). To date, only the brown shrike (*Lanius cristatus*) (Fig. 1.6 B; Chiu *et al*., 2011), and the Malay night heron (*Gorsakius* *melanolophus*) (Norval *et al*., 2011b) have been recorded as avian predators of free-living *A. sagrei* in Taiwan. However, due to its relatively small size and the high densities this species can attain, it can be expected that a variety of predators would prey upon *A. sagrei* wherever it occurs, and it is thus very likely that other species also prey on *A. sagrei* in Taiwan.

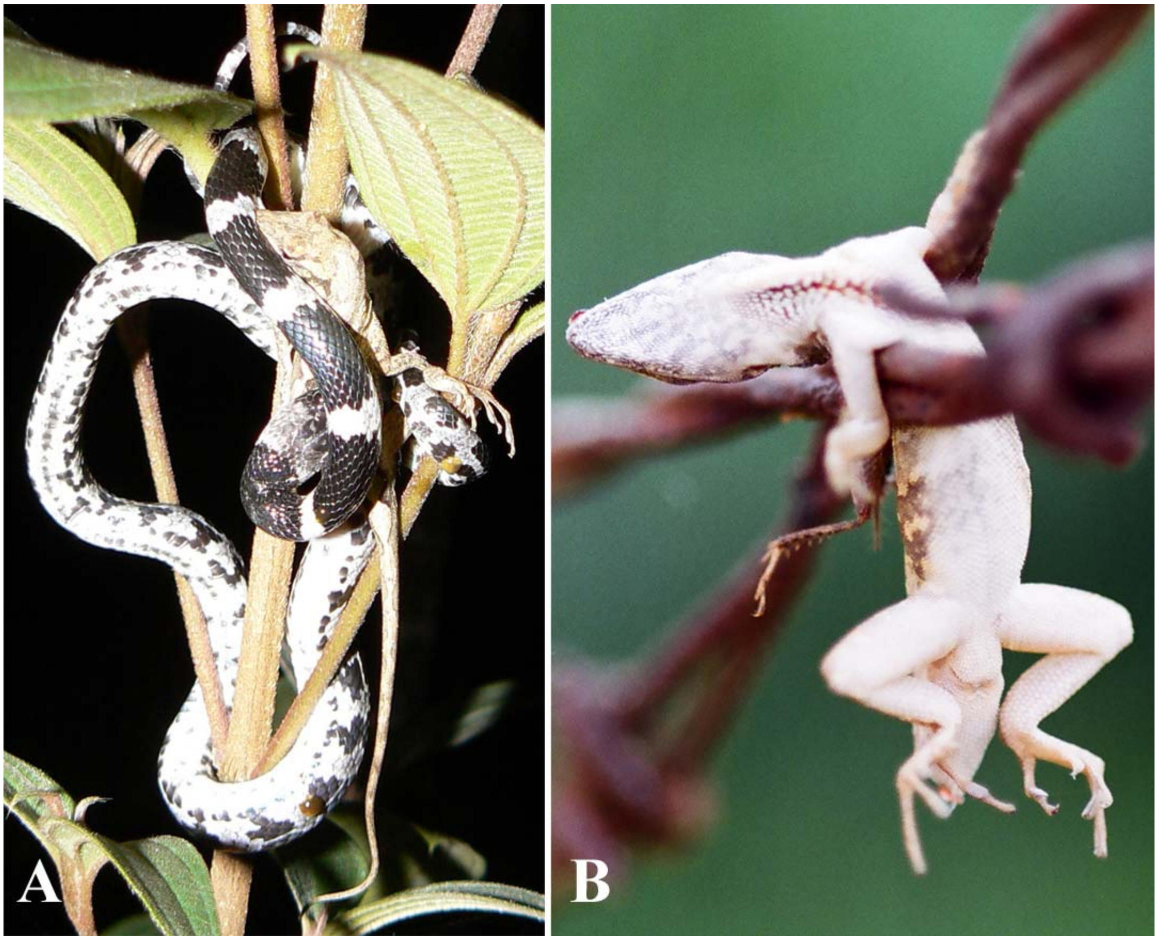

Figure 1.6. An *Anolis sagrei* female, captured by a *Lycodon ruhstrati ruhstrati*, biting the snake (retaliation) in an attempt to escape (A), and an adult *Anolis sagrei* male that was wedged by a *Lanius cristatus* between two wires of a barbed wire fence (B).

To date, no studies have been conducted to determine the predation pressure that these predators exert upon *A. sagrei* in Taiwan. Still, *A. sagrei* with broken or regenerated tails are fairly frequently recorded in southwestern Taiwan (Table 1.4; Norval, *unpublished* *data*). This kind of situation can also be expected to exist in eastern Taiwan since many of the recorded predators of *A. sagrei* in southwestern Taiwan also occur in eastern Taiwan. The data should be interpreted with caution though, because tail-break frequencies do not indicate predation pressure (Schoener, 1979; Schoener and Schoener 1980b), and since the *A. sagrei* specimens were collected from various habitats, and no survival rates, density, and predator diversity data is available, little can be inferred from the available data.

Table 1.4. The numbers (N) of *Anolis sagrei* specimens collected in Santzepu, southwestern Taiwan, in the years 2002 to 2009, the means and standard deviations of their snout-vent lengths (SVL), and percentages of the sampled lizards that had original tails, regenerated tails, or broken tails (a broken tail that lacked indications of regeneration).

	Males					Females				
Year	**N**	**SVL**	**with original tails**	**with regenerated tails**	**with broken tails**	**N**	**SVL**	**with original tails**	**with regenerated tails**	**with broken tails**
2002	169	51.1 ± 6.2	70.4	17.8	11.8	175	40.5 ± 3.7	58.3	36.0	5.7
2003	54	50.0 ± 6.2	63.0	31.4	5.6	40	39.7 ± 3.9	45.0	47.5	7.5
2004	210	47.4 ± 7.9	69.0	16.2	14.8	142	37.9 ± 4.8	70.4	13.4	16.2
2005	17	45.0 ± 7.6	64.7	23.5	11.8	10	36.2 ± 5.8	90.0	10.0	0.0
2006	13	44.5 ± 8.5	69.2	30.8	0.0	3	38.3 ± 4.7	66.7	33.3	0.0
2007	143	41.8 ± 9.1	70.6	16.8	12.6	148	35.3 ± 5.5	70.9	14.2	14.9
2008	118	44.9 ± 7.7	74.6	21.2	4.2	121	38.3 ± 5.1	67.8	20.7	11.5
2009	22	45.4 ± 8.4	72.7	22.7	4.6	48	38.4 ± 6.4	64.6	18.8	16.6

Throughout its range, native and introduced, *A. sagrei* is infected by a variety of parasites (Table 1.5). *Anolis sagrei* may impact native species indirectly by potentially introducing parasites into newly colonized environments (Goldberg *et al.*, 1995; Goldberg and Bursey, 2000; Goldberg *et al.*, 2002a; Norval *et al.*, 2011a). Nematodes that have been recorded from *A. sagrei* specimens collected in Taiwan are *C. penneri* (believed to have

Table 1.5. Reported eco- and endoparasites of *Anolis sagrei*. (* - indicates larvae; ** - indicates species that have undergone revision and may thus have been incorrectly identified)

Class	Parasite	Locality	Reference
Acanthocephala	*Acanthocephalus bufonis*	Hawaii	Goldberg and Bursey, 2000; Goldberg *et al*., 2002a
	Centrorhynchus sp.	Bahamas	Goldberg *et al*., 1994
Arachnida	*Amblyomma torrei*	Cuba	Rodriguez Schettino, 1999
Conoidasida	*Haemogregarina* sp.	Cuba	Rodriguez Schettino, 1999
Eucestoda	*Oochoristica* sp.	Hawaii	Goldberg *et al*., 2002a
Nematoda	*Abbreviata* sp. *	Cuba	Coy Otero and Barus, 1979
	Acuariidae *	Hawaii	Goldberg *et al*., 2002a
	Atractis opeatura	Cuba	Coy Otero and Barus, 1979
	Atractis scelopori	Hawaii	Goldberg and Bursey, 2000; Goldberg *et al*., 2002a
	Cyrtosomum penneri	Florida	Goldberg *et al*., 1994
		Taiwan	Norval *et al*., 2011a; Norval *et al*., 2014b
	Cyrtosomum scelopori	Bahamas	Goldberg *et al*., 1994
		Cuba	Barus and Coy Otero, 1969; Coy Otero, 1970; Coy Otero and Barus, 1973; Coy Otero and Barus, 1979
		Florida	Price and Underwood, 1984
	Oswaldocruzia lenteixeirai	Bahamas	Goldberg *et al*., 1994
		Cuba	Coy Otero and Barus, 1979
	Ozolaimus monhystera	Cuba	Coy Otero and Barus, 1979
	Parapharyngodon sp.	Taiwan	Norval *et al*., 2011a
	Parapharyngodon cubensis	Bahamas	Goldberg *et al*., 1994
		Cuba	Barus and Coy Otero, 1969; Coy Otero and Barus, 1979
	Physaloptera squamatae	Bahamas	Goldberg *et al*., 1994
		Cuba	Coy Otero and Barus, 1979
		Florida	Price and Underwood, 1984; Goldberg *et al*., 1994
		Hawaii	Goldberg and Bursey, 2000; Goldberg *et al*., 2002a
	Physalopteridae gen. sp.	Cuba	Coy Otero and Barus, 1979
	Physocephalus sp. *	Hawaii	Goldberg and Bursey, 2000; Goldberg *et al*., 2002a
	Porrocaecum sp. *	Bahamas	Goldberg *et al*., 1994
		Cuba	Coy Otero and Barus, 1979
	Skrjabinoptera phrynosoma	Cuba	Barus and Coy Otero, 1969; Coy Otero and Barus, 1979
	Strongyloides sp.	Bahamas	Goldberg *et al*., 1994
	Trichospirura teixeirai	Cuba	Coy Otero and Barus, 1979
Pentastomida	*Kiricephalus pattoni*	Taiwan	Norval *et al*., 2009b
	Raillietiella frenatus	Hawaii	Goldberg and Bursey, 2000; Goldberg *et al*., 2002a
Trematoda	*Mesocoelium americanum*	Florida	Calhoun and Dronen, 2012
	Mesocoelium monas **	Florida	Price and Underwood, 1984; Sellers and Graham, 1987
		Hawaii	Goldberg and Bursey, 2000
	Mesocoelium sociale	Taiwan	Norval *et al*., 2011a; Norval *et al*., 2014b
	Platynosomum fastosum *	Florida	Eckerlin and Leigh, 1962
		Hawaii	Goldberg and Bursey, 2000
	Urotrema scabridum	Bahamas	Goldberg *et al*., 1994
		Cuba	Coy Otero, 1970
		Florida	Sellers and Graham, 1987; Goldberg *et al*., 1994
	Urotrema wardi	Cuba	Coy Otero, 1970

been introduced into Taiwan along with *A. sagrei*) and *Parapharyngodon* sp. Since the *Parapharyngodon* specimen could not be identified to the species level (Norval *et al*., 2011a), it is not known if it is a species introduced into Taiwan along with *A. sagrei* or whether it is an acquired parasite. The pentastome, *Kiricephalus pattoni* (Norval *et al*., 2009b; Fig. 1.7), and the digenean, *Mesocoelium sociale* (reported as *Mesocoelium monas*; Norval *et al*., 2011a; Norval *et al*., 2014b), have also been found to infect *A. sagrei* in Taiwan, but because these two parasite species have been recorded from various native amphibians and reptiles (Table 1.6 and 1.7), it is suggested that these are acquired parasites of *A. sagrei* in Taiwan.

Figure 1.7. A *Kiricephalus pattoni* nymph (indicated by the red arrow) under the skin of a dissected female *Anolis sagrei* specimen, collected in Santzepu, southwestern Taiwan.

Two cases of hepatic granulomas were reported from *A. sagrei* specimens collected in Taiwan (Norval *et al*., 2005). One was due to a fungal infection, but the cause of the other could not be determined (Norval *et al*., 2005). An abnormal testis, due to unknown

Table 1.6. Amphibians and reptiles from Taiwan that have been reported as hosts of the pentastome, *Kiricephalus pattoni* (* - indicates nymphs)

Host		Reference
Frogs	*Duttaphrynus melanostictus* *	Riley and Self, 1980
	Fejervarya limnocharis *	Riley and Self, 1980
Lizards	*Hemidactylus frenatus* *	Riley and Self, 1980
	Japalura swinhonis *	Riley and Self, 1980; Norval *et al*., 2014a; Norval *et al*., 2014b
	Plestiodon elegans *	Norval *et al*., 2014a
Snakes	*Amphiesma sauteri* *	Riley and Self, 1980
	Amphiesma stolatum *	Riley and Self, 1980; Norval *et al*., 2014a
	Boiga kraepelini *	Riley and Self, 1980
	Bungarus multicinctus multicinctus *	Riley and Self, 1980; Lai *et al*., 2004
	Cyclophiops major *	Riley and Self, 1980
	Daboia russellii siamensis *	Riley and Self, 1980
	Deinagkistrodon acutus *	Riley and Self, 1980
	Dinodon rufozonatum rufozonatum *	Riley and Self, 1980; Norval *et al*., 2014a
	Elaphe carinata	Riley and Self, 1980
	Elaphe porphyracea *	Riley and Self, 1980
	Enhydris chinensis *	Riley and Self, 1980
	Enhydris plumbea *	Riley and Self, 1980
	Lycodon ruhstrati ruhstrati *	Norval *et al*., 2009a; Norval *et al*., 2012a
	Naja atra *	Riley and Self, 1980
	Orthriophis taeniurus friesei *	Riley and Self, 1980; Lai *et al*., 2004
	Protobothrop mucrosquamatus *	Riley and Self, 1980; Lai *et al*., 2004
	Psammodynastes pulverulentus *	Riley and Self, 1980
	Ptyas korros	Riley and Self, 1980
	Ptyas mucosa	Riley and Self, 1980; Lai *et al*., 2004
	Rhabdophis swinhonis *	Riley and Self, 1980
	Sibynophis chinensis chinensis *	Norval *et al*., 2008
	Sinonatrix annularis *	Riley and Self, 1980
	Sinonatrix percarinata suriki *	Riley and Self, 1980
	Trimeresurus stejnegeri stejnegeri *	Riley and Self, 1980
	Xenochrophis piscator *	Riley and Self, 1980
	Zaocys dhumnades	Riley and Self, 1980

Table 1.7. Amphibians and reptiles from Taiwan that have been reported as hosts of the digenean, *Mesocoelium sociale*.

	Host	Reference
Frogs	*Duttaphrynus melanostictus*	Fischthal and Kuntz, 1975
	Fejervarya limnocharis	Fischthal and Kuntz, 1975
Lizards	*Eutropis longicaudata*	Goldberg *et al*., 2014
	Japalura swinhonis	Fischthal and Kuntz, 1975
	Plestiodon elegans	Norval *et al*., 2014b
	Sphenomorphus indicus	Norval *et al*., 2014b
Snakes	*Amphiesma stolatum*	Fischthal and Kuntz, 1975

causes (Norval *et al*., 2006), and a gular cyst, most likely as a result of a *K. pattoni* infection (Norval *et al*., 2009a), have also been recorded from *A. sagrei* specimens collected in Taiwan. The only other clinical condition reported from the *A. sagrei* population in Taiwan, was a deformed hind limb (polydactyly; Fig. 1.8) of an *A. sagrei* male collected from Chisintang (Norval *et al*., 2009c).

Figure 1.8. An *Anolis sagrei* male, collected from Chisintang, Hualien County, eastern Taiwan, with an extra foot on the right hind limb.

1.3. SIGNIFICANCE OF THE STUDY

By mapping all the localities where *A. sagrei* has been recorded in Taiwan from 2001 to date, a description of the known distribution can be provided, and can form a basis upon which future distribution, expansion and dispersal studies can be based. In this study such a description will be made by incorporating the GPS positions, of localities where *A. sagrei* had previously been recorded in Taiwan with the GPS positions of any new localities where they are recorded, to create an up-to-date presence/absence distribution map of this species.

Although some dominant plant species are sometimes listed in descriptions pertaining to the habitats utilized by *A. sagrei* (e.g. Salzburg, 1984; Calsbeek, 2009), the habitat descriptions in most studies either entail the structural habitats (e.g. Schoener, 1975; Losos *et al*., 1993) or the types of habitats used by these lizards (e.g. Schoener, 1968; Collette, 1961). An understanding of the characteristics of the habitat types these lizards occur in, can provide an indication of which habitat types can be expected to be invaded, which in turn could be instrumental in the management and forecasting of the expected range expansion of *A. sagrei* in Taiwan. In order to identify the characteristics of the habitat types utilised by *A. sagrei* in Taiwan, a description will be made of the plant communities, using the modified Braun-Blanquet cover abundance scale, in some of the habitats *A. sagrei* is known to occur in.

In Taiwan, *A. sagrei* is known to exist in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan (Norval *et al*., 2002), and Chisintang, Hualien County, eastern Taiwan (Chang, 2007), which are *ca*. 125 km apart and is divided by the Central Mountain Range, which is the highest part of Taiwan and has several peaks that are higher than 3 000 m in altitude (Galewsky *et al*., 2006). The southwestern population was recorded first, and samples from this population have been morphologically compared with individuals from other parts of the world to confirm the identification of the species (Norval *et al*., 2002). Even though the eastern and southwestern populations are most likely from the same founder population, this still needs to be confirmed. In this study, *A. sagrei* specimens that were collected in Chisintang, will be compared with the previously described specimens collected in Santzepu, to determine if they are similar, which would provide additional evidence that they are from the same founder population. Since some morphological differences exist between the sexes (Lee, 1985), the sexes will also be compared separately.

Reproductive cycle studies are essential because the reproductive biology of a species is a crucial aspect of its natural history, and an understanding of the natural history and field ecology of herpetofauna are essential for successful conservation and management programs (Bury, 2006). Because stored fat often provides the energy required for reproduction in lizards (Derickson, 1976), and because the liver plays a vital part in fat metabolism and storage (Schaffner, 1998), examinations of the fat and liver cycles are often important parts of lizard reproductive cycle studies (e.g. Lin and Cheng, 1986; Huang, 1997; Amat *et al*., 2000; Ramírez-Bautista *et al*., 2009). *Anolis* stores most of its fat in a pair of visceral abdominal fat bodies (corpora adiposa), and measures of these abdominal fat bodies are ideal for tracking fat cycling patterns (Dessauer, 1955; Derickson, 1976). The reproductive and fat body cycles of *A. sagrei* has been described for populations in Belize (Sexton and Brown, 1977), Florida (Lee *et al*., 1989), and Jamaica (Licht and Gorman, 1970). Although the reproductive cycle of *A. sagrei* in Taiwan has been studied (Norval *et al*., 2012b), the fat body cycle has not yet been described. For the purpose of this study both the fat body and liver weight cycles of *A. sagrei* will be described, and the associations between these cycles and the reproductive cycles, as well as potential meteorological factors, will be examined. This information will contribute to the understanding of the reproductive biology of *A. sagrei* not only in Taiwan, but also as a species.

The overall objective of this study was to contribute to the understanding of the *A. sagrei* populations in Taiwan and their natural history.

1.4. KEY QUESTIONS

To meet the above-mentioned objective the following key questions will be addressed in this study:

1.4.1. What is the current known distribution of *A. sagrei* in Taiwan?

1.4.2. What are the characteristics of the habitat types that *A. sagrei* are mostly observed in in Taiwan?

1.4.3. What intersexual intralocality, and interlocality intrasexual morphological variations exist among the *A. sagrei* specimens from the two study sites?

1.4.4. What are the abdominal fat body and liver weight cycles of *A. sagrei* in Taiwan, and what associations are there between these cycles and the reproductive cycles and meteorological factors that may regulate them?

1.5. DISSERTATION OUTLINE

The layout and contents of this dissertation are described below:

1. Chapter 1 provides a brief introduction to the biology of lizards, and a description of the study species and its biology. This chapter also explains the significance of this

study and provides the key questions that were addressed.

2. Chapter 2 provides geographical and general descriptions of Taiwan as well as the climate, geography, and land utilisation of the two study sites in southwestern and eastern Taiwan.
3. Chapter 3 describes the materials and methods utilised for creating the known distribution maps of *A. sagrei* in Taiwan as well as the methods used for determining the characteristics of the plant communities in areas inhabited by *A. sagrei*. Detailed descriptions are also made of the characteristics examined in the interlocality intrasexual and intralocality intersexual comparisons of *A. sagrei* specimens collected from the two study sites in Taiwan. Finally, the methods utilised for investigating the fat body and liver weight cycles of *A. sagrei* in the southwestern Taiwan study site are described.
4. Chapter 4 provides a description of the known distribution of *A. sagrei* in Taiwan, plant communities classified and characteristics of the habitats in which *A. sagrei* were found to occur within the two study sites.
5. Chapter 5 provides the result of the intralocality intersexual and interlocality intrasexual comparisons of *A. sagrei* specimens collected from the two study sites in Taiwan. The potential factors that influence the similarities and variations in the results, as well as the conclusion pertaining to the source populations are discussed.
6. Chapter 6 describes the abdominal fat body and liver weight cycles of *A. sagrei* from the southwestern Taiwan study site. The correlations between the abdominal fat body weight, liver weight, and reproductive cycles, as well as climatic factors that may influence them are discussed.

7. Chapter 7 provides the results of this study that will be incorporated with the available information pertaining to *A. sagrei* in Taiwan to provide a discussion of what can be expected to happen with this species in Taiwan. Some management recommendations are also made.

1.6. REFERENCES

Amat, F., Llorente, G.A., and Carretero, M.A. 2000. Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range. *Amphibia-Reptilia* 21: 463-476.

Andrews, R., and Rand, A.S. 1974. Reproductive effort in anoline lizards. *Ecology* 55: 1317-1327.

Arnold, E.N. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History* 18:127–169.

Arnold, E.N. 1988. Caudal autotomy as a defense. pp. 236-273. In: Gans, C., and Huey, R.B. (eds.) 1988. *Biology of the Reptilia*. Vol.16. Alan R. Liss Inc., New York.

Ballinger, R.E., and Tinkle, D.W. 1979. On the cost of tail regeneration to body growth in lizards. *Journal of Herpetology* 13: 374-375.

Barus, V., and Coy Otero, A. 1969. Systematic survey of nematodes parasitizing lizards (Sauria) in Cuba. *Helminthologia* 10: 329-346.

Bateman, P.W., and Fleming, P.A. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology* 277: 1-14.

Beaton, G. 2008. Geographic distribution. *Anolis* (= *Norops*) *sagrei* (Brown anole). *Herpetological Review* 39: 237.

Beck, D.D. 1990. Ecology and behavior of the Gila monster in southwestern Utah. *Journal of Herpetology* 24: 54-68.

Birchard, G.F. 2004. Effects of incubation temperature. pp. 103–123 In: Deeming, D.C. (ed.) 2004. *Reptilian Incubation: Environment, Evolution, and Behaviour*. Nottingham University Press, Nottingham.

Bishop, D.C. 2005. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 36: 336.

Blackburn, D.G. 1982. Evolutionary origins of viviparity in the reptilia. I. Sauria. *Amphibia-Reptilia* 3: 185-205.

Boundy, J. 2004. Amphibian and reptile distribution records for Louisiana. *Herpetological Review* 35: 194-196.

Boundy, J., and Gregory, B. 2012. Amphibian and reptile distribution records for Louisiana - II. *Herpetological Review* 43: 113-114.

Branch, B. 1998. *Field Guide to Snakes and Other Reptiles of Southern Africa*. Struik Publishers (Pty) Ltd., Cape Town.

Brown, K.M., and Sexton, O.J. 1973. Stimulation of reproductive activity of female *Anolis sagrei* by moisture. *Physiological Zoology* 46: 168-172.

Bull, C.M. 1987. A population study of the viviparous Australian lizard *Trachydosaurus rugosus*. *Copeia* 1987: 749-757.

Bull, C.M. 2000. Monogamy in lizards. *Behavioural Processes* 51: 7-20.

Bull, C.M., and Pamula, Y. 1998. Enhanced vigilance in monogamous pairs of the lizard, *Tiliqua rugosa*. *Behavioral Ecology* 9: 452-455.

Bull, J.J. 1980. Sex determination in reptiles. *The Quarterly Review of Biology* 55: 3-21.

Burgess, J. 2012. Cuban brown anoles (*Anolis sagrei*) in the Turks & Caicos Islands. *IRCF Reptiles and Amphibian* 19: 263-264.

Bursey, C.R., Goldberg, S.R., Telford, S.R. Jr., and Vitt, L.J. 2012. Metazoan endoparasites of 13 species of Central American anoles (Sauria: Polychrotidae: *Anolis*) with a review of the helminth communities of Caribbean, Mexican, North American, and South American anoles. *Comparative Parasitology* 79: 75-132.

Bury, B.R. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. *Herpetological Conservation and Biology* 01: 56-61.

Butler, H., Camp, C.D., Greer, G.C., Jensen, J.B., Olive, D., Stevenson, D.J., and Stohlgren, K.M. 2012. New county records of amphibian and reptile in Georgia, USA. *Herpetological Review* 43: 453-456.

Calderon, R., Cedeño-Vázquez, J.R., and Pozo, C. 2003. New distributional records for amphibians and reptiles from Campeche, México. *Herpetological Review* 34: 269-272.

Calhoun, D.M., and Dronen, N.O. 2012. A reevaluation of specimens of *Mesocoelium monas* (Platyhelminthes: Digenea: Mesocoeliidae) from the Natural History Museum, UK and the United States National Parasite Collection, USA. *Zootaxa* 3589: 1-29.

Calsbeek, R. 2009. Experimental evidence that competition and habitat use shape the individual fitness surface. *Journal of Evolutionary Biology* 22: 97-108.

Calsbeek, R., Bonneaud, C., Prabhu, S., Manoukis, N., and Smith, T.B. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards.

Evolutionary Ecology Research 09: 495-503.

Campbell, T.S. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. *Herpetological Review* 27**:** 155-157.

Campbell, T.S. 1999. Consequences of the Cuban brown anole invasion in Florida: it's not easy being green. *Anolis Newsletter* 05: 12-21.

Campbell, T.S. 2003. The introduced brown anole (*Anolis sagrei*) occurs in every county in Peninsular Florida. *Herpetological Review* 34: 173-174.

Campbell, T.S., and Gerber, G.P. 1996. *Anolis sagrei* (Brown anole). Saurophagy. *Herpetological Review* 27: 200.

Campbell, T.S., and Hammontree, J.T. 1995a. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 26: 107.

Campbell, T.S., and Hammontree, J.T. 1995b. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 26: 107.

Cannatella, D.C., and de Queiroz, K. 1989. Phylogenetic systematics of the anoles: is a new taxonomy warranted? *Systematic Zoology* 38: 57-69.

Chang, N.C. 2007. A new discovered alien lizard of Hualien – *Anolis sagrei*. *Quarterly of Natural Conservation* 57: 37-41. (In Chinese)

Chiu, P.K., Norval, G., Chu, H.P., and Mao, J.J. 2011. Two records of brown shrikes (*Lanius cristatus* Linnaeus, 1758) preying on brown anoles (*Anolis sagrei* Duméril & Bibron, 1837) in Taiwan. *Herpetology Notes* 04: 87-89.

Christman, S.P., Young, C.A., Gonzalez, S., Hill, K., Navratil, G., and Delis, P. 2000. New records of amphibians and reptiles from Hardee County, Florida. *Herpetological Review* 31: 116-117.

Church, G. 1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*. *Copeia* 1962: 262-269.

Cochran, P.A. 1990. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 21: 22.

Cogger, H.G. 2000. *Reptiles and Amphibians of Australia*. 6th edition. Reed New Holland. Sydney.

Collette, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum of Comparative Zoology at Harvard College* 125: 137-162.

Conant, R., and Collins, J.T. 1991. *The Peterson Field Guide Series: a Field Guide to Reptiles and Amphibians*. *Eastern and Central North America*. 3rd edition. Houghton Mifflin, Boston.

Cooper, W.E. Jr. 2000. Food chemical discriminations by an herbivorous lizard, *Corucia zebrata*. *Journal of Experimental Zoology* 286: 372-378.

Cooper, W.E. Jr., Pérez-Mellado, V., Baird, T.A., Caldwell, J.P., and Vitt, L.J. 2004. Pursuit deterrent signalling by the Bonaire whiptail lizard *Cnemidophorus murinus*. *Behaviour* 141: 297-311.

Corwin, C.M., Linzey, A.V., and Linzey, D.W. 1977. Geographic distribution. *Anolis sagrei sagrei* (Cuban brown anole). *Herpetological Review* 8: 84.

Costantini, D., Dell'Omo, G., Casagrande, S., Fabiani, A., Carosi, M., Bertacche, V., Marquez, C., Snell, H., Snell, H., Tapia, W., and Gentile, G. 2005. Inter-population variation of carotenoids in Galápagos land iguanas (*Conolophus subcristatus*). *Comparative Biochemistry and Physiology, Part B* 142: 239-244.

Cox, R.M., and Calsbeek, R. 2010. Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution* 64: 1321-1330.

Coy Otero, A. 1970. Contribucion al concocimiento de la helmintofauna de los saurios Cubanos. *Ciencias* 4: 1-50. (In Spanish)

Coy Otero, A., and Barus, V. 1973. Notes on nematodes of the genus *Cyrtosomum* (Atractidae) parasitic in Cuban lizards (Sauria). *Folia Parasitologica* 20: 297-305.

Coy Otero, A., and Barus, V. 1979. Nematodes parasitizing Cuban reptiles. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovaca* 13: 1-43.

Cuellar, O. 1966. Oviducal anatomy and sperm storage structures in lizards. *Journal of Morphology* 119: 7-20.

Darevsky, I.S., Kupriyanova, L.A., and Uzzell, T. 1985. Parthenogenesis in reptiles. pp. 411-526. In: Gans, C., and Billet, F. (eds.) 1985. *Biology of the Reptilia*. Vol. 15. John Wileyand Sons, Inc., New York.

Davis, M.A., and Thompson, K. 2000. Eight ways to be a colonizer; two ways to be an invader. *Bulletin of the Ecological Society of America* 81: 226-230.

Delaney, D.M., Reedy, A.M., Mitchell, T.S., Durso, A.M., Durso, K.P., Morrison, E.J., and Warner, D.A. 2013. *Anolis sagrei* (Brown anole). Nest-site choice. *Herpetological Review* 44: 314.

Derickson, W.K. 1976. Lipid storage and utilization in reptiles. *American Zoologist* 16: 711-723.

Dessauer, H.C. 1955. Seasonal changes in the gross organ composition of the lizard, *Anolis carolinensis*. *Journal of Experimental Zoology* 128: 1-12.

Doughty, P., and Shine, R. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* 79: 1073-1083.

Du Toit, A., Mouton, P. le F.N., and Flemming, A.F. 2003. Aseasonal reproduction and high fecundity in the Cape grass lizard, *Cordylus anguinus*, in a fire-prone habitat. *Amphibia-Reptilia* 24: 471-482.

Duellman, W.E., and Schwartz, A. 1958. Amphibians and reptiles of southern Florida. *Bulletin of the Florida State Museum* 3: 181-324.

Echternacht, A.C., Wilson, M.A., Michaud, E.J., and MacDonald, D.M. 1995. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 26: 107.

Eckerlin, R.P., and Leigh, W.H. 1962. *Platynosomum fastosum* Kossack, 1910 (Trematoda: Dicrocoeliidae) in South Florida. *Journal of Parasitology* 48: 49 (Supplement).

Evans, L.T. 1938. Cuban field studies on territoriality of the lizard, *Anolis sagrei*. *Journal of Comparative Psychology* 26: 97-125.

Evans, S.E. 2003. At the feet of the dinosaurs: the early history and radiation of lizards. *Biological Reviews* 78: 513-551.

Fischthal, J.H., and Kuntz, R.E. 1975. Some trematodes of amphibians and reptiles from Taiwan. *Proceedings of the Helminthological Society of Washington* 42: 1-13.

Flanagan, S.P., and Bevier, C.R. 2014. Do male activity and territory quality affect female association time in the nrown anole, *Anolis sagrei*? *Ethology* 120: 365-374.

Fläschendräger, A. 2010. Cuban brown anoles (*Anolis sagrei*) in St. Maarten. *IRCF*

Reptiles and Amphibian 17: 121-122.

Fox, W. 1963. Special tubules for sperm storage in female lizards. *Nature* 198: 500-501.

Franz, R., Morgan, G.S., and Davies, J.E. 1987. Some recent introductions of reptiles in the Cayman Islands, West Indies. *Herpetological Review* 18: 10-11.

Fulbright, M.C., Flaherty, J.P., and Gienger, C.M. 2013. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 44: 624-625.

Funk, R.S., and Moll, D. 1979. Geographic distribution. *Anolis s. sagrei* (Cuban brown anole). *Herpetological Review* 10: 102.

Galewsky, J., Stark, C.P., Dadson, S., Wu, C.C., Sobel, A.H., and Horng, M.J. 2006. Tropical cyclone triggering of sediment discharge in Taiwan. *Journal of Geophysical Research* 03: F03014, doi:10.1029/2005JF000428.

Garman, S. 1887. On West Indian Iguanidae and on West Indian Scincidae in the collection of the Museum of Comparative Zoology at Cambridge, Mass., U.S.A. *Bulletin of the Essex Institute* 19: 1-29.

Gerber, G.P. 1999. A review of intraguild predation and cannibalism in *Anolis*. *Anolis Newsletter* 05: 28-39.

Godley, J.S., Lohrer, F.E., Layne, J.N., and Rossi, J. 1981. Distributional status of an introduced lizard in Florida: *Anolis sagrei*. *Herpetological Review* 12: 84-86.

Goldberg, S.R., and Bursey, C.R. 2000. Transport of helminths to Hawaii via the brown anole, *Anolis sagrei* (Polychrotidae). *Journal of Parasitology* 86: 750-755.

Goldberg, S.R., Bursey, C.R., and Cheam, H. 1995. Helminth parasites of three sympatric lizards from Grand Cayman Island, *Anolis conspersus*, *Anolis sagrei* (Polychridae) and *Leiocephalus carinatus* (Tropiduridae). *Caribbean Journal of*

Science 31: 339-340.

Goldberg, S.R., Bursey, C.R., and Kraus, F. 2002a. Seasonal variation in the helminth community of the brown anole, *Anolis sagrei* (Sauria: Polychrotidae), from Oahu, Hawaii. *American Midland Naturalist* 148: 409-415.

Goldberg, S.R., Bursey, C.R., Norval, G., Arreola, J., and Mao, J.J. 2014. *Eutropis longicaudata* (Long-tailed sun skink). Endoparasites. *Herpetological Review* 45: 127-128.

Goldberg, S.R., Bursey, C.R., and Tawil, R. 1994. Helminth parasites of the bark anole, *Anolis distichus* and the brown anole, *Anolis sagrei* (Polychridae) from Florida and the Bahamas. *Caribbean Journal of Science* 30: 275-277.

Goldberg, S.R., Kraus, F., and Bursey, C.R. 2002b. Reproduction in an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawaii. *Pacific Science* 56: 163-168.

Greene, B.T., Yorks, D.T, Parmer-Lee, J.S. Jr., Powell, R., and Henderson, R.W. 2002. Discovery of *Anolis sagrei* in Grenada with comments on its potential impact on native anoles. *Caribbean Journal of Science* 38: 270-272.

Guyer, C., and Savage, J.M. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). *Systematic Zoology* 35: 509-531.

Hahn, W.E., and Tinkle, D.W. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *Journal of Experimental Zoology* 158: 79-86.

Harrison, A., and Poe, S. 2012. Evolution of an ornament, the dewlap, in females of the lizard genus *Anolis*. *Biological Journal of the Linnean Society* 106: 191-201.

Hasson, O., Hibbard, R., and Ceballos, G. 1989. The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Canadian Journal of Zoology* 67: 1203-1209.

Henderson, R.W., and Powell, R. 2005. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 36**:** 467.

Hennessy, J. 2010. Parthenogenesis in an ornate Nile monitor, *Varanus ornatus*. *Biawak* 4: 26-30.

Heulin, B., Ghielmi, S., Vogrin, N., Surget-Groba, Y., and Guillaume, C.P. 2002. Variation in eggshell characteristics and in intrauterine egg retention between two oviparous clades of the lizard *Lacerta vivipara*: Insight into the oviparity–viviparity continuum in squamates. *Journal of Morphology* 252: 255-262.

Holbrook, J.D. 2012. *Anolis sagrei* (Brown anole). Prey. *Herpetological Review* 43: 641.

Huang, S.C., Norval, G., and Tso, I.M. 2008a. Predation by an exotic lizard, *Anolis sagrei*, alters the ant community structure in betelnut palm plantations in southern Taiwan. *Ecological Entomology* 33: 569-576.

Huang, S.C., Norval, G., Wei, C.S., and Tso, I.M. 2008b. Effects of the brown anole invasion and betelnut palm planting on arthropod diversity in southern Taiwan. *Zoological Science* 25: 1121-1129.

Huang, W.S. 1997. Reproductive cycle of the ovipарious lizard *Japalura brevipes* (Agamidae: Reptilia) in Taiwan, Republic of China. *Journal of Herpetology* 31: 22-29.

Huang, W.S. 2006. Ecological characteristics of the skink, *Mabuya longicaudata*, on a tropical East Asian Island. *Copeia* 2006**:** 293-300.

Huang, W.S. 2007. Ecology and reproductive patterns of the agamid lizard *Japalura swinhonis* on an East Asian island, with comments on the small clutch sizes of island lizards. *Zoological Science* 24: 181-188.

Huang, W.S., and Pike, D.A. 2011. Climate change impacts on fitness depend on nesting habitat in lizards. *Functional Ecology*, published online 14 April 2011, doi:10.1111/j.1365-2435.2011.01855.x.

Huey, R.B., and Pianka, E.R. 1977. Natural selection for juvenile lizards mimicking noxious beetles. *Science* 195: 201-203.

Huey, R.B., and Pianka, E.R. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.

Jackson, D.R. 2007. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 38: 481-482.

Jaksić, F.M., and Busack, S.D. 1984. Apparent inadequacy of tail-loss figures as estimates of predation upon lizards. *Amphibia-Reptilia* 5: 177-179.

Jensen, J.B., Stevenson, D.J., Graham, S., Wallace, M.P. Sr., Muise, C., Muise, T., Safer, A.B., Snow, F., Preston, R. Jr., Greer, G.C., and Camp, C.D. 2011. Additional distributional records of amphibians and reptiles in Georgia, USA. *Herpetological Review* 42: 250-255.

Johnson, C.R. 1975. Defensive display behaviour in some Australian and Papuan-New Guinean pygopodid lizards, boid, colubrid and elapid snakes. *Zoological Journal of the Linnean Society* 56: 265-282.

King, W., and Krakauer, T. 1966. The exotic herpetofauna of southeast Florida. *Quarterly Journal of the Florida Academy of Sciences* 29: 144-154.

Kishinami, M.L., and Kishinami, C.H. 1996. New records of lizards established on Oahu. *Bishop Museum Occasional Papers* 46: 45-46.

Koenig, J., Shine, R., and Shea, G. 2001. The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? *Wildlife Research* 28: 215-227.

Kolbe, J.J., Glor, R.E., Schettino, L.R., Lara, A.C., Larson, A., and Losos, J.B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431: 177-181.

Kraus, F. 2002. New records of alien reptiles in Hawai‘i. *Bishop Museum Occasional Papers* 69: 48-52.

Kraus, F. 2003. New records of alien plants and animals in Hawai‘i. *Bishop Museum Occasional Papers* 74: 76-78.

Kraus, F. 2006. New records of alien lizards from Maui County. *Bishop Museum Occasional Papers* 88: 61-62.

Kraus, F. 2009. *Alien Reptiles and Amphibians, a Scientific Compendium and Analysis*. Invading Nature: Springer Series in Invasion Biology 4. Springer, New York.

Krusling, P.J., Ferner, J.W., and Patterson, J. 1995. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 26: 108.

Krysko, K.L., and Granatosky, M.C. 2010. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 41: 511.

Krysko, K.L., and Wasilewski, J.A. 2012. *Anolis sagrei* (Brown anole). Saurophagy. *Herpetological Review* 43: 477-478.

Kuo, C.Y., Lin, Y.S., and Lin, Y.K. 2007. Resource use and morphology of two sympatric *Japalura* lizards (Iguania: Agamidae). *Journal of Herpetology* 41: 713-723.

Lai, C.H., Kuo, Y.C., Tung, K.C., and Wang, J.S. 2004. A survey of endoparasitic infections of snakes in Taiwan. *Taiwan Veterinary Journal* 30: 26-32. (In Chinese)

Landwer, A.J., Ferguson, G.W., Herber, R., and Brewer, M. 1995. Habitat use of introduced and native anoles (Iguanidae: *Anolis*) along the northern coast of Jamaica. *The Texas Journal of Science* 47: 45-52.

Leal, M. 1999. Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Animal Behaviour* 58: 521-526.

Lee, J.C. 1985. *Anolis sagrei* in Florida: phenetics of a colonizing species I. Meristic characters. *Copeia* 1985: 182-194.

Lee, J.C. 1987. *Anolis sagrei* in Florida: phenetics of a colonizing species II. Morphometric characters. *Copeia* 1987: 458-469.

Lee, J.C. 1992. *Anolis sagrei* in Florida: phenetics of a colonizing species III. West Indian and Middle American comparisons. *Copeia* 1992: 942-954.

Lee, J.C. 2000. *A Field Guide to the Amphibians and Reptiles of the Maya World: the Lowlands of Mexico, Northern Guatemala, and Belize*. Cornell University Press, New York.

Lee, J.C., Clayton, D., Eisenstein, S., and Perez, I. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989: 930-937.

Lenk, P., Eidenmueller, B., Staudter, H., Wicker, R., and Wink, M. 2005. A parthenogenetic *Varanus*. *Amphibia-Reptilia* 26: 507-514.

Les, A.M. 2013. *Anolis sagrei* (Cuban brown anole). Aggressive behavior. *Herpetological Review* 44: 137-138.

Levey, C.A. 2011. *Anolis sagrei* (Brown anole). Defensive behavior. *Herpetological Review* 42: 427-428.

Licht, P. and Gorman, G.C. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *University of California Publications in Zoology* 95: 1-52.

Lin, C.F., Chen, Y.L., and Tsai, Y.F. 2004. A production of four successive clutches of eggs by a female grass lizard (*Takydromus stejnegeri* van Denburgh) in captivity. *Endemic Species Research* 06: 35–40.

Lin, J.Y., and Cheng, H.Y. 1986. Annual reproductive and lipid storage patterns of the agamid lizard, *Japalura swinhonis mitsukurii* in southern Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 25: 13-23.

Losos, J.B. 2009. *Lizards in an Evolutionary Tree*: *Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, California.

Losos, J.B., Marks, J.C., and Schoener, T.W. 1993. Habitat use and ecological interaction of an introduced and native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes on anole introductions. *Oecologia* 95: 525-532.

Losos, J.B., Schoener, T.W., and Spiller, D.A. 2003. Effects of immersion in seawater on egg survival in the lizard *Anolis sagrei*. *Oecologia* 137: 360-362.

Losos, J.B., and Spiller, D.A. 1999. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* 80: 252-258.

Luo, L.G., Ding, G.H., and Ji, X. 2010. Income breeding and temperature-induced plasticity in reproductive traits in lizards. *The Journal of Experimental Biology*

213: 2073-2078.

Mattison, C. 1997. *Lizards of the World*. Facts on File Inc., New York.

Mausfeld, P., Schmitz, A., Böhme, W., Misof, B., Vrcibradic, D., Rocha, C.F.D. 2002. Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean Archipelago of Fernando de Noronha (Brazil): necessity of partitioning the Genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). *Zoologischer Anzeiger* 241: 281-293.

Mautz, W.J., and Shaffer, M.B. 2011. Colonization of Hawaii Island by the brown anole (*Anolis sagrei*). *Herpetological Review* 42: 508-509.

McAllister, C.T., Trauth, S.E., and Harris, C.S. 2003. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 34: 261-262.

McCoid, M.J. 2006. Geographic distribution. *Norops sagrei* (Brown anole). *Herpetological Review* 37: 361.

McConnachie, S., and Whiting, M. 2003. Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*. *African Zoology* 38: 57-65.

McMann, S., and Paterson, A.V. 2012. Display behavior of resident brown anoles (*Anolis sagrei*) during close encounters with neighbors and non-neighbors. *Herpetological Conservation and Biology* 07: 27-37.

Means, D.B. 1990. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 21: 96.

Means, D.B. 1996. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 27: 151-152.

Means, D.B., Means, R.C., and Means, R.P.M. 2008. Geographic distribution. *Anolis* (= *Norops*) *sagrei* (Brown anole). *Herpetological Review* 39: 366.

Medel, R.G., Jiménez, J.E., Fox, S.F., and Jaksić, F.M. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* 53: 321-324.

Meshaka, W.E. Jr. 2011. A runaway train in the making: the exotic amphibians, reptiles, turtles, and crocodilians of Florida. Monograph 1. *Herpetological Conservation and Biology* 6: 1-101.

Meshaka, W.E. Jr., Butterfield, B.P., and Hauge, J.B. 2004. *The Exotic Amphibians and Reptiles of Florida*. Krieger Publishing Company, Florida.

Meylan, P. 1977. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 08: 39.

Minton, S.A., and Minton, M.R. 1984. Geographic distribution. *Anolis sagrei*. *Herpetological Review* 15: 77.

Mouton, P. le F.N., Flemming, A.F., and Kanga, E.M. 1999. Grouping behaviour, tail-biting behaviour and sexual dimorphism in the armadillo lizard (*Cordylus cataphractus*) from South Africa. *Journal of Zoology* 249: 1-10.

Murphy-Walker, S., and Haley, S.R. 1996. Functional sperm storage duration in female *Hemidactylus frenatus* (Family Gekkonidae). *Herpetologica* 52: 365-373.

Myers, S. 1978. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 9: 107-108.

Myers, S. 1981. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 12: 13.

Naya, D.E., Veloso, C., Muñoz, J.L.P., and Bozinovic, F. 2007. Some vaguely explored (but not trivial) costs of tail autotomy in lizards. *Comparative Biochemistry and Physiology, Part A* 146: 189-193.

Nicholson, K.E., Crother, B., Guyer, C., and Savage, J.M. 2012. It is time for a new classification of anoles (Squamata: Dactyloidae). *Zootaxa* 3477: 1-108.

Nicholson, K.E., Paterson, A.V., and Richards, P.M. 2000. *Anolis sagrei* (Brown anole). Cannibalism. *Herpetological Review* 31: 173-174.

Norval, G. 2007. A report on male *Anolis sagrei* saurophagy in Chiayi County, Taiwan. *Herpetological Bulletin* 102: 34-37.

Norval, G., Bursey, C.R., Goldberg, S.R., and Mao, J.J. 2008. A record of *Kiricephalus pattoni* as a parasite of *Sibynophis chinensis chinensis* from Chiayi County, Taiwan. *Sauria* 30: 49-50.

Norval, G., Bursey, C.R., Goldberg, S.R., and Mao, J.J. 2009a. The first record of *Kiricephalus pattoni* Stephens, 1908 as a parasite of *Lycodon ruhstrati ruhstrati* Fischer, 1886 from Chiayi County, Taiwan. *Herpetology Notes* 2: 79-80.

Norval, G., Bursey, C.R., Goldberg, S.R., Mao, J.J., and Slater, K. 2011a. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), in southwestern Taiwan. *Pacific Science* 65: 383-390.

Norval, G., Bursey, C.R., Goldberg, S.R., Tung, C.L., and Mao, J.J. 2009b. *Norops sagrei* (Brown anole) pathology and endoparasite. *Herpetological Bulletin* 107: 42-44.

Norval, G., Chiu, P.K., Chu, H.P., and Mao, J.J. 2011b. An instance of predation on the brown anole (*Anolis sagrei* Duméril & Bibron, 1837) by a Malay night heron

(*Gorsakius melanolophus* Swinhoe, 1865). *Herpetology Notes* 04: 05-07.

Norval, G., Dieckmann, S., Huang, S.C., Mao, J.J., Chu, H.P., and Goldberg, S.R. 2011c. Does the tokay gecko (*Gekko gecko* [Linnaeus, 1758]) occur in the wild in Taiwan? *Herpetology Notes* 4: 203-205.

Norval, G., Goldberg, S.R., Bursey, C.R., and Mao, J.J. 2014a. Notes on *Kiricephalus pattoni* nymphs, recorded as subcutaneous lumps in some squamates from the same locality in southwestern Taiwan, Republic of China. *Comparative Parasitology* 81: 122-124.

Norval, G., Goldberg, S.R., Bursey, C.R., Dieckmann, S., and Mao, J.J. 2012a. A description of parasites from mountain wolf snakes, *Lycodon ruhstrati ruhstrati* (Serpentes: Colubridae), from two localities in western Taiwan. *Asian Journal of Conservation Biology* 1: 130-133.

Norval, G., Goldberg, S.R., and Mao, J.J. 2012b. The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan. *Russian Journal of Herpetology* 19: 75-81.

Norval, G., Goldberg, S.R., Bursey, C.R., Mao, J.J., and Slater, K. 2014b. Internal parasites of lizards from Taiwan. *Herpetological Conservation and Biology* 9: 484-494.

Norval, G., Hsiao, W.F., Huang, S.C., and Chen, C.K. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russian Journal of Herpetology* 17: 131-138.

Norval, G., Hsiao, W.F., Lin, C.C., and Huang, S.C. 2011d. Ambushing the supply line: a report on *Anolis sagrei* predation on ants in Chiayi County, Taiwan. *Russian*

Journal of Herpetology 18: 39-46.

Norval, G., Huang, S.C., and Mao, J.J. 2007a. Mountain wolf snake (*Lycodon r. ruhstrati*) predation on an exotic lizard, *Anolis sagrei*, in Chiayi County, Taiwan. *Herpetological Bulletin* 101: 13-17.

Norval, G., Huang, S.C., Mao, J.J., and Goldberg, S.R. 2012c. Notes on some dietary items of *Eutropis longicaudata* (Hallowell, 1857), *Japalura polygonata xanthostoma* Ota, 1991, *Plestiodon elegans* (Boulenger, 1887), and *Sphenomorphus indicus* (Gray, 1853) from Taiwan. *Herpetology Notes* 5: 453-456.

Norval, G., Huang, S.C., Mao, J.J., Goldberg, S.R., and Slater, K. 2012d. Additional notes on the diet of *Japalura swinhonis* (Agamidae), from southwestern Taiwan, with comments about its dietary overlap with that of sympatric *Anolis sagrei* (Polychrotidae). *Basic and Applied Herpetology* 26: 87-97.

Norval, G., and Mao, J.J. 2007. Can *Anolis sagrei* be unintentionally transported to new localities in bamboo stem bundles? *Sauria* 29: 51-54.

Norval, G., and Mao, J.J. 2008. An instance of arboricolous predation by a mountain wolf snake (*Lycodon ruhstrati ruhstrati* [Fischer, 1886]) on a brown anole (*Norops sagrei* Duméril & Bibron, 1837). *Sauria* 30: 59-62.

Norval, G., and Mao, J.J. 2011. *Dinodon rufozonatum rufozonatum* (Cantor, 1842) attempted predation on *Anolis sagrei* Duméril & Bibron, 1837, in Chiayi County, Taiwan. *Notes and Newsletter of Wildlifers (NOW)* 15: 14-16. (In Chinese)

Norval, G., and Mao, J.J. 2013a. An instance of a brown anole (*Anolis sagrei* Duméril & Bibron, 1837) feeding on the sap of a banana plant (*Musa sapientum* L.).

Herpetology Notes 6: 501-502.

Norval, G., and Mao, J.J. 2013b. An instance of *Anolis sagrei* eggs remaining viable after an extended exposure to excessively wet conditions. *Herpetology Notes* 6: 167-169.

Norval, G., Mao, J.J., and Chu, H.P. 2004. *Mabuya longicaudata* (Long-tailed skink). Predation. *Herpetological Review* 35: 393-394.

Norval, G., Mao, J.J., and Goldberg, S.R. 2012c. A record of a green anole (*Anolis carolinensis* Voigt, 1832), from the wild in southwestern Taiwan. *Herpetology Notes* 5: 95-97.

Norval, G., Mao, J.J., Bursey, C.R., and Goldberg, S.R. 2009c. A deformed hind limb of an invasive free-living brown anole (*Anolis sagrei* Duméril & Bibron, 1837) from Hualien City, Taiwan. *Herpetology Notes* 02: 219-221.

Norval, G., Mao, J.J., Chu, H.P., and Chen, L.C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.

Norval, G., and Norval, A.W. 2007. A description of opportunistic foraging behavior of the striped skink (*Trachylepis punctatissima*) in an urban setting**.** *Sauria* 29: 43-46.

Norval, G., Tso, I.M., and Huang, S.C. 2007b. A study of predation by the brown anole (*Norops sagrei*) on spiders in Chiayi County, Taiwan. *Russian Journal of Herpetology* 14: 191-198.

Norval, G., Tung, C.L., and Cooper, J.E. 2005. A report of hepatic granuloma in free-living brown anoles (*Anolis sagrei*) in Taiwan: two cases. *Herpetological Bulletin*

93: 9-13.

Norval, G., Tung, C.L., and Cooper, J.E. 2006. *Anolis sagrei* (Brown anole). Testicular pathology. *Herpetological Review* 37: 219-220.

Nussbaum, R.A. 1981. Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. *Oecologia (Berl)* 49: 8-13

Oliver, J.A. 1950. *Anolis sagrei* in Florida. *Copeia* 1950: 55-56.

Overall, K.L. 1994. Lizard egg environments. pp. 51-72. In: Vitt, L.J., and Pianka, E.R. (eds.) 1994. *Lizard Ecology: Historical and Experimental Perspectives*. Princeton University Press, Princeton, New Jersey.

Parmley, D. 2002. Northernmost record of the brown anole (*Anolis sagrei*) in Georgia. *Georgia Journal of Science* 60: 191-193.

Pianka, E.R., and Pianka, H.D. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in western Australia. *Copeia* 1970: 90-103.

Pianka, E.R., and Vitt, L.J. 2003. *Lizards*: *Windows to the Evolution of Diversity*. University of California Press, Berkley.

Platt, S.G., and Fontenot, L.W. 1994. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 25: 33.

Poe, S. 2013. 1986 Redux: New genera of anoles (Squamata: Dactyloidae) are unwarranted. *Zootaxa* 3626: 295-299.

Poulin, B., Lefebvre, G., Rand, A.S. Rand. 1995. *Hemidactylus frenatus* (House gecko). Foraging. *Herpetological Review* 26: 205.

Powell, R., and Pansza, J.M. 2005. Geographic distribution. *Anolis sagrei* (Cuban brown anole). *Herpetological Review* 36: 201.

Price, W.W., and Underwood, H. 1984. Intestinal helminths of the Cuban anole *Anolis sagrei sagrei*, from Tampa, Florida. *Florida Scientist* 47: 205-207.

Rabe, R.W., Powell, R.L., Claunch, C.J., and Montalvo, E.O. 2012. Geographic distribution. *Anolis sagrei* (Cuban brown anole). *Herpetological Review* 43: 304.

Ramírez-Bautista, A., Hernández-Ramos, D., Martinez, A.R., and Marshall, J.C. 2009. Fat bodies and liver mass cycles in *Sceloporus grammicus* (Squamata: Phrynosomatidae) from southern Hidalgo, Mexico. *Herpetological Conservation and Biology* 04: 164-170.

Reaney, L.T., Yee, S., Losos, J.B., and Whiting, M.J. 2012. Ecology of the flap-necked chameleon *Chamaeleo dilepis* in southern Africa. *Breviora* 532: 1-18

Reed, A.R., and LaDuc, T.J. 2012. *Anolis sagrei* (Brown anole). *Herpetological Review* 43: 444.

Reedy, A.M., Cox, C.L., Cox, R.M., and Calsbeek, R. 2013a. *Anolis sagrei* (Brown anole). Sexual cannibalism. *Herpetological Review* 44: 661-662.

Reedy, A.M., Zaragoza, D., and Warner, D.A. 2013b. Maternally chosen nest sites positively affect multiple components of offspring fitness in a lizard. *Behavioral Ecology* 24: 39-46.

Regalado, R. 1998. Approach distance and escape behavior of three species of Cuban *Anolis* (Squamata, Polychrotidae). *Caribbean Journal of Science* 34: 211-217.

Riley, J., and Self, T.J. 1980. On the systematics and life-cycle of the pentastomid genus *Kiricephalus* Sambon 1922 with descriptions of three new species. *Systematic Parasitology* 1: 127-140.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of

Florida, Gainesville, Florida.

Röll, B., and von Düring, M.U.G. 2008. Sexual characteristics and spermatogenesis in males of the parthenogenetic gecko *Lepidodactylus lugubris* (Reptilia, Gekkonidae). *Zoology* III: 385-400.

Rosenberg, H.I., and Russell, A.P. 1980. Structural and functional aspects of tail squirting: a unique defense mechanism of *Diplodactylus* (Reptilia: Gekkonidae). *Canadian Journal of Zoology* 58: 865-881.

Ruibal, R. 1964. An annotated checklist and key to the anoline lizards of Cuba. *Bulletin of the Museum of Comparative Zoology* 130: 473-520.

Salzburg, M.A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. *Ecology* 65: 14-19.

Sanger, T.J., Hime, P.M., Johnson, M.A., Diani, J., and Losos, J.B. 2008. Laboratory protocols for husbandry and embryo collection of *Anolis* lizards. *Herpetological Review* 39: 58-63.

Sanger, T.J., Losos, J.B., and Gibson-Brown, J.J. 2008. A developmental staging series for the lizard genus *Anolis*: A new system for the integration of evolution, development, and ecology. *Journal of Morphology* 269: 129-137.

Sanz Ochotorena, A., and Uribe Aranzábal, M.C. 1999. Ciclo gonadal y de los cuerpos grasos de *Anolis sagrei* (Sauria: Iguanidae) en Ciudad de La Habana. *Revista de Biología* 13: 26-32. (In Spanish)

Sarre, S.D., Georges, A., and Quinn, A. 2004. The ends of a continuum: genetic and temperature-dependent sex determination in reptiles. *BioEssays* 26: 639-645.

Schaffner, F. 1998. *The liver*. pp. 485-531. In: Gans, C., and Gaunt, A.S. (eds.) 1998.

Biology of the Reptilia. Vol. 19. Society for the Study of Amphibians and Reptiles, New York.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.

Schoener, T.W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs* 45: 233-258.

Schoener, T.W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60: 1110-1115.

Schoener, T.W., and Schoener, A. 1976. The ecological context of female pattern polymorphism in the Lizard *Anolis sagrei*. *Evolution* 30: 650-658.

Schoener, T.W., and Schoener, A. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978: 390-405.

Schoener, T.W., and Schoener, A. 1980a. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *Journal of Animal Ecology* 49: 19-53.

Schoener, T.W., and Schoener, A. 1980b. Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* 1980: 839-850.

Schoener, T.W., and Schoener, A. 1982a. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* 63: 809-823.

Schoener, T.W., and Schoener, A. 1982b. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* 39: 1-16.

Schoener, A, and Schoener, T.W. 1984. Experiments on dispersal: short-term floatation of insular anoles, with review of similar abilities in other terrestrial animals. *Oecologia (Berlin)* 63: 289-294.

Schoener, T.W., and Spiller, D.A. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381: 691-694.

Schoener, T.W., Spiller, D.A., and Losos, J.B. 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? *Ecological Monographs* 72: 383-407.

Schulte, J.A., Valladares, J.P., and Larson, A. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and phylogenetic taxonomy of iguanian lizards. *Herpetologica* 59: 399-419.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Scott, M.P. 1984. Agonistic and courtship displays of male *Anolis sagrei*. *Breviora* 479: 1-22.

Sellers, L.G., and Graham, G. 1987. Trematodes of Cuban brown anoles, *Anolis sagrei sagrei,* from Florida. *Proceedings of the Helminthological Society of Washington* 54: 266-267.

Sever, D.M., and Hamlett, W.C. 2002. Female sperm storage in reptiles. *Journal of Experimental Zoology* 292: 187-199.

Sexton, O.J., and Brown, K.M. 1977. The reproductive cycle of an iguanid lizard *Anolis sagrei*, from Belize. *Journal of Natural History* 11: 241-250.

Shea, G. 1981. Notes on the reproductive biology of the eastern bluetongue skink, *Tiliqua scincoides*. *Herpetofauna* 12: 16-23.

Sherbrooke, W.C., and Middendorf, G.A. 3rd. 2001. Blood-squirting variability in horned lizards (Phrynosoma). *Copeia* 2001: 1114-1122.

Shieh, C.J., Juan, L.Y., and Lue, K.Y. 1986. The study of the feeding habit of *Sphenomorphus indicus* in Ha-Pen area, Taipei County. Biological Bulletin of National Taiwan Normal University 21: 73-84. (In Chinese)

Shine, R. 1990. Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae). *Biological Journal of the Linnean Society* 40: 11-20.

Shine, R., and Bull, J.J. 1979. The evolution of live-bearing in lizards and snakes. *American Naturalist* 113: 905-923.

Skelton, C., and Parmley, D. 2005. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review*. 36: 467.

Somma, L.A. 2013. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 44: 107.

Spawls, S., Howell, K., Drewes, R., and Ashe, J. 2002. *A Field Guide to the Reptiles of East Africa*. Academic Press, London.

Spiller, D.A., and Schoener, T.W. 1988. An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs* 58: 57-77.

Spiller, D.A., and Schoener, T.W. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83: 150-161.

Spiller, D.A., and Schoener, T.W. 1994. Effects of top and intermediated predators in a terrestrial food web. *Ecology* 75: 182-196.

Spiller, D.A., and Schoener, T.W. 1997. Folivory on islands with and without insectivorous lizards: an eight-year study. *Oikos* 78: 15-22.

Spiller, D.A., and Schoener, T.W. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* 79: 503-516.

Steffen, J., and Birkhead, R. 2007. Geographic distribution. *Norops sagrei* (Brown anole). *Herpetological Review* 38: 353.

Steiner, T.M., and McLamb, L.T. 1985. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 16: 115.

Stevenson, D., and Crowe, D. 1992. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 23: 89.

Stuart-Fox, D., Whiting, M.J., and Moussalli, A. 2006. Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. *Biological Journal of the Linnean Society* 88: 437-446.

Surget-Groba, Y, Heulin, B., Guillaume, C.P., Thorpe, R.S., Kupriyanova, L., Vogrin, N., Maslak, R., Mazzotti, S., Venczel, M., Ghira, I., Odierna, G., Leontyeva, O., Monney, J.C., and Smith, N. 2001. Intraspecific phylogeography of *Lacerta vivipara* and the evolution of viviparity. *Molecular Phylogenetics and Evolution* 18: 449-459.

Swanson, C.L., Swanson, R.L., and Lee, J.E. 2014. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 45: 91.

Tan, H.H., and Lim, K.K.P. 2012. Recent introduction of the brown anole *Norops sagrei* (Reptilia: Squamata: Dactyloidae) to Singapore. *Nature in Singapore* 5: 359-362.

Telemeco, R.S., and Baird, T.A. 2011. Capital energy drives production of multiple clutches whereas income energy fuels growth in female collared lizards *Crotaphytus collaris*. *Oikos* 120: 915-921.

Thawley, C.J. 2011. Geographic distribution. *Anolis* (*Norops*) *sagrei* (Brown anole). *Herpetological Review* 42: 239-240.

Thomas, R.A., Thomas, P.J., Coulson, J.O., and Coulson, T. 1990. Geographic distribution. *Anolis sagrei sagrei* (Brown anole). *Herpetological Review* 21: 22.

Tinkle, D.W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *American Naturalist* 103: 501-516.

Toda, M., Takahashi, H., Nakagawa, N., and Sukigara, N. 2010. Ecology and control of the green anole (*Anolis carolinensis*), an invasive alien species on the Ogasawara Islands. pp. 145-152. In: Kawakami, K., and Okochi, I. (eds.) 2010. *Restoring the Oceanic Island Ecosystem. Impact and Management of Invasive Alien Species in the Bonin Islands*. Springer-Verlag Tokyo, Springer Japan, Tokyo.

Tokarz, R.R. 1992. Male mating preference for unfamiliar females in the lizard *Anolis sagrei*. *Animal Behaviour* 44: 843-849.

Tokarz, R.R., and Beck, J.W. Jr. 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test for behavioural interference. *Animal Behaviour* 35: 722-734.

Townsend, J.H., and Lindsay, C.R. 2001. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 32: 192.

Townsend, J.H., Krysko, K.L., Reppas, A.T., and Sheehy, C.M. 2002. Noteworthy records for introduced reptiles and amphibians from Florida, USA. *Herpetological Review* 33: 75.

Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Sites, J.W. Jr., Kuczynski, C.A., Wiens, J.J., and Reeder, T.W. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Molecular Phylogenetics and Evolution* 61: 363-380.

Trillmich, K.G.K., and Trillmich, F. 1986. Foraging strategies of the marine iguana, *Amblyrhynchus cristatus*. *Behavioral Ecology and Sociobiology* 18: 259-266.

Turnbough, N.W. 2006. Geographic distribution. *Norops* (=*Anolis*) *sagrei* (Brown anole). *Herpetological Review* 37: 361.

Turnbough, N.W. 2012. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 43: 101.

Van Wyk, J.H., and Mouton, P. le F.N. 1996. The reproductive cycles of the oviparous lizards *Platysaurus capensis* and *P. minor*: evidence supporting a viviparity-oviparity reversal in the Cordylidae. *Amphibia-Reptilia* 17: 115-129.

Viets, B.E., Ewert, M.A., Talent, L.G., and Nelson, C.E. 1994. Sex-determining mechanisms in squamate reptiles. *Journal of Experimental Zoology* 270: 45-56.

Viets, B.E., Tousignant, A., Ewert, M.A., Nelson, C.E., and Crews, D. 1993. Temperature-dependent sex determination in the leopard gecko, *Eublepharis macularius*. *Journal of Experimental Zoology* 265: 679-683.

Vitt, L.J., Congdon, J.D., and Dickson, N.A. 1977. Adaptive strategies and energetics of tail autonomy in lizards. *Ecology* 58: 326-337.

Wall, M., and Shine, R. 2013. Ecology and behaviour of Burton’s legless lizard (*Lialis burtonis*, Pygopodidae) in tropical Australia. *Asian Herpetological Research* 4: 9−21.

Wapstra, E., Olsson, M., Shine, R., Edwards, A., Swain, R., and Joss, J.M.P. 2004. Maternal basking behaviour determines offspring sex in a viviparous reptile.

Proceedings of the Royal Society of London. Series B: Biological Sciences (Suppl. 4) 271: S230-S232.

Warner, D.A., Bonnet, X., Hobson, K.A., and Shine, R. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology* 77: 1242-1249.

Warner, D.A., Lovern, M.B., and Shine, R. 2007. Maternal nutrition affects reproductive output and sex allocation in a lizard with environmental sex determination. *Proceedings of the Royal Society B* 274: 883-890.

Warner, D.A., Moody, M.A., Telemeco, R.S., and Kolbe, J.J. 2012. Egg environment have large effects on embryonic development, but have minimal consequences for hatchling phenotypes in an invasive lizard. *Biological Journal of the Linnean Society* 105: 25-41.

Watts, P.C., Buley, K.R., Sanderson, S., Boardman, W., Ciofi, C., Gibson, R. 2006. Parthenogenesis in Komodo dragons. *Nature* 444: 1021-1022.

Wiley, M.P., Ferrara, A.M., and Fontenot, Q.C. 2007. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review*. 38: 217.

Williams, A.A., and Comeaux, J. 2008. Geographic distribution. *Anolis* (= *Norops*) *sagrei* (Brown anole). *Herpetological Review* 39: 366.

Williams, E.E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *The Quarterly Review of Biology* 44: 345-389.

Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. *Evolutionary Biology* 6: 47-89.

Wilson, L.D., and Porras, L. 1983. The ecological impact of man on the South Florida herpetofauna. *University of Kansas museum of Natural History Special Publications* 9: 1-89.

Winegarner, C.E., Robertson, W.B. Jr., and Hoffman, W. 1984. Geographic distribution. *Anolis sagrei sagrei* (Cuban brown anole). *Herpetological Review* 15: 77-78.

Wood, A. 2010. Geographic distribution. *Anolis* (=*Norops*) *sagrei* (Cuban brown anole). *Herpetological Review* 41: 243.

Wygoda, M.L., and Bain, J.R. 1980. Geographic distribution. *Anolis sagrei* (Cuban brown anole). *Herpetological Review* 11: 115.

Yamashiro, S., Toda, M., and Ota, H. 2000. Clonal composition of the parthenogenetic gecko, *Lepidodactylus lugubris*, at the northernmost extremity of its range. *Zoological Science* 17: 1013-1020.

Yokoyama, M. 2012. Reptiles and amphibians introduced on St. Martin, Lesser Antilles. *IRCF Reptiles and Amphibians* 19: 271-279.

Yoshimura, M., and Okochi, I. 2005. A decrease in endemic odonates in the Ogasawara Islands, Japan. *Bulletin of the Forestry and Forest Products Research Institute* 4: 45-51.

Zamora-Abrego, J.G., García-Vázquez, U.O., Nieto-Montes De Oca, A., and Canseco-Márquez, L. 2006. Geographic distribution. *Anolis sagrei* (Brown anole). *Herpetological Review* 37: 493.

Zhang, Y.P., and Ji, X. 2004. Sexual dimorphism in head size and food habits in the blue-tailed skink *Eumeces elegans*. *Acta Zoologica Sinica* 50: 745-752. (In Chinese)

Zug, G.R., Vitt, L.J., and Caldwell, J.P. 2001. *Herpetology. An Introductory Biology of Amphibians and Reptiles*. 2nd edition. Academic Press, San Diego.

CHAPTER 2 – STUDY AREAS

2.1. INTRODUCTION

Taiwan, formerly known as Formosa, is an island in the Pacific Ocean (Fig. 2.1), between the northern latitudes 20º 50' and 25º 20' (Hsu *et al*., 2002), and is located *ca*. 150 km southeast from the coastline of China (Central Geological Survey). The island is spindle shaped and *ca*. 385 km in length (from north to south) and *ca*. 143 km in width at its widest point, and has a total area of *ca*. 35 960 km² (Hsu *et al*., 2002; Central Geological Survey). Taiwan was formed as a result of the uplifting of parts of the earlier forms of the Eurasian Plate, during collisions with the Philippine Sea Plate (Anderson, 2001). About half of Taiwan's land surface is mountainous, and about a third of the land surface consists of foothills and peaks that exceed 1 000 m in elevation, including *ca*. 200 peaks with elevations exceeding 3 000 m (*The Republic of China Yearbook 2012*, 2012). The eastern and western sides of Taiwan are divided into two unequal parts by the Central Mountain Range (Central Geological Survey), which is the highest part of Taiwan and has several peaks that are higher than 3 000 m in elevation (Galewsky *et al*., 2006). In northern Taiwan a second range, the Hsuehshan Range, extends distinctively west from the Central Mountain Range (Central Geological Survey). East of the Central Mountain Range is the Coastal Range, which is *ca*. 140 km in length and has a width of *ca*. 10 km (Central Geological Survey). The Central Mountain Range and Coastal Range form a longitudinal valley, which extends for *ca*. 150 km and has an average width of less than 5 km (Central Geological Survey). The Coastal Range has a steep gradient, which levels out into a relatively narrow coastal plane that is bordered on the east by the Pacific Ocean

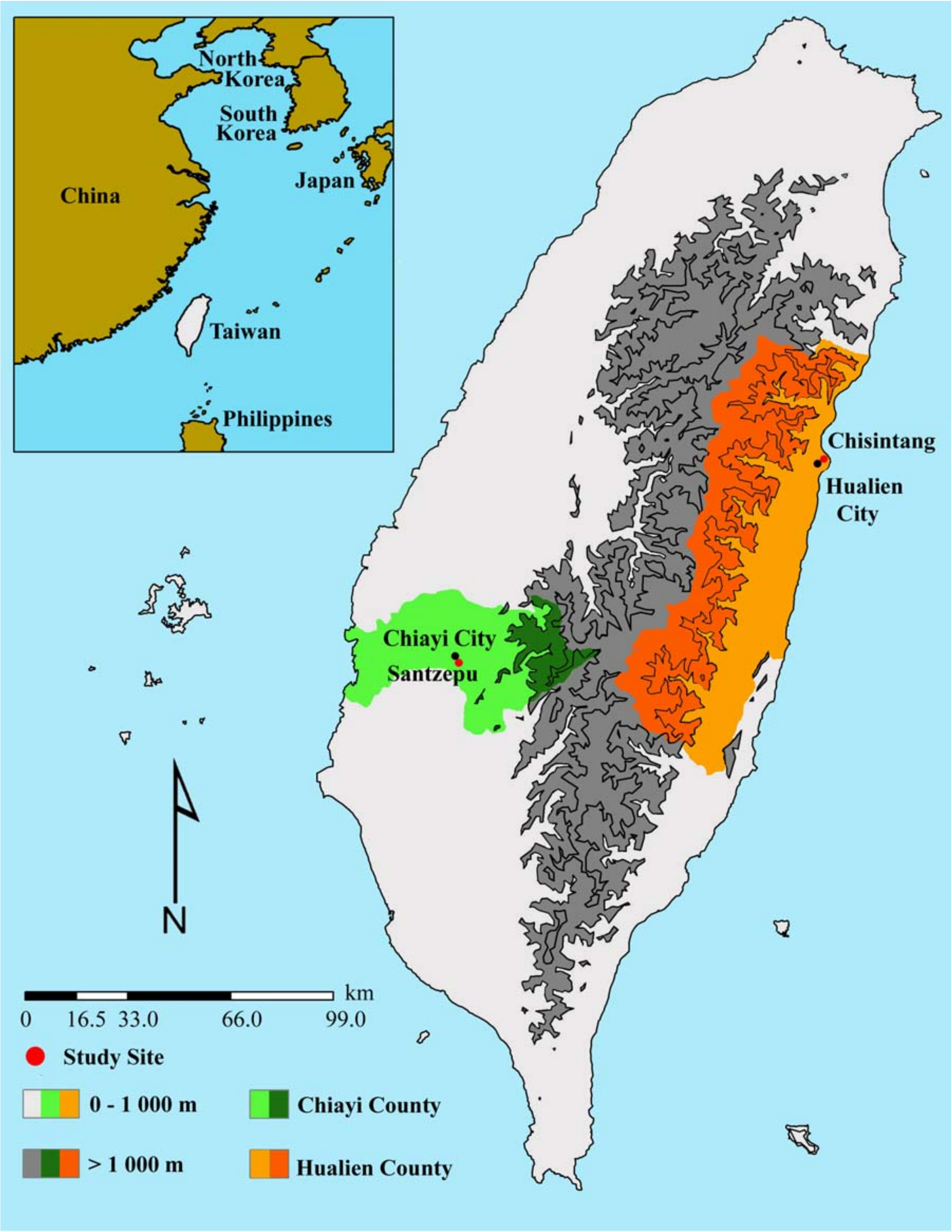

Figure 2.1. A map of Taiwan, indicating the positions of Chiayi County (green shaded area), Chiayi City, Santzepu, Hualien County (orange shaded area), Hualien City, and Chisintang.

(Central Geological Survey). From west to east, and extending along the length of the island, Taiwan has the following lithotectonic belts: the Coastal Plain, the Western Foothills, the Hsuehshan Range, the Backbone Range, the basement complex, and the Coastal Range (Ernst and Jahn, 1987).

Taiwan is located within a subtropical zone, and generally experiences high temperatures and torrential rains, usually associated with typhoons (Hsu *et al*., 2002). Due to the latitudinal proximity of the island, and its topography, the island has four climatic zones: tropical, subtropical, temperate, and frigid (Hsieh *et al*., 1994; Hsu *et al*., 2002; Table 2.1).

Table 2.1. The climate zones of Taiwan, and their associated altitudinal zones, altitudes, vegetation zones, and temperatures.

Climate zone	Altitudinal zone	Altitude (m)	Vegetation zone	Temperate (ºC)
Tropical	Plains and foothills	< 500	Ficus-Machilus	> 23
Subtropical	Submontane	500 – 1 500	Machilus-Castanopsis	17 – 23
Warm-temperate	Montane	1 500 – 2 000	Quercus (lower)	14 – 17
Temperate		2 000 – 2 500	Quercus (upper)	11 – 14
Cool-temperate	Upper montane	2 500 – 3 100	Tsuga-Picea	8 – 11
Cold-temperate	Subalpine	3 100 – 3 600	Abies	5 – 8
Frigid (Subarctic)	Alpine	> 3 600	Alpine vegetation	< 5

2.2. STUDY SITES

Chiayi County is situated in southwestern Taiwan (Fig. 2.1), and has a total surface area of 1 903 km² (Chiayi County Government). From west to east, the Coastal Plain, the Western Foothills, and the Hsuehshan Range lithotectonic belts extend through it. The geology of the Coastal Plain consists primarily of alluvium, well-bedded, but poorly consolidated clastic sediments, and gravels (Ernst and Jahn, 1987). Those of the Western Foothills, and the Hsuehshan Range consist primarily of argillites, carbonaceous metasandstones, quartzose, and slates (Ernst and Jahn, 1987). The mean minimum and maximum temperatures of this area are 19.4 ºC and 28.2 ºC respectively (Fig. 2.2 A), with an overall mean of 23.1 ºC (Taiwanese Central Weather Bureau). January is usually the coldest month and July the hottest (Taiwanese Central Weather Bureau) (Fig. 2.2 A). July is the month with the most sunshine duration (Fig. 2.2 B), and this area has an overall mean monthly sunshine duration of 172.2 hours. Chiayi County has a humid climate, and the overall mean monthly relative humidity is 80.6 %. The area usually experiences some precipitation throughout the year (Fig. 2.2 C), and on average the annual precipitation is 1 774.3 mm, of which the most normally falls in August (Taiwanese Central Weather Bureau) (Fig. 2.2 C).

Santzepu, Sheishan District, is situated in central southern Chiayi County (Fig. 2.1; N23º25'42", E120º29'06"). The area is fairly flat, with a few foothills in the eastern parts. Small stands of secondary forests, fallow fields, cultivated fields, a county government nursery, and several smaller private nurseries are the main habitat types in this area. Several crop types, of which rice is the most common, are cultivated in this area (Table 2.2). Ten amphibian and 26 reptile species have been recorded in this locality (Table 2.3), and the initial records of *A. sagrei* populations in Taiwan were from this area (Norval *et al*., 2002). For this study, Santzepu and the neighbouring areas in which *A. sagrei* has been recorded will be used as a study site (from this point on termed the southwestern study site).

Hualien County, which has a total surface area of 4 628 km², is situated in eastern Taiwan

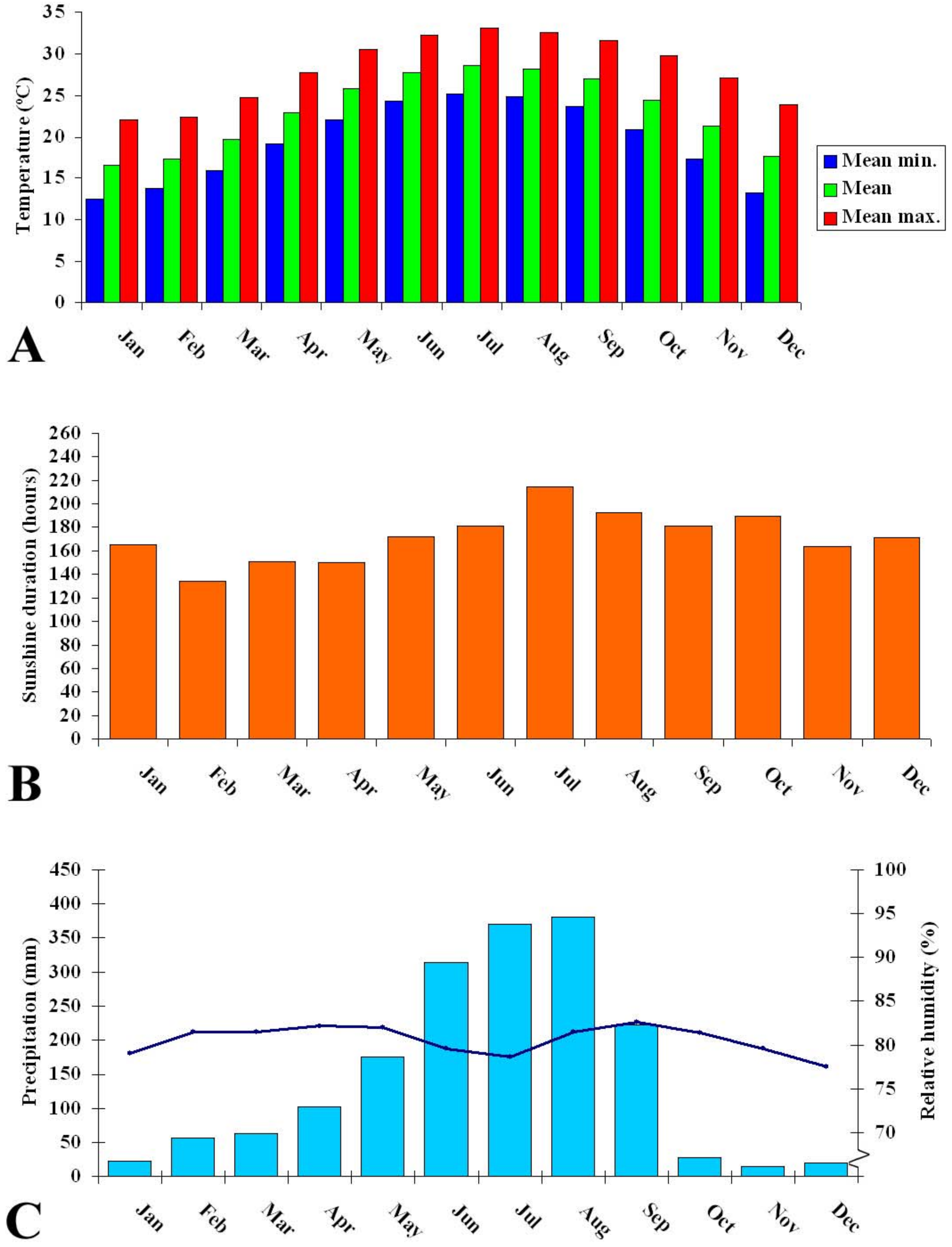

Figure 2.2. The monthly mean minimum, mean maximum and mean temperatures (A), monthly mean sunshine duration (B), and monthly mean precipitation (C) of Chiayi County, recorded during the period 1981-2010 (Taiwanese Central Weather Bureau).

Table 2.2. Agricultural crops, cultivated in Santzepu and Chisintang.

Family	Species	Common name	Santzepu	Chisintang
Annonaceae	*Annona squamosa*	Sugar apple		X
Araceae	*Colocasia esculenta*	Taro	X	
Arecaceae	*Areca catechu*	Betelnut	X	
Arecaceae	*Cocos nucifera*	Coconut		X
Bromeliaceae	*Ananas comosus*	Pineapple	X	
Cactaceae	*Hylocereus undatus*	Dragon fruit	X	
Caricaceae	*Carica papaya*	Papaya	X	
Cucurbitaceae	*Luffa cylindrica*	Vietnamese luffa	X	
Lamiaceae	*Mesona chinensis*	Grass jelly	X	
Lamiaceae	*Perilla frutescens*	Chinese basil	X	
Musaceae	*Musa sapientum*	Latundan banana	X	
Myrtaceae	*Psidium guajava*	Guava	X	
Poaceae	*Oryza sativa*	Asian rice	X	
Rubiaceae	*Coffea arabica*	Coffee	X	
Rutaceae	*Citrus × sinensis*	Orange	X	
Rutaceae	*Citrus aurantifolia*	Key lime	X	
Rutaceae	*Citrus grandis*	Pomelo	X	
Sapindaceae	*Litchi chinensis*	Lychee	X	
Solanaceae	*Capsicum annuum*	Chili pepper	X	

(Fig. 2.1) (Hualien County Government). From west to east, the Backbone Range, the basement complex, and the Coastal Range lithotectonic belts extend through it. The geology of the Backbone Range consists primarily of phyllitic and slaty metaclastic rocks (Ernst and Jahn, 1987). That of the basement complex consists primarily of sediments, and gravels (Hualien County Government), while the Coastal Range is comprised mainly of lava flow, volcanic rock fragments fused by heat and andesite (Central Geological Survey). The mean minimum and maximum temperatures of this area are 20.7 ºC and 26.8 ºC respectively (Fig. 2.3 A), with an overall mean of 23.4 ºC (Taiwanese Central Weather Bureau). As in Chiayi County, January is usually the coldest month, but in Hualien County August is usually the hottest month (Taiwanese Central Weather Bureau) (Fig. 2.3 A). July is the month with the most sunshine duration (Fig. 2.3 B), and this area has an overall mean monthly sunshine duration of 125.3 hours. Hualien County also has a

Table 2.3. Reptiles and amphibians that have been recorded to occur in Santzepu and Chisintang.

	Family	Species	Santzepu	Chisintang
Frogs	Bufonidae	*Duttaphrynus melanostictus*	X	X
	Dicroglossidae	*Fejervarya limnocharis*	X	X
	Hylidae	*Hyla chinensis*	X	
	Microhylidae	*Microhyla fissipes*	X	X
		Microhyla heymonsi	X	
		Micryletta stejnegeri	X	
	Rhacophoridae	*Chirixalus idiootocus*	X	
		Polypedates braueri	X	X
		Rhacophorus moltrechti	X	
	Ranidae	*Hylarana guentheri*	X	
Terrapins	Geoemydidae	*Cuora flavomarginata*	X	
		Ocadia sinensis	X	
Lizards	Agamidae	*Japalura swinhonis*	X	X
	Dactyloidae	*Anolis sagrei*	X	X
	Gekkonidae	*Hemidactylus frenatus*	X	X
		Hemiphyllodactylus typus typus		X
		Lepidactylus lugubris		X
	Lacertidae	*Takydromus formosanus*	X	
		Takydromus kuehnei	X	
		Takydromus luyeanus		X
		Takydromus stejnegeri	X	
	Scincidae	*Eutropis longicaudata*	X	X
		Eutropis multifasciata	X	
		Plestiodon chinensis formosensis		X
		Plestiodon elegans	X	X
		Sphenomorphus indicus	X	
Snakes	Colubridae	*Amphiesma stolatum*	X	
		Cyclophiops major		X
		Dinodon rufozonatum rufozonatum	X	X
		Elaphe carinata	X	
		Lycodon ruhstrati ruhstrati	X	
		Oligodon formosanus	X	
		Orthriophis taeniurus friesei	X	
		Ptyas korros	X	X
		Ptyas mucosa	X	X
		Sibynophis chinensis chinensis	X	
		Xenochrophis piscator	X	
	Elapidae	*Bungarus multicinctus multicinctus*	X	X
		Naja atra	X	X
	Typhlopidae	*Ramphotyphlops braminus*	X	
	Viperidae	*Daboia russellii siamensis*		X
		Protobothrops mucrosquamatus	X	X

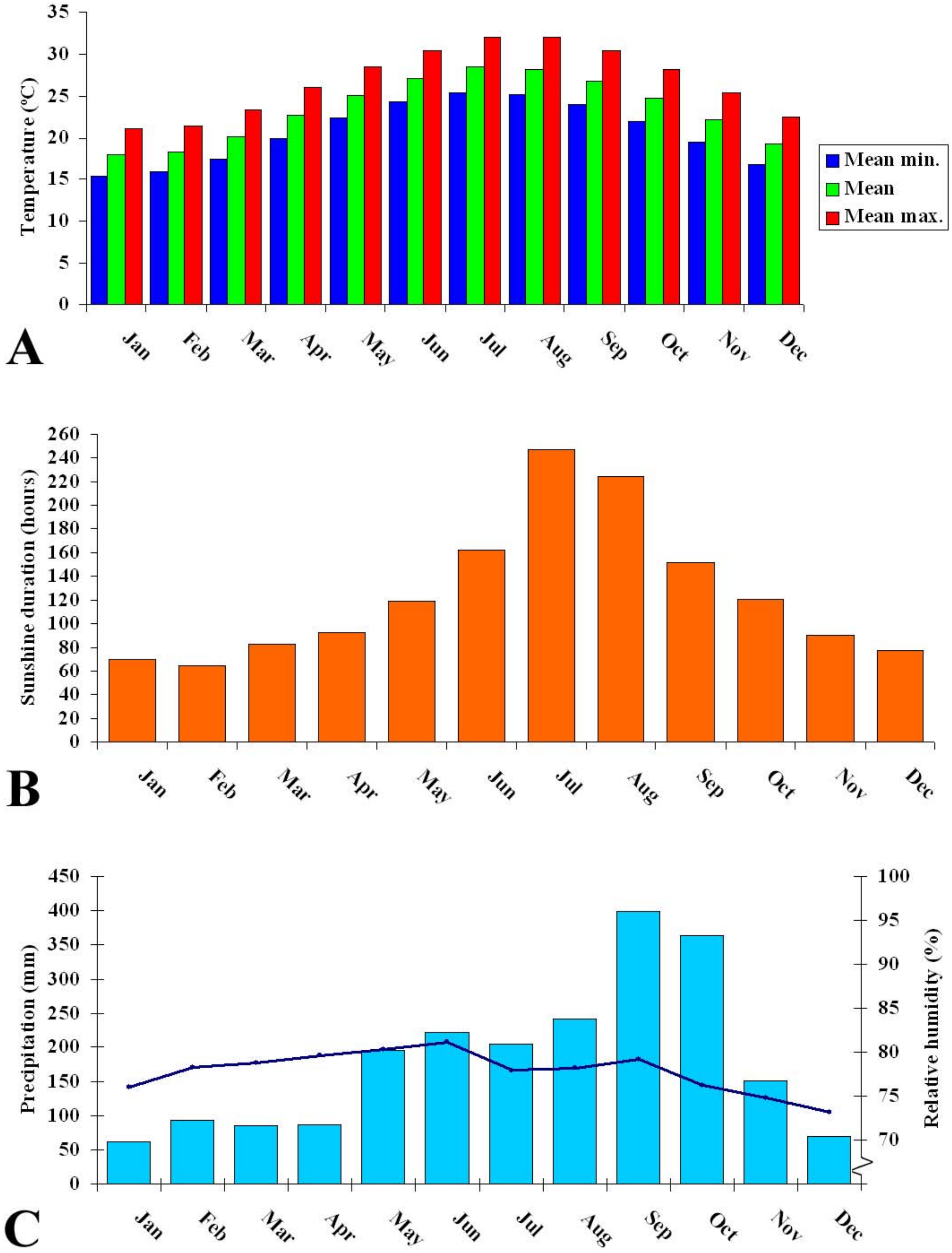

Figure 2.3. The monthly mean minimum, mean maximum and mean temperatures (A), monthly mean sunshine duration (B), and monthly mean precipitation (C) of Hualien County, recorded during the period 1981-2010 (Taiwanese Central Weather Bureau).

humid climate, and the overall mean monthly relative humidity is 77.8 %. As in Chiayi County, the area usually experiences some precipitation throughout the year (Fig. 2.3 C), and on average the annual precipitation is 2 176.8 mm, of which the most usually falls in September (Taiwanese Central Weather Bureau) (Fig. 2.3 C).

After the initial records of *A. sagrei* populations in Santzepu, these lizards were also recorded in Chisintang (Chang, 2007), which is situated in northeastern Hualien County (Fig. 2.1; N24º01'22", E121º37'49"). Santzepu and Chisintang are *ca*.125 km apart and are divided by the Central Mountain Range. The terrain in Chisintang is fairly flat, with a few foothills in the western parts. Secondary forests, fallow fields, cultivated fields, and an area that is currently being developed into a geology park, which will exhibit various rock types from Taiwan, are the main habitat types in this area. Only a few crop types are cultivated in this area (Table 2.2), and 4 amphibian and 17 reptile species have been recorded in this locality (Table 2.3). For this study, Chisintang and the neighbouring areas in which *A. sagrei* has been recorded will be used as a study site (from this point on termed the eastern study site).

2.3. REFERENCES

Anderson, M. 2001. Taiwan: An Active Continental Subduction Zone. [online]. Available at: http://www.geo.arizona.edu/~anderson/taiwan/tai_index.html (accessed 12th of August, 2013).

Central Geological Survey, MOEA. [online]. Available at: http://www.moeacgs.gov.tw/english2/index.jsp (accessed 06th of August, 2013).

Chang, N.C. 2007. A new discovered alien lizard of Hualien – *Anolis sagrei*. *Quarterly of Natural Conservation* 57: 37-41. (In Chinese)

Chiayi County Government. [online]. Available at: http://www.cyhg.gov.tw/wSite/mp? mp =12 (accessed 09th of August, 2013).

Ernst, W.G., Jahn, B.M. 1987. Crustal accretion and metamorphism in Taiwan, a post-Palaeozoic mobile belt. *Philosophical Transactions of the Royal Society of London* A321: 129-161.

Galewsky, J., Stark, C.P., Dadson, S., Wu, C.C., Sobel, A.H., and Horng, M.J. 2006. Tropical cyclone triggering of sediment discharge in Taiwan. *Journal of Geophysical Research* 03: F03014, doi:10.1029/2005JF000428.

Hsieh, C.F., Shen, C.F., and Yang, K.C. 1994. *Introduction to the flora of Taiwan, 3: floristics, phytogeography, and vegetation*. pp. 7-18. In: Huang, T.C., Keng, H., Shieh, W.C., Tsai, J.L., Hu, J.M., Shen, C.F., and Yang, K.C. (eds.) 1994. *Flora of Taiwan*. Vol. 1. 2nd edition. Department of Botany, National Taiwan University, Taipei.

Hsu, L.P., Huang, C.C., Huang, C.C., Chou, M.Y. 2002. *The Beauty of Formosan Nature*. Council for Cultural Affairs, Executive Yuan, Taipei, Taiwan.

Hualien County Government. [online]. Available at: http://www.hl.gov.tw/bin/home.php? Lang=en (accessed 09th of August, 2013).

Norval, G., Mao, J.J., Chu, H.P., and Chen, L.C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.

Taiwanese Central Weather Bureau. [online]. Available at: http://www.cwb.gov.tw/V6e/index.htm (accessed 06th of August, 2013).

The Republic of China Yearbook 2012. 2012. Executive Yuan, Taipei, Taiwan.

CHAPTER 3 – MATERIALS AND METHODS

3.1. DISTRIBUTION AND HABITATS

3.1.1. DISTRIBUTION

Anolis sagrei was recorded for the first time in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan during 2000 (Norval *et al*., 2002), and in Chisintang, Hualien County, eastern Taiwan, during 2006 (Chang, 2007). Since these first observations, surveys (Table 3.1) were conducted on an *ad hoc* basis in areas where these lizards were potentially thought to occur. Because *A. sagrei* usually perches conspicuously on tree trunks and other objects in open sunny areas (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004; Norval *et al*., 2011b), the surveys usually entailed visually searching for active or basking animals in habitats likely to be used by these lizards. When *A. sagrei*, or any other lizard species was observed, the locality's GPS coordinates were recorded. After an area has been surveyed or after the presence of *A. sagrei* had been confirmed, the observer moved (by walking or riding a scooter) to the next site. Since these surveys were done to only determine the presence of *A. sagrei* in the localities, the lizards were not counted. For this study additional surveys were conducted in a similar fashion in Santzepu in areas adjacent (< 500 m away) to where *A. sagrei* had previously been recorded.

In addition to this, localities where *A. sagrei* specimens have been collected as part of research on this lizard species in Taiwan, unpublished distribution records in Chiayi County and Hualien County, provided by other researchers (Table 3.1; M.H. Chuang,

Table 3.1. Activities in which the GPS coordinates of *Anolis sagrei* distribution observations were recorded, as well as the duration (number of days), number of workers, and effort involved. (? – data not available; N.A. – not applicable)

Period	**Activity**	**Number of days**	**Number of workers**	**Effort (minutes/day)**
Nov. 2001 to Oct. 2013	Survey on an *ad hoc* basis for the presence of *Anolis sagrei* in potential habitats in the southwestern study site (Norval, *unpublished data*).	76	1	86.1 ± 64.4
Jan. 2002 to Mar. 2003	Collect *Anolis sagrei* in the southwestern study site for diet and reproductive studies (Norval *et al*., 2010; Norval *et al*., 2012; Norval, *unpublished data*).	83	1	78.7 ± 53.9
Apr., Aug., and Nov. 2005	*Anolis sagrei* and *Japalura swinhonis* population estimates in a secondary forest fragment and neighboring *Areca catechu* plantation in the southwestern study site as part of an impact study (Huang *et al*., 2008; Norval, *unpublished data*).	10	2	241.8 ± 131.3
Jun. 2005 to Sep 2008	Species diversity study in a secondary forest fragment (five funnel traps) and neighboring *Areca catechu* plantation (seven funnel traps) in the southwestern study site (Norval, *unpublished data*).	1043	N.A.	1403.6 ± 62.1
Jan. to Aug. 2007, and Oct. and Nov. 2008	Collect *Anolis sagrei* in the southwestern study site for an eradication trial (Norval, *unpublished data*).	23	1	87.2 ± 41.5
Sep. 2007 to Sep. 2008	Collect *Anolis sagrei* in the southwestern study site for a parasite study (Norval *et al*., 2011a; Norval, *unpublished data*).	12	1	136.7 ± 43.1
Mar. to Aug. 2009	Collect lizards with funnel traps in a secondary forest fragment (five traps) and neighboring *Areca catechu* plantation (seven traps) in the southwestern study site for a parasite study (Norval *et al*., 2014; Norval, *unpublished data*).	65	N.A.	1387.0 ± 25.2
Mar. to Jul. 2009	Collect *Anolis sagrei* in the southwestern study site for a parasite study and predation trials (Norval *et al*., 2014; Norval, *unpublished data*).	5	1	76.2 ± 47.9
Jul. 2009	Collect *Anolis sagrei* in the eastern study site for a parasite study and morphological comparisons (Norval *et al*., 2014; J.J. Mao, *personal communication*).	1	?	?
Aug. 2011 to Apr. 2012	Survey by volunteers of the Wild Bird Society of Hualien for the presence of *Anolis sagrei* in potential habitats in Hualien County (Y.J. Yang, *personal communication*).	?	?	?
Oct. 2011 to Sep. 2012	Surveys for the presence of *Anolis sagrei* in the southwestern study site as part of a dispersal pattern study (Wang, 2013; G.Q. Wang, *personal communication*).	87	5	*ca*. 265
Oct. 2012 to Oct. 2013	Survey and trial removal of *Anolis sagrei* by volunteers in Hualien County (Y.J. Yang, *personal communication*).	13	5.4 ± 5.3	?
2012 to 2014	Surveys for the presence of *Anolis sagrei* in Chiayi County (M.H. Chuang, *personal communication*).	?	?	?
Jul. 2003 to Jul. 2014	Records of chance sightings of *Anolis sagrei* while moving around in the southwestern study site (Norval, *unpublished data*).	43	1	N.A.

pers. com.[1]; J.J. Mao, *pers. com.*[2]; G.Q. Wang, *pers. com.*[3]; Y.J. Yang, *pers. com.*[4]), were also incorporated into the distribution data collected during surveys. Using Arcview GIS8.3 GPS, GIS User Community aerial photographs of the study areas were divided into 100 x 100 m grids. The GPS coordinates of all the localities where *A. sagrei* specimens were recorded, over the period late 2001 to mid 2014, were used to plot in which grids these lizards were recorded, to create current presence/absence distribution maps of this species in Taiwan. Conservative estimates of the distribution of this species in Taiwan were then made by counting the number of grids in which these lizards were recorded.

3.1.2. HABITAT CHARACTERISTICS

For the vegetation surveys, minimum plot sizes were determined in betel nut palm (*Areca catechu*) plantations (*n* = 3), a cemetery (*n* = 1), fallow agricultural fields (*n* = 2), fruit orchards (*n* = 3), parks (*n* = 2), roadsides (*n* = 2), and secondary forest fragments (*n* = 2). In each of these 15 localities, a species curve was determined for the recorded plant species, and using the method of minimal area as described by Kent and Coker (1992), the minimum plot size was derived from that. The minimum plot sizes ranged from 1 x 4 m to 8 x 8 m. For practical purposes and ease of use in the field it was decided that all plots would be rounded off to the nearest 5 m and that no plot would be smaller than 5 x 1 m. Thus a plot size of 10 x 10 m (as opposed to 8 x 8 m) was chosen for this study in

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habitats that could accommodate this plot size. The smallest plot size used was 5 x 1 m. The numbers of the various sample plot sizes used in this study are indicated in Table 3.2.

Table 3.2. The numbers of the various sample plot sizes used for the vegetation surveys in the two study sites.

Plot size	Eastern study site	Southwestern study site
10 x 10 m	4	104
10 x 5 m	–	18
10 x 1 m	5	25
5 x 5 m	–	3
5 x 2 m	6	–
5 x 1 m	–	1

The vegetation surveys were conducted in areas where *A. sagrei* has been recorded in the two study sites, and to which access could be gained. Military facilities such as the air base in Hualien, and private properties of which the owners did not permit access could thus not be used for vegetation surveys. Since *A. sagrei* was recorded in a few localities in the eastern study site, only 15 sample plots were placed in this locality. In the southwestern study site a total of 141 sample plots were placed. An additional 10 sample plots were placed in the southwestern study site in localities, such as secondary forest fragments, where *A. sagrei* has not been recorded, but that were within 100 m from localities where these lizards did occur.

To identify the plant communities within the habitat type being investigated, sample plots were placed, based on the principle of the Zurich-Montpellier (Braun-Blanquet) school (Poore, 1955; Kent and Coker, 1992; Brown *et al*., 2013), in a stratified random way in localities with homogeneous vegetation of the perceived plant community, i.e. areas such as ecotones that do not have homogeneous vegetation were avoided. This was to ensure that all variations in the habitats were included. Where possible, a minimum of three sample plots per identified habitat type were placed. Within each sample plot all plant species were identified and recorded, and the percentage of the plot covered by each species was estimated by using the modified Braun-Blanquet cover abundance scale (Kent and Coker, 1992):

r – one or a few species.

+ – less than 5 % of total area of stand and irregular appearance.

1 – abundant, but with low cover; or less abundant, but with a greater cover, but less than 5 % of the total surface of the stand.

2 – abundant, but less than 5 % cover, or 5 % - 25 % cover of total surface of the stand.

3 – 25 % - 50 % cover of total stand surface, irrespective of the number of individuals.

4 – 50 % - 75 % cover of total stand surface, irrespective of the number of individuals.

5 – 75 % - 100 % cover of total stand surface, irrespective of the number of individuals.

Plants that could not be identified in the field were allocated reference field numbers. The leaves, flowers, and/or fruit, as well as the growth form of unidentified plants were then photographed for later identification by a botanist and for future reference.

The extent (as a percentage) to which the sample plot was covered by the crowns of trees, shrubs, herbaceous plants, grasses, and rocks, as well as the height of the vegetation (in metres) were visually estimated. Additional environmental data recorded included: aspect (presented in cardinal degrees); slope, with the aid of a clinometer (Clinometer/Compass Tandem - SS001380011, Suunto, Vantaa, Finland); degree of erosion, based on the type (sheet, rill, or gully erosion; Brady and Weil, 2002) and visual estimate of the percentage of the plot affected by erosion; soil texture, estimated by rubbing some of the soil between the tips of the index finger and thumb (Harpstead *et al*., 2001); and soil pH, measured with a soil tester (DM-15, Takemara Electric Works, Ltd., Tokyo, Japan). Any reptiles and/or amphibians observed within the sample plot while the vegetation data was being collected were also noted.

The vegetation of sample plot 96 in the southwestern study site was found to consist of only *Ananas comosus* (pineapple), and did thus not meet the requirements for the vegetation analysis (i.e. it is not a community with plant associations), and was therefore excluded from the plant community analysis and description. In addition to that, due to equipment malfunctions, no soil soil pH data was collected from the sample plots placed in the eastern study site.

The floristic data were entered into the floristic database, TURBOVEG (Hennekens, 1996; Hennekens, 1998), from where the data was exported into the JUICE program (Tichý, 2002). The modified Weighted Two-Way Indicator Species Analysis (TWINSPAN) algorithm (Tichý *et al*., 2007), contained in JUICE, was used to derive a first approximation of the floristic data. TWINSPAN groups sample plots and divides the floristic data based on the internal heterogeneity to produce a classification hierarchy (Poore, 1955; Kent and Coker, 1992; Brown *et al*., 2013). Further refinement of the classification was achieved by affecting Braun-Blanquet procedures (Barbour *et al*., 1987; Kent and Coker, 1992; Brown *et al*., 2013). The constancy of a species is the number of sample plots within which the species occurs (Kent and Coker, 1992). For description, the constancy of plant species in each community was determined by using the following formula:

constancy = (the number of sample plots in a community in which the species is present x 100) / the total number of sample plots in the community

3.2. MORPHOLOGICAL MEASUREMENTS

Thirty *A. sagrei* specimens (male = 8; female = 22) that were collected in 2009 in Chisintang, Hualien County, eastern Taiwan (eastern study site), and 36 *A. sagrei* specimens (male = 19; female = 19), collected during 2000, from Santzepu, Sheishan District, Chiayi County, southwestern Taiwan (southwestern study site) were used in this study to compare morphological characteristics of *A. sagrei* from these different locations. The 36 *A. sagrei* specimens from the southwestern study site, were used for morphologically comparisons with conspecifics from other parts of the world to confirm the identification of the species (Norval *et al*., 2002). The comparisons were made based on methods suggested by G. Köhler (*pers. com.*[5]). For this study the same methods were employed to determine the morphological characteristics of the *A. sagrei* from the eastern study site.

Morphological characteristics that were recorded included (Fig. 3.1): the snout-vent length (SVL), measured from the anterior tip of the snout to the posterior margin of the vent; tail length (TL), measured from the posterior margin of the vent to the tip of the tail;

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head length (HL), measured from the tip of the rostral to the posterior margin of the ear opening; and left hind shank length (LHS), measured from the knee to the ankle. All the morphometric characters were measured with a dial calliper (505-666 D15F, Mitutoyo Corporation, Kanagawa, Japan) to the nearest 0.1 mm.

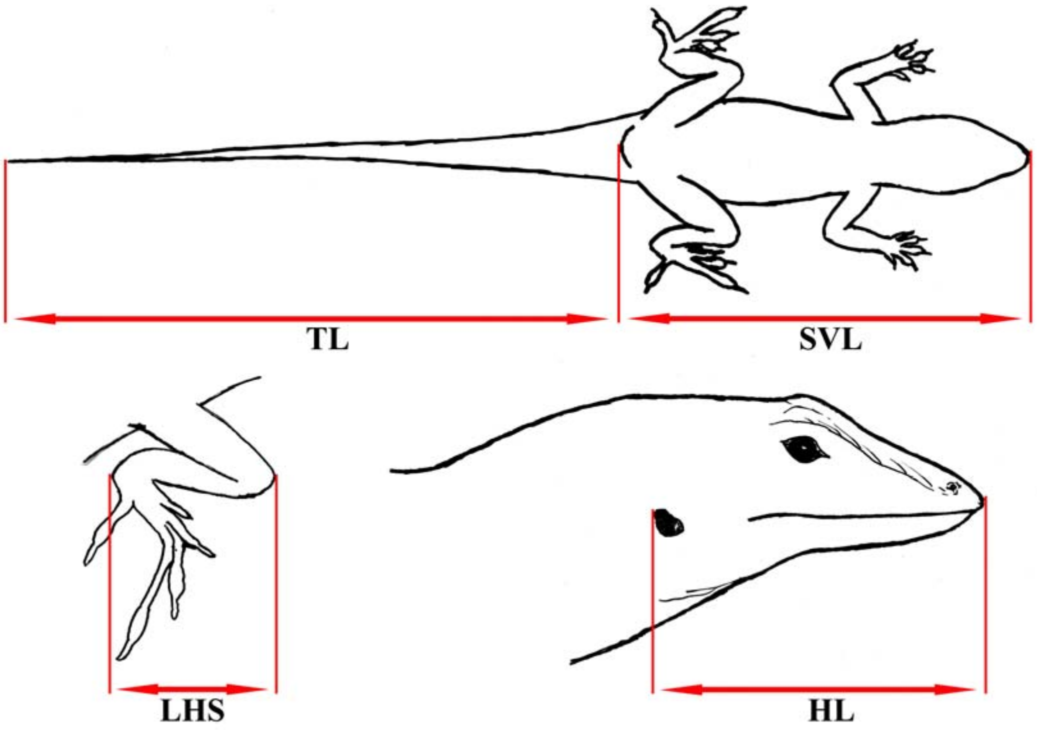


Figure 3.1. Diagrams illustrating how the snout-vent length (SVL), tail length (TL), head length (HL), and left hind shank length (LHS) were measured.

The following meristic (scalation) characters were also recorded (Fig. 3.2): a count of the interorbital (IO), as well as the interpariental/interorbitals (IP/IO) scales; the number of scales in the second row of scales between the canthal ridges (2. Canth.); the number of internasal (IN) scales, not including the supranasal scales; the number of scales in the second loreal scale row; the number of scales between the subocular scales and supralabials (SO/SPL); and the number of supralabials (SPL), not including the rostral,

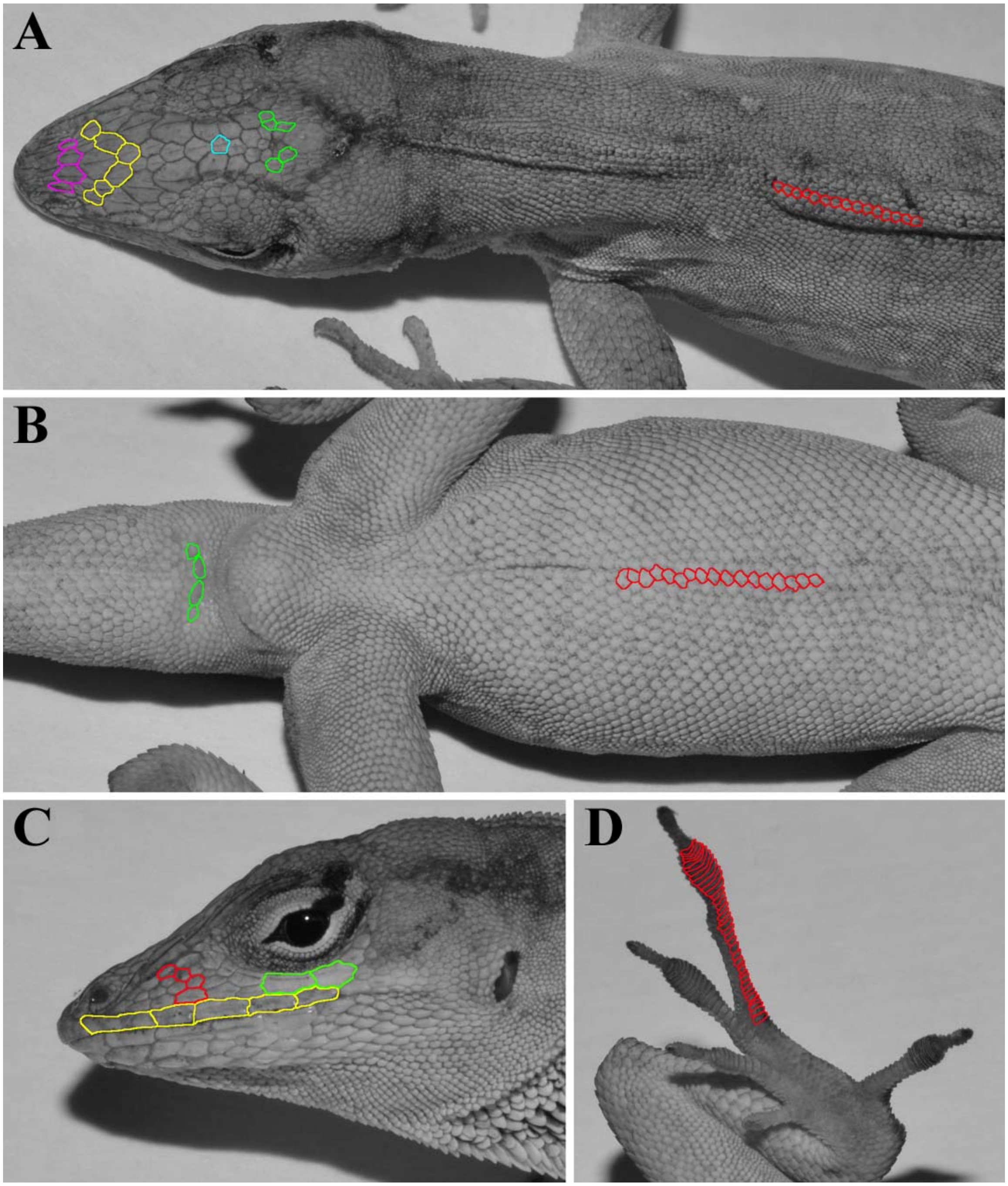


Figure 3.2. Images, indicating the (A) mid dorsal scales (Dors. 5 mm; red), interpariental/interorbital scales (IP/IO; green), interorbital scales (IO; blue), second row of scales between the canthal ridges (2. Canth.; yellow), internasal scales (IN; pink), (B) mid ventral scales (Ventr. 5 mm; red) enlarged postanal scale (PA; green), (C) supralabial scales (SPL; yellow), second row of loreal scales (red), subocular scales (SO; green), and (D) the lamellae scales under the 4th toe on the left hind foot.

only counted to the centre of the eye, and not the entire length of the upper lip. The number of lamellae under the 4th toe (the longest toe) on the left hind foot, as well as the number of enlarged postanal (PA) scales was also counted. In addition, the number of scales in a 5-mm length along the centre of the dorsal (Dors. 5 mm) and ventral (Ventr. 5 mm) sides, one head length from the neck, was also counted. Bilateral (left and right) characteristics were only recorded on the left side during this study.

Because *A. sagrei* employs caudal autotomy as a defensive mechanism, analysis and comparisons based on tail lengths were not feasible. In addition, the dorsal scales of a female from Chiayi, and the 4th toe of the left hind foot of a female from Hualien were damaged, and therefore the relative data were thus excluded from the respective analyses (Table 3.3).

Table 3.3. The sample sizes of the morphometric and meristic characters of the brown anole (*Anolis sagrei*) specimens from the eastern and southwestern study sites, used in this study. (* - data was only collected on the left lateral side of the head of the lizards)

	Eastern study site		**Southwestern study site**	
	Male	**Female**	**Male**	**Female**
Snout-vent length (SVL) (mm)	8	22	19	19
Tail length (TL) (mm)	8	22	19	19
Head length (HL) (mm) *	8	22	19	19
Left hind shank length (LHS) (mm)	8	22	19	19
Interorbital (IO) scale count	8	22	19	19
Interpariental/interorbital (IP/IO) scale count	8	22	19	19
Supralabials (SPL) scale count *	8	22	19	19
2nd row of scales between the canthal ridges (2. Canth.) scale count	8	22	19	19
Internasal (IN) scale count	8	22	19	19
Left hind foot 4th toe lamellae scale count	8	21	19	19
Enlarged postanal (PA) scale count	8	22	19	19
2nd loreal scale row scale count *	8	22	19	19
5 mm. Dorsal scale count	8	22	19	19
5 mm. Ventral scale count	8	22	19	18

Due to variations in the sizes of the *A. sagrei* specimens used in this study, the head length (HL), left hind shank length (LHS), dorsal (Dors. 5 mm) and ventral (Ventr. 5

mm) scale counts, were expressed as proportionate indices (HL or LHS/SVL x 100; or scale count/5 x SVL).

The normality of the distribution of the data was verified with one-sample Kolmogorov-Smirnov tests. Log data transformation did not normalise the distribution of some of the skewed recorded data of both sexes. As a result intersexual variation within localities and interlocality variation within sexes were analysed in a univariate fashion, using the untransformed data, by the Mann-Whitney *U*-test, using the statistics software package Instat (Vers. 3.0b, Graphpad Software, San Diego, CA). Statistical significance was set at 95 % confidence level (i.e. $p \leq 0.05$).

3.3. REPRODUCTIVE BIOLOGY

Meteorological data of the study area, for the period March 2002 to March 2003, was obtained from the Taiwanese Central Weather Bureau website (Taiwanese Central Weather Bureau), and was reported for Chiayi City which is located about 5 km from the study area. Daily photoperiods for Chiayi City were calculated using the online sunrise and sunset calculator of the Graduate Institute of Astronomy website (Graduate Institute of Astronomy).

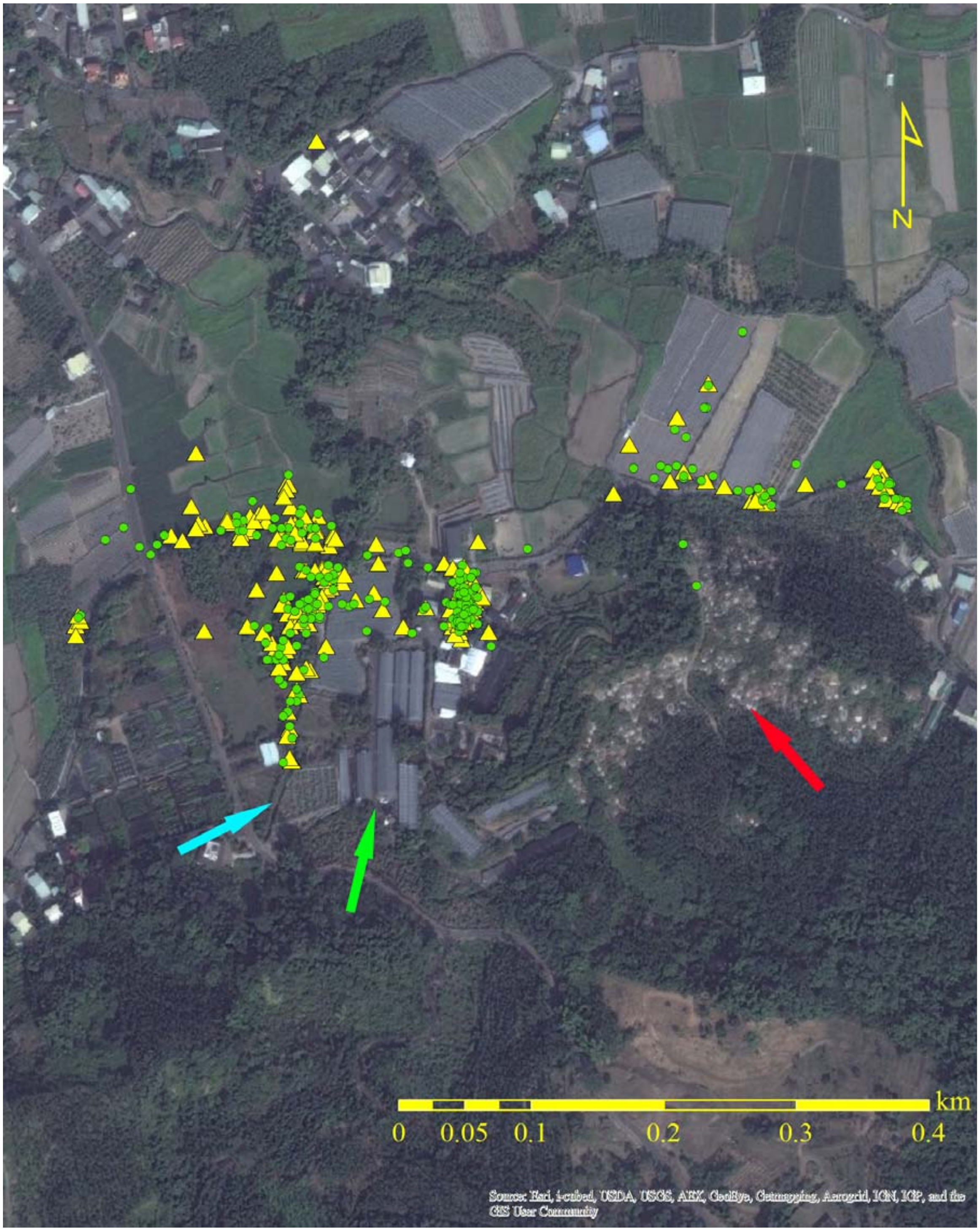
Between the 4th of March 2002 and the 28th of March 2003, male and female *A. sagrei* specimens, were collected monthly (Table 3.4) by hand or with a fine-meshed fishing scoop net, along the road; from agricultural fields; along a creek; and from a cemetery in the area surrounding a plant nursery (23º25'51"N, 120º28'30"E) in Santzepu, Sheishan

District, Chiayi County, southwestern Taiwan (Fig. 3.3).

Table 3.4. The numbers of brown anole (*Anolis sagrei*) specimens collected, and the monthly sampled specimens used in the reproductive biology and caudal autotomy analyses.

	Collected specimens		**Reproductive biology**		**Caudal autotomy**	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**
Mar 2002	17	17	17	15	0	15
Apr 2002	16	22	15	22	13	20
May 2002	17	19	17	19	13	19
Jun 2002	15	20	15	19	13	18
Jul 2002	17	18	16	17	15	17
Aug 2002	19	15	17	15	0	15
Sep 2002	20	17	20	17	15	13
Oct 2002	22	16	21	16	20	16
Nov 2002	12	20	12	15	11	15
Dec 2002	14	12	14	11	14	10
Jan 2003	21	11	18	10	18	10
Feb 2003	18	12	18	11	15	10
Mar 2003	15	17	15	17	15	15

At the point of capture, the GPS location was recorded and the specimen was allocated a field number. Upon returning from the field, each lizard was euthanised with ether (Shimakyu's Pure Chemicals, Osaka, Japan), and the snout-vent length (SVL) and tail length (TL) were measured with a transparent plastic ruler to the nearest mm by the same person. The tail was scored as complete or broken, based on its morphology (Fig. 3.4), and if the animal had experienced caudal autotomy, the regenerated portion was measured with a transparent plastic ruler to the nearest mm. The lizard was also weighed to the nearest 0.1 g with an electronic scale (YC e68, Shanghai Yong Cheng Scale Co. Ltd. Shanghai, China), and after making a mid-ventral incision, the stomach, abdominal fat bodies of both sides and the liver were removed. The abdominal fat bodies and the livers were weighed (wet weight) to the nearest 0.01 g with an electronic scale (FX-1200, A & D Weighing, California, U.S.A.).



Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, and the GIS User Community

Figure 3.3. An aerial view of the agricultural fields, the creek (blue arrow), the cemetery (red arrow), and the plant nursery (green arrow) in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan, where the brown anole (*Anolis sagrei*) specimens were collected for the reproductive biology study. The localities where the lizards were collected are indicated by green dots (for males) and yellow triangles (for females).

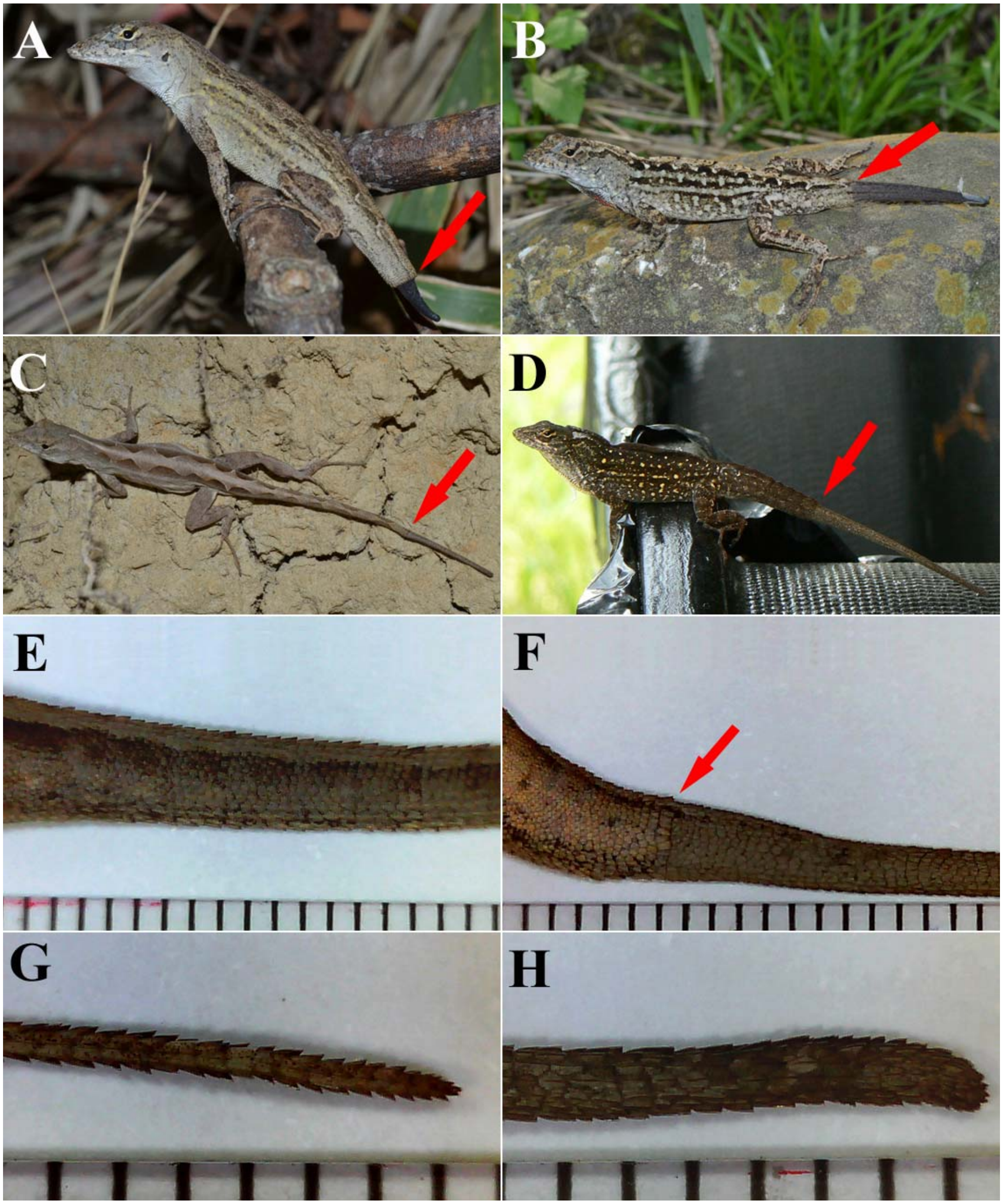


Figure 3.4. During early (A and B) and more advanced stages (C and D) of tail regeneration, the regenerated tails (indicated by red arrows) of *Anolis sagrei* females (A and C) and males (B and D) can be distinguished from what remains of the original tail by differences in coloration and patterns. Closer examination will also reveal that the scales of an original tail (E) differ from a regenerated tail (F), and the tip of the former is sharper and narrower (G) than that of the latter (H).

All the specimens, except for the right testes (removed prior to fixation), stomachs and stomach contents, were fixed in 10 % formalin (Kojima Chemical Co. Ltd., Sayama, Japan) for 24 hours, after which they were preserved in 75 % alcohol (Taiwan Sugar Corporation, Tainan City, Taiwan). The stomachs and their contents were placed individually in vials filled with 75 % alcohol. The testes were treated as required for histology. To eliminate factors such as inconsistent tail lengths due to caudal autotomy, and the weight of stomach and gut contents, the organ weights of the *A. sagrei* specimens used in this study were expressed as proportionate indices (abdominal fat bodies or liver weight/SVL x 100). All the descriptions and analyses were then based on these indices.

To determine the reproductive status of the males, the gonad (testis) on the right hand side was removed, fixed in 100 % Bouin's solution[6] for four hours after which it was transferred to 75 % alcohol. The testes were taken to Chiayi Christian Hospital's cytology laboratory, where they were dehydrated with a tissue processor (ETP-300CV, Sakura, Tokyo, Japan), embedded in paraffin with an embedder (Tissue-Tek® AutoTEC® Automated Embedder, Sakura, Tokyo, Japan), sectioned with a microtome (RM 2125 RTS, Leica, Wetzlar, Germany) at 5 µ, mounted on glass slides, and stained with Harris' hematoxylin followed by eosin counterstain. The testicular tissue samples were examined microscopically, and each sample was assigned to one of four stages in the testicular cycle: (1) immature – spermatogonia and spermatocytes are present, but it is not possible to state when spermiogenesis will begin; (2) regressed – seminiferous tubules contained spermatogonia and Sertoli cells only; (3) recrudescent – seminiferous tubules exhibited markedly increased cellularity, with primary spermatocytes predominating; or (4)

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[6] Bouin's solution is a fixative made of a mixture of picric acid (saturated; 75 ml), formaldehyde (37-40 %; 25 ml) and glacial acetic acid (5 ml).

spermiogenic – sperm, spermatids, and metamorphosing spermatids abundant (Goldberg *et al*., 2002).

To determine the reproductive condition of the females, the left ovaries were visually examined *in situ*, and assigned to one of four stages of the ovarian cycle: (1) inactive – no yolk deposition; (2) yolk deposition in one or more ovarian follicles; (3) oviductal eggs present and yolk deposition in one or more ovarian follicles; or (4) oviductal eggs present, and no yolk deposition in ovarian follicles (Goldberg *et al*., 2002).

The size at which sexual maturity was reached was based on the presence of sperm, spermatids, and metamorphosing spermatids in males. In the females the presence of oviductal eggs, enlarged vitellogenic follicles, or both indicated sexual maturity. Only individuals that were at a sexually mature size were used in this study (Table 3.4).

Before the data could be analysed it was necessary to determine whether caudal autotomy (tail loss) had an influence on the abdominal fat body weight and/or liver weight of lizards that had experienced caudal autotomy and regenerated their tails. Male (n = 21) and female (n = 11) lizards that had experienced caudal autotomy, but showed no indications of caudal regeneration, were excluded from this analysis, because the possibility that the autotomy, which often involved just the tip of the tail, may have occurred during the capturing process could not be ruled out. No *A. sagrei* male specimens, with regenerated autotomised tails, were collected in March and August 2002 and therefore sampled male specimens from these months were thus also excluded from the analysis. The monthly sampled specimens used in the caudal autotomy analyses are indicated in Table 3.4.

The normality of the distribution of the data was verified with one-sample Kolmogorov-Smirnov tests. Log data transformation did not normalise the distribution of the mean liver weight indices (LWI) of the female lizards that had not experienced caudal autotomy and those that had. As a result, the Mann-Whitney *U*-test, was used to compare the monthly variations in the mean abdominal fat body weight indices (AFBWI) and mean LWI of the male and female lizards that had not experienced caudal autotomy and those that had, using the untransformed data.

No statistically significant variations in the monthly mean AFBWI and monthly mean LWI of male and female lizards that had not experienced caudal autotomy and those that had were noted, so the relevant data of the respective sexes, irrespective of their tail condition, were pooled for the reproductive biology study. The monthly sampled specimens used in the reproductive biology study are indicated in Table 3.4. Since log data transformation did not normalise the distribution of the SVL, AFBWI, or LWI data of both sexes, the Kruskal-Wallis Test (Nonparametric ANOVA) was used to test for significant monthly variations in the medians of the SVL, AFBWI, or LWI. Spearman's rank correlation coefficient (r_s) was used in a univariate fashion to examine the relationships between the monthly proportion of reproductive lizards, monthly AFBWI, monthly LWI, monthly mean precipitation, monthly mean temperature, and monthly mean photoperiod. The SVL, AFBWI, and LWI of the males and females sampled in

March 2002 and March 2003 were analysed in a univariate fashion using the unpaired *t*-test with Welch correction, or, where the assumptions of the *t*-test were substantially violated (i.e. non-normal distribution), by the Mann-Whitney *U*-test. The data was analysed with the statistics software package Prism 6 (Graphpad Software, San Diego, CA). Statistical significance was set at 95 % confidence level (i.e. $p \leq 0.05$). For description, the period of high reproductive activity of the males was considered the period in which > 50 % of the adult males were spermiogenic, and for the females the period in which > 50 % of the adult females there was yolk deposition in one or more ovarian follicles and/or oviductal eggs were present

3.4. REFERENCES

Barbour, M.G., Burk, J.H., and Pitts, W.D. 1987. *Terrestrial Plant Ecology. 2nd Edition*. The Benjamin/Cummings Publishing Company, Inc, Massachusetts.

Brady, N.C., and Weil, R.R. 2002. *The Nature and Properties of Soils.* 13th edition. Pearson Education Inc., New Jersey.

Brown, L.R., du Preez, P.J., Bezuidenhout, H., Bredenkamp, G.J., Mostert, T.H.C., and Collins, N.B. 2013. Guidelines for phytosociological classifications and descriptions of vegetation in southern Africa. *Koedoe* 55: 1-10.

Chang, N.C. 2007. A new discovered alien lizard of Hualien – *Anolis sagrei*. *Quarterly of Natural Conservation* 57: 37-41. (In Chinese)

Graduate Institute of Astronomy, National Central University. [online]. Available at: http ://www.astro.ncu.edu.tw/index_e.shtml?p=outreach/sunriseset/index.html (accessed 03rd of June, 2013).

Goldberg S.R., Kraus F., and Bursey C.R. 2002. Reproduction in an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawaii. *Pacific Science* 56: 163-168.

Harpstead, M.I., Sauer, T.J., and Bennett, W.F. 2001. *Soil Science Simplified.* 4th edition. Iowa State University Press, Iowa.

Hennekens, M. 1996. *TURBOVEG, A Software Package for Input, Processing, and Presentation of Phytosociological Data. User's Guide, Version 2001*. IBN-DLO Wageningen, NL and University of Lancaster, UK.

Hennekens, S. 1998. *TURBOVEG: Clipper Database Management Software for Storage, Selection, and Export of Vegetation Data (Relevés).* Green World Research, Wageningen, Netherlands.

Huang, S.C., Norval, G., Wei, C.S., and Tso, I.M. 2008. Effects of the brown anole invasion and betelnut palm planting on arthropod diversity in southern Taiwan. *Zoological Science* 25: 1121-1129.

Kent, M., and Coker, P. 1992. *Vegetation Description and Analysis, a Practical Approach*. John Wiley & Sons, Chichester.

Lee, J.C. 2000. *A Field Guide to the Amphibians and Reptiles of the Maya World: The Lowlands of Mexico, Northern Guatemala, and Belize*. Cornell University Press, New York.

Meshaka, W.E. Jr., Butterfield, B.P., and Hauge, J.B. 2004. *The Exotic Amphibians and Reptiles of Florida*. Krieger Publishing Company, Florida.

Norval, G., Bursey, C.R., Goldberg, S.R., Mao, J.J., and Slater, K. 2011a. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei*

(Squamata: Polychrotidae), in southwestern Taiwan. *Pacific Science* 65: 383-390.

Norval, G., Chiu, P.K., Chu, H.P., and Mao, J.J. 2011b. An instance of predation on the brown anole (*Anolis sagrei* Duméril & Bibron, 1837) by a Malay night heron (*Gorsakius melanolophus* Swinhoe, 1865). *Herpetology Notes* 04: 05-07.

Norval, G., Goldberg, S.R., and Mao, J.J. 2012. The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan. *Russian Journal of Herpetology* 19: 75-81.

Norval, G., Goldberg, S.R., Bursey, C.R., Mao, J.J., and Slater, K. 2014. Internal parasites of lizards from Taiwan. *Herpetological Conservation and Biology* 9: 484-494.

Norval, G., Hsiao, W.F., Huang, S.C., and Chen, C.K. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russian Journal of Herpetology* 17: 131-138.

Norval, G., Mao, J.J., Chu, H.P., and Chen, L.C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.

Poore, M.E.D. 1955. The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet system. *Journal of Ecology* 43: 226-244.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of Florida, Gainesville, Florida.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Taiwanese Central Weather Bureau. [online]. Available at: http://www.cwb.gov.tw/V6e/index.htm (accessed 06th of June, 2013).

Tichý, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451-453.

Tichý, L., Roleček, J., Zelený, D., and Chytrý, M. 2007. *New Stopping Rules For TWINSPAN*. European Vegetation Survey, 16th Workshop, March 22-27, 2007.

Wang, G.Q. 2013. *Modeling the Dispersal Pattern of Brown Anole (Anolis sagrei) Population in Samtzepu, Chiayi County, Taiwan*. M.Sc. dissertation. National Cheng Kung University, Tainan, Taiwan, R.O.C.

CHAPTER 4 – A DESCRIPTION OF THE KNOWN DISTRIBUTION RANGE OF *ANOLIS SAGREI* IN TAIWAN AND THE CHARACTERISTICS OF THE HABITATS THIS SPECIES OCCURS IN

4.1. INTRODUCTION

Throughout the native and introduced distribution range of *A. sagrei*, it has been noted that this species utilises open sunny habitats and that it is well adapted to areas disturbed by humans (Ruibal, 1964; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004). In the original description of *A. sagrei* as an invasive species in Taiwan it was also stated that this species seems to prefer disturbed areas with low or no ground covering (Norval *et al*., 2002). However, for the management and forecasting of the expected range expansion of *A. sagrei* in Taiwan, a better understanding of the characteristics of the habitat types these lizards occur in is needed. Therefore, herein in addition to a description of the current known distribution of *A. sagrei* in Taiwan, a classification and description of the characteristics of the habitat types these lizards occur in will also be made.

4.2. RESULTS

4.2.1. *KNOWN DISTRIBUTION WITHIN STUDY SITES*

In the southwestern study site, *A. sagrei* specimens were recorded in one locality in the East District of Chiayi City (Fig. 4.1). In Chiayi County, they were recorded in one locality in Suantou (Liujiao Township), and numerous localities in the area in and

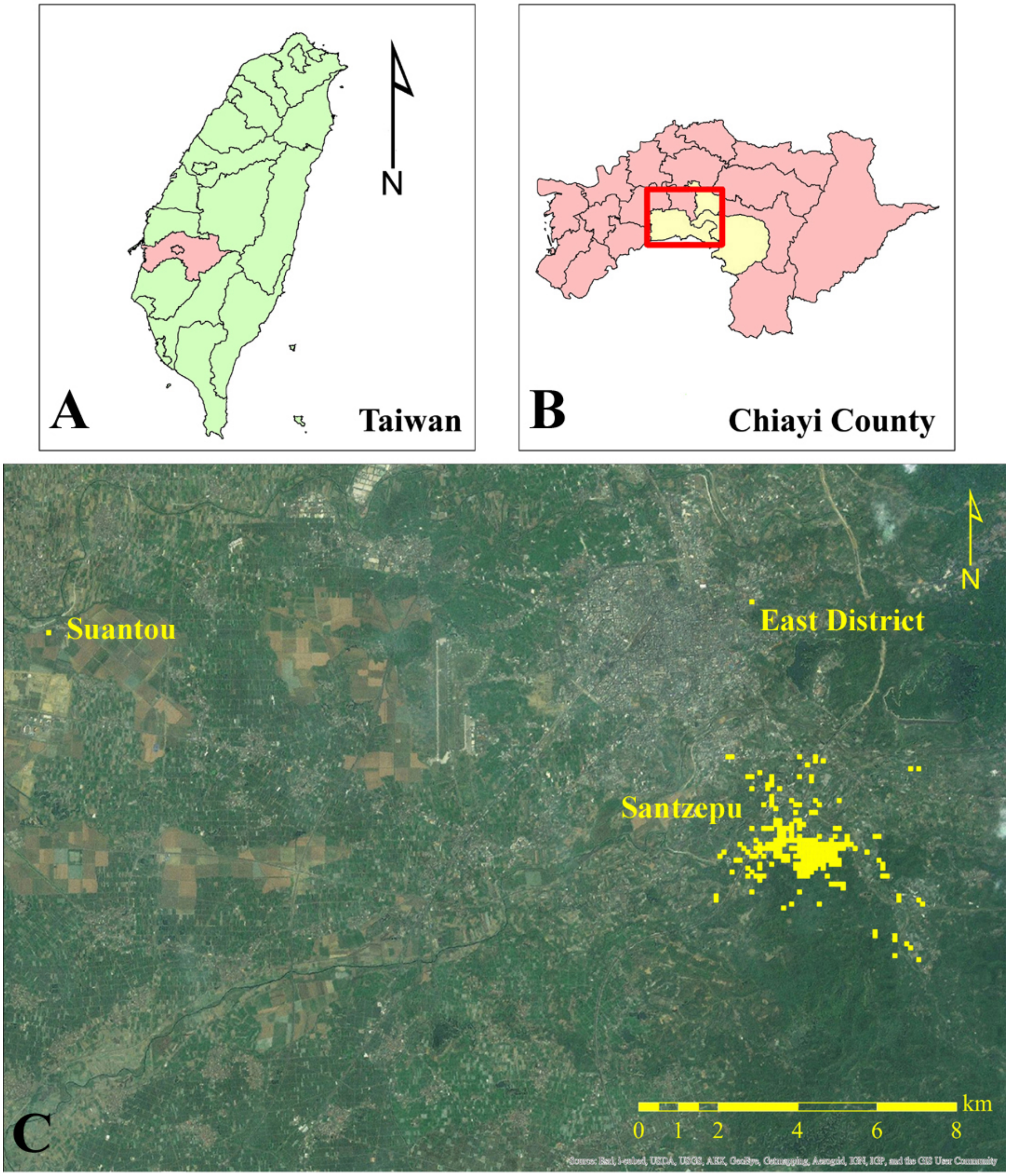


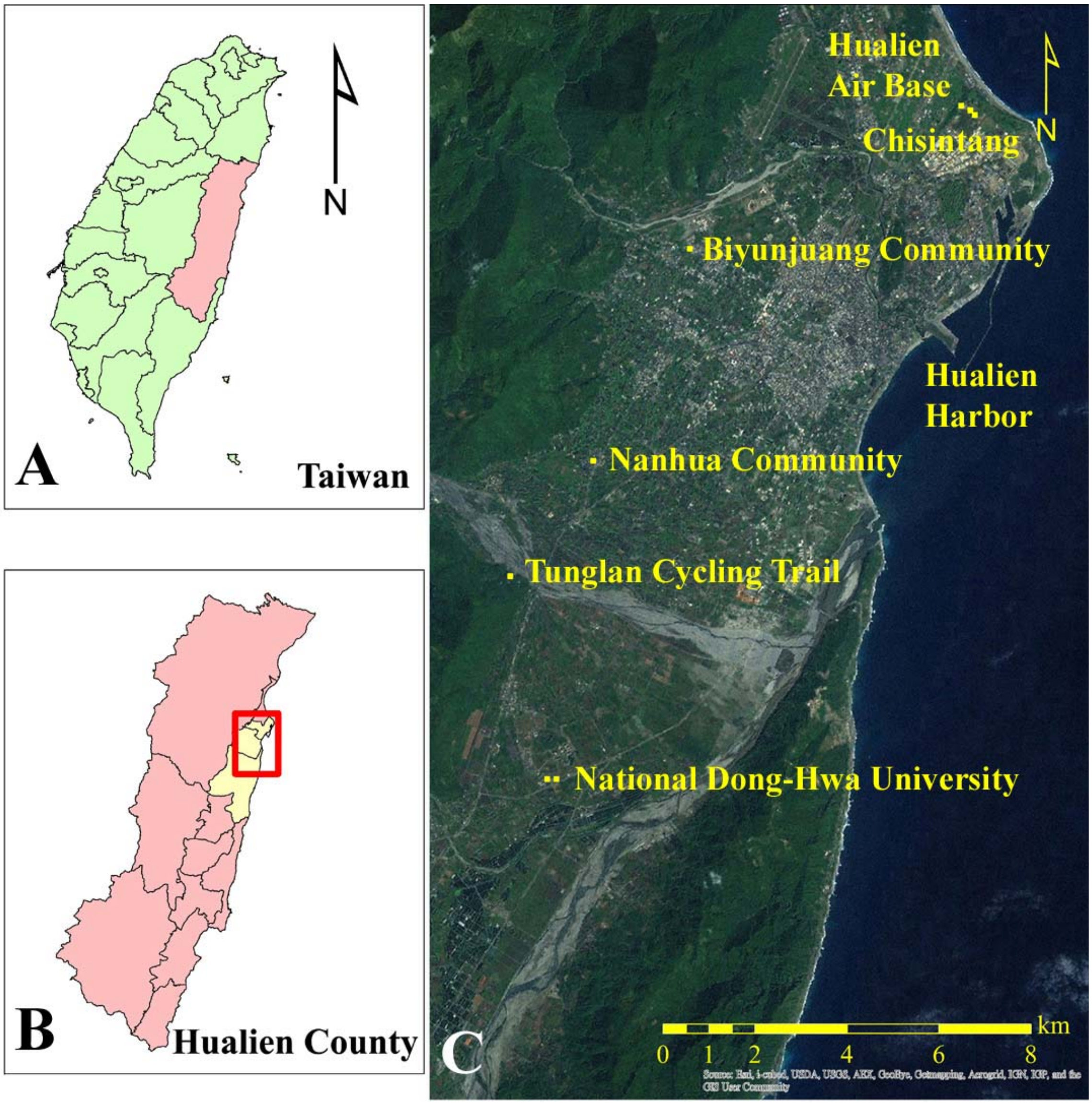
Figure 4.1. The position of Chiayi County, southwestern Taiwan (a), the study area (red rectangle in b), and the distribution of the one hectare plots (yellow squares) in which *Anolis sagrei* were recorded within this locality (c) (total area of distribution = 237 hectares).

surrounding Santzepu (Fig. 4.1). The lizards were recorded in a variety of habitats, such as roadside and urban gardens, parks, cemeteries, fruit orchards and other agricultural fields.

In the eastern study site, *A. sagrei* specimens were recorded in two localities in Chisintang, one locality near the Hualien Air Base, one locality along the Tunglan Cycling Trail, and two localities at National Dong-Hwa University, all located in Hualien County (Fig. 4.2). They were also found in one locality in Biyunjuang Community and one in Nanhua Community, both located in the outskirts of Hualien City (Fig. 4.2). The lizards were found in urban gardens, fallow fields, *Cocos nucifera* (coconut) plantations, an area that is currently being developed into a geology park (to exhibit various rock types from Taiwan), and the edges of roadside secondary forests.

4.2.2. *VEGETATION DESCRIPTION*

A total of 305 plant species belonging to 84 families were recorded in the southwestern study site. Flowering plants were represented by the Dicotyledoneae with 207 species in 63 families, and Monocotyledoneae with 87 species in 14 families (Table 4.1). The non-flowering plants were represented by Pteridophytes with 11 species in seven families (Table 4.1). Ten families dominated the flora of this study. The four largest families were the Asteraceae with 24 species, reflecting 7.9 % of the total flora, the Cyperaceae with 18 species representing 5.9 % of the flora, Euphorbiaceae with 20 species, representing 6.6% of the flora, and the Poaceae with 46 species, representing 15.1 % of the flora of the southwestern study site. These were followed by much smaller, but still significant families, represented by the Leguminosae with 17 species (5.6 %), Malvaceae with 8 species (2.6 %), Rubiaceae with 11 species (3.6 %), and Moraceae, Solanaceae and Verbenaceae with 6 species, each representing 2 % (total of 6 % together) of the flora of the study site. These 10 families represented 53.3 % of the flora of the southwestern



Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, and the GIS User Community

Figure 4.2. The position of Hualien County, eastern Taiwan (a), the study area (red rectangle in b), and the distribution of the one hectare plots (yellow squares) in which *Anolis sagrei* were recorded within this locality (c) (total area of distribution = 8 hectares).

study site, while the other 74 families reflected the remaining 46.7 % with a total of 143 different plant species.

A total of 111 plant species belonging to 52 families were recorded in the eastern study site. Flowering plants were represented by the Dicotyledoneae with 85 species in 41 families, and Monocotyledoneae with 23 species in nine families (Table 4.2). The non-

Table 4.1. A list of the plant families identified in the southwestern study site in Chiayi County, indicating the number of genera and species in each family (a species list is given in Appendix 4.1).

Family name	Genera	Species	Family name	Genera	Species	Family name	Genera	Species
DICOTYLEDONEAE			Lythraceae	1	4	Tiliaceae	1	1
Acanthaceae	1	1	Malvaceae	1	8	Ulmaceae	1	1
Altingiaceae	1	1	Melastomataceae	1	1	Umbelliferae	1	1
Amaranthaceae	1	3	Meliaceae	1	1	Urticaceae	1	2
Anacardiaceae	1	2	Menispermaceae	1	2	Verbenaceae	1	6
Apocynaceae	1	3	Moraceae	1	6	Vitaceae	1	4
Aristolochiaceae	1	1	Myristicaceae	1	1	MONOCOTYLEDONEAE		
Asteraceae	1	24	Myrsinaceae	1	2	Agavaceae	1	1
Basellaceae	1	1	Myrtaceae	1	5	Araceae	1	5
Bignoniaceae	1	1	Oleaceae	1	3	Arecaceae	1	3
Bombacaceae	1	1	Onagraceae	1	3	Asparagaceae	1	1
Boraginaceae	1	4	Oxalidaceae	1	3	Bromeliaceae	1	1
Brassicaceae	1	1	Papilionaceae	1	3	Commelinaceae	1	2
Buddlejaceae	1	1	Passifloraceae	1	2	Cyperaceae	1	18
Cactaceae	1	1	Plantaginaceae	1	1	Dioscoreaceae	1	1
Capparidaceae	1	1	Plumbaginaceae	1	1	Liliaceae	1	1
Caricaceae	1	1	Polygonaceae	1	4	Musaceae	1	1
Caryophyllaceae	1	1	Portulacaceae	1	1	Poaceae	1	46
Chenopodiaceae	1	1	Rosaceae	1	1	Smilacaceae	1	3
Combretaceae	1	1	Rubiaceae	1	11	Typhaceae	1	1
Convolvulaceae	1	5	Rutaceae	1	5	Zingiberaceae	1	3
Crassulaceae	1	1	Sapindaceae	1	4	PTERIDOPHYTA		
Cucurbitaceae	1	2	Sapotaceae	1	2	Cupressaceae	1	1
Ebenaceae	1	1	Scrophulariaceae	1	3	Cycadaceae	1	1
Euphorbiaceae	1	20	Solanaceae	1	6	Equisetaceae	1	1
Labiatae	1	1	Sphenocleaceae	1	1	Podocarpaceae	1	1
Lamiaceae	1	2	Symplocaceae	1	1	Pteridaceae	1	4
Lauraceae	1	4	Theaceae	1	3	Schizaeaceae	1	1
Leguminosae	1	17	Thymelaeaceae	1	1	Thelypteridaceae	1	2
						Total	**84**	**305**

flowering plants were represented by Pteridophytes with three species in two families (Table 4.2).

Eight families dominated the flora of the eastern study site. Similar to the southwestern study site, the two largest families were the Asteraceae with nine species, reflecting 8.1 % of the total flora, and the Poaceae with 10 species, representing 9 % of the flora of the

Table 4.2. A list of the plant families identified in the eastern study site in Hualien County, indicating the number of genera and species in each family (a species list is given in Appendix 4.2).

Family name	Genera	Species
DICOTYLEDONEAE		
Amaranthaceae	1	1
Annonaceae	1	1
Apocynaceae	1	1
Araliaceae	1	4
Asteraceae	1	9
Balsaminaceae	1	1
Berberidaceae	1	1
Bombacaceae	1	1
Chenopodiaceae	1	1
Clusiaceae	1	1
Elaeagnaceae	1	1
Euphorbiaceae	1	4
Lamiaceae	1	3
Leguminosae	1	3
Lythraceae	1	2
Magnoliaceae	1	3
Melastomataceae	1	1
Moraceae	1	4
Myrsinaceae	1	1
Myrtaceae	1	2
Nyctaginaceae	1	1
Ochnaceae	1	1
Oleaceae	1	2
Onagraceae	1	1
Oxalidaceae	1	3
Phyllanthaceae	1	2
Piperaceae	1	1
Ranunculaceae	1	1
Rosaceae	1	2
Rubiaceae	1	3
Rutaceae	1	2
Sapindaceae	1	2
Solanaceae	1	4
Staphyleaceae	1	1
Theaceae	1	1
Tiliaceae	1	1
Ulmaceae	1	2
Umbelliferae	1	1
Urticaceae	1	4
Verbenaceae	1	4
Vitaceae	1	1
MONOCOTYLEDONEAE		
Araceae	1	3
Arecaceae	1	3
Asparagaceae	1	1
Commelinaceae	1	1
Laxmanniaceae	1	1
Liliaceae	1	1
Poaceae	1	10
Smilacaceae	1	1
Zingiberaceae	1	2
PTERIDOPHYTA		
Podocarpaceae	1	1
Thelypteridaceae	1	2
Total	**52**	**111**

study site. These were followed by the Araliaceae, Euphorbiaceae, Moraceae, Solanaceae, Urticaceae and Verbenaceae, all with four species, each representing 3.6 % of the flora of the study site. These eight families represented 38.7 % of the flora of the eastern study site, while the other 44 families reflect the remaining 61.3 % with a total of 68 different plant species.

4.2.3. *PLANT COMMUNITY CLASSIFICATION AND DESCRIPTIONS*

a) The southwestern study site

The results from the vegetation analysis resulted in the identification of seven plant communities that can be grouped into three main communities:

1. *Alocasia odora-Panicum maximum* community
    1.1. *Alocasia odora-Panicum maximum-Miscanthus floribundus* sub-community
    1.2. *Alocasia odora-Panicum maximum-Trema orientalis* sub-community
2. *Cynodon dactylon* community
    2.1. *Cynodon dactylon-Axonopus affinis* sub-community
    2.2. *Cynodon dactylon-Cuphea hyssopifolia* sub-community
    2.3. *Cynodon dactylon-Polygonum multiflorum* sub-community
    2.4. *Cynodon dactylon-Acalypha australis* sub-community
3. *Echinochloa colona-Eleusine indica* community

The traits of the seven plant communities are summarised in Table 4.3. Overall the vegetation is characterised by the prominence of the forbs *Bidens pilosa* and *Phyllanthus urinaria*, and the grass, *Panicum maximum*, all from species group M (Table 4.4). These species will therefore not necessarily be mentioned in each description of the different plant communities. All references to species groups in the descriptions refer to Table 4.4.

1. *Alocasia odora-Panicum maximum* community

This community occurs on low-elevation foothills, and flat plain areas. The vegetation comprises pioneer and sub-climax species that establish after agricultural activities have taken place in these areas. The vegetation range in height from short (< 0.5 m) in the artificial grasslands and plantation understories to tall (> 5 m) in the secondary forests. In some of the agricultural areas, bare ground patches are visible, while in the secondary forests, the vegetation cover is usually very high (> 75 %). A total of 200 species were

Table 4.3. The ranges of the estimated vegetation and rockiness cover of the seven plant communities identified in the southwestern study site. The number of species recorded, the ranges of the number of species per sample plot, the ranges of the number of species per m², as well as the soil types, the ranges of the soil pH, the ranges of the slope, and the ranges of aspect recorded in each community are also given. Where applicable, the mean and standard deviation is given in parenthesis (mean ± SD).

	***Alocasia odora-Panicum maximum* community**		***Cynodon dactylon* community**				***Echinochloa colona-Eleusine indica* community**
	***Alocasia odora-Panicum maximum-Miscanthus floribundus* sub-community**	***Alocasia odora-Panicum maximum-Trema orientalis* sub-community**	***Cynodon dactylon-Axonopus affinis* sub-community**	***Cynodon dactylon-Cuphea hyssopifolia* sub-community**	***Cynodon dactylon-Polygonum multiflorum* sub-community**	***Cynodon dactylon-Acalypha australis* sub-community**	
Tree cover *	5 – 85	0 – 90	0	0 – 80	0 – 50	0 – 60	0 – 80
Shrub cover *	0 – 25	0 – 10	<1	5 – 80	<1 – 5	0 – 30	0 – 80
Herb cover *	<1 – 90	0 – 50	5 – 90	<1 – 25	0 – 80	1 – 60	<1 – 90
Grass cover *	<1 – 75	<1 – 90	10 – 90	<1 – 80	15 – 65	<1 – 80	<1 – 80
Rockiness *	0 – 1	0 – 45	0	0 – 30	0	0 – 30	0 – 70
Number of species recorded	68	172	48	56	20	74	178
Number of species per sample plot	6 – 21 (16.0 ± 4.5)	10 – 44 (24.8 ± 8.9)	18 – 26 (21.3 ± 3.6)	10 – 32 (20.0 ± 9.3)	4 – 17 (10.5 ± 9.2)	14 – 34 (21.3 ± 6.4)	5 – 32 (15 .4 ± 5.6)
Number of species per m²	0.1 – 0.2 (0.2 ± 0.1)	0.1 – 0.9 (0.3 ± 0.2)	0.2 – 0.4 (0.3 ± 0.1)	0.1 – 2.6 (1.2 ± 1.1)	0.1 – 0.3 (0.2 ± 0.2)	0.1 – 0.5 (0.3 ± 0.1)	0.1 – 3.2 (0.6 ± 0.7)
Soil type	sandy clayish, clayish, or sandy	sandy clayish, clayish,	sandy clayish	sandy clayish, sandy loam, or loam	sandy clayish	sandy clayish, clayish,	sandy clayish, clayish, or loam
Soil pH	3.8 – 6.6 (5.7 ± 0.7)	3.8 – 7.0 (5.9 ± 0.7)	4.6 – 5.7 (5.2 ± 0.5)	5.2 – 6.4 (5.9 ± 0.5)	4.5 – 5.4 (5.0 ± 0.6)	5.2 – 6.4 (5.9 ± 0.4)	3.0 – 7.0 (5.7 ± 0.7)
Slope	0 – 5º (1.0 ± 1.7)	0 – 50º (15.2 ± 12.4)	1 – 4º (3.0 ± 1.0)	1 – 34º (8.0 ± 14.5)	0º	0 – 12º (2.1 ± 4.4)	0 – 65º (5.0 ± 12.3)
Aspect	0 – 180º	0 – 299º	0º	0 – 180º	0º	0 – 180º	0 – 214º

* - These values were based on visual estimates and are not accurate enough for mean and standard deviation calculations.

identified within this community, with a mean of 22 (± 9.3 SD) species per sample plot, and 0.3 (± 0.2 SD) species per m².

The community is characterised by species from species groups A. The vegetation is dominated by the tuberous *Alocasia odora* (species group A), the forb *B. pilosa*, and the grass *P. maximum* (species group M). Thepalm *Areca catechu*, and the tree *Macaranga tanarius* (species group A) are co-dominant throughout this community, with constancies ranging from 36.4 % to 80.0 %. The fern *Lygodium japonicum* (species group A), weedy forbs *Drymaria diandra* (species group L), *Ipomoea cairica*, and *Mikania micrantha*, and the woody shrub *Melastoma candidum*, and the trees *Cinnamomum camphora*, and *Machilus zuihoensis* (species group A) are conspicuous in this community, with constancies ranging from 25.5 % to 52.7 %.

1.1. *Alocasia odora-Panicum maximum-Miscanthus floribundus* sub-community

This sub-community occurs in the secondary forest areas, which grow along the creek that flows through the study site, neglected *A. catechu* plantations, and roadsides. These areas are fairly flat, and experience limited disturbances, in the form of annual application of herbicides in the *A. catechu* plantations prior to harvesting, or when typhoons pass over the study site, which reduces the vegetation cover by defoliating trees and shrubs (Norval, *pers. obs.*). In the *A. catechu* plantations and roadsides the soil is sandy clayish or clayish, while in the secondary forest the soil is sandy. Gullies were present in sample plots 140 (*A. catechu* plantation), 145 and 146 (secondary forest) where water drains from within the secondary forest and the *A. catechu* plantations during heavy rains.

This sub-community is characterised by species from species group B. The vegetation is dominated by the palm *A. catechu*, the tuberous *A. odora*, the weedy vine *M. micrantha* (species group A), and the grass *Miscanthus floridulus* (species group B), with constancies ranging from 46.2 % to 76.9 %. The tree *Averrhoa carambola* is dominant in sample plots 143 and 150. The fern *Christella acuminata* (species group B), the forbs *Costus speciosus*, *Callerya reticulata*, and *Maesa perlaria* var. *perlaria*, the grass *Oplismenus hirtellus*, and the semi-woody shrubs *M. candidum* (species group A), and *Clerodendrum paniculatum* (species group B), are conspicuous in this community, with constancies ranging from 30.8 % to 53.9 %.

The spectacled toad (*Duttaphrynus melanostictus*), marshland frog (*Fejervarya limnocharis*), dark-sided chorus frog (*Microhyla heymonsi*), Stejneger's paddy frog (*Micryletta stejnegeri*), long-tailed skink (*Eutropis longicaudata*), Asian house gecko (*Hemidactylus frenatus*), Swinhoe's tree lizard (*Japalura swinhonis*), elegant skink (*Plestiodon elegans*), and striped keelback (*Amphiesma stolata*) were recorded in sample plots placed within the *A. catechu* plantations and secondary forest. The checkered keelback (*Xenochrophis piscator*) was also recorded in sample plots placed within the *A. catechu* plantations and secondary forest, but only in those (sample plots 147 and 148) that tended to be waterlogged during the rainy season. The Günther's frog (*Hylarana guentheri*), ornamented pygmy frog (*Microhyla fissipes*), white-lipped tree frog (*Polypedates braueri*), Moltrecht's tree frog (*Rhacophorus moltrechti*), Kühne's grass lizard (*Takydromus kuehnei*), and Indian forest skink (*Sphenomorphus indicus*), were only recorded in sample plots placed within the secondary forest and sample plots in the *A. catechu* plantations with high vegetation cover. *Anolis sagrei* was only recorded in sample plots placed within the *A. catechu* plantations and roadside areas with a low vegetation cover.

1.2. *Alocasia odora-Panicum maximum-Trema orientalis* sub-community

This sub-community occurs on areas such as small secondary forest fragments located among agricultural fields, *A. catechu* plantations, mixed *A. catechu* and banana (*Musa sapientum*) plantations, bamboo plantations, a small artificial grassland, a park on a hill and a roadside. The areas are primarily located on slopes, and experience occasional disturbances due to farming practices, weeding, and/or typhoons and heavy rains. The sample plots placed within bamboo (*Dendrocalamus latiflorus*) stands (sample plots 134 and 137), and a roadside (sample plot 123) had sandy soil, while sample plots placed within some of the secondary forest fragments (sample plot 82), *A. catechu* plantations (sample plots 3 and 136), mixed *A. catechu* and *M. sapientum* plantations (sample plots 77, 78, 79, 80 and 135), and the cemetery (sample plot 122) had sandy clayish soil. All the other sample plots had clayish soil. Sheet erosion, rills, furrows and gullies were noted in various sample plots in areas where the vegetation cover was low.

This sub-community is characterised by species from species group C, and is co-dominated by the tree *Trema orientalis* (species group C), the grass *P. maximum*, and the forbs *B. pilosa*, and *P. urinaria* (species group M), with constancies ranging from 52.4 %

to 83.3 %. The tuberous *A. odora*, the weedy vine *M. micrantha* (species group A), and the forbs *Ageratum conyzoides*, *Ipomoea obscura*, and *Passiflora suberosa* (species group L) are present throughout this sub-community, with constancies ranging from 45.2 % to 73.8 %. The fern *Cyclosorus parasiticus*, the forb *Oxalis corniculata*, the shrub *Flueggea virosa*, and the trees *Acacia confusa*, and *Litchi chinensis* (species group C) are conspicuous in this community, with constancies ranging from 26.2 % to 40.5 %.

The tree lizard, *J. swinhonis* and the frog *M. stejnegeri* were the only species recorded in sample plots placed within the secondary forest fragments. *Anolis sagrei* was the only species observed in sample plot 123, which was located on the roadside. The frog *F. limnocharis* and the lizard *A. sagrei* were the only vertebrates observed in sample plots 134 and 137, placed within the *D. latiflorus* stands. No amphibians and reptiles were observed in most of the sample plots placed within the artificial grassland, but in sample plot 12, which was shady due to a high tree canopy cover (*ca*. 80%), and sample plot 13, which bordered an area with a high tree cover, the lizards *E. longicaudata*, *J. swinhonis*, and *S. indicus* were observed. In most of the sample plots placed within the park *A. sagrei*, *H. frenatus*, and *J. swinhonis* were observed to be sympatric. However, in sample plot 62, which had a shaded undergrowth and dense canopy cover, only *J. swinhonis* and *Takydromus formosanus* were observed. *Duttaphrynus melanostictus*, *A. sagrei*, and *E. longicaudata* were observed in the sample plots placed within the *A. catechu* plantations. In sample plots placed within the mixed *A. catechu* and *M. sapientum* plantations, the lizards *A. sagrei*, *E. longicaudata*, *H. frenatus*, *J. swinhonis*, *P. elegans*, *S. indicus*, and *T. formosanus* were observed, although not always sympatric. *Anolis sagrei*, *E.*

longicaudata, and *H. frenatus* were observed within sample plots placed within *M. sapientum* plantations. Only *A. sagrei*, and *J. swinhonis* were observed within sample plot 122, which was placed within the cemetery.

2. *Cynodon dactylon* community

This community occurs primarily on flat plain areas. The vegetation consists mostly of pioneer and sub-climax species that establish after disturbances due to natural (typhoons and heavy rains) and/or human activities (primarily agriculture). The vegetation range in height from short (< 0.5 m) in the small artificial grassland areas, fallow fields, a cemetery, and roadsides, to tall trees (> 2 m) in orchards. In all the areas, except for the grassland, bare ground is visible in open patches in the vegetation cover. A total of 355 species were recorded in this community, with a mean of 17 (± 9.8 SD) species per sample plot, and 0.5 (± 0.7 SD) species per m^2.

The *Cynodon dactylon* community is characterised by the dominance of the grass, *Cynodon dactylon* (species group D), with a constancy of 88.9 %. The forbs *Solanum nigrum* (species group L), and *B. pilosa*, the grass *P. maximum* (species group M), and the sedge *Kyllinga brevifolia* (species group L) are present throughout this community, with constancies ranging from 27.8 % to 72.2 %.

2.1. *Cynodon dactylon-Axonopus affinis* sub-community

This sub-community comprises of a small artificial grassland that is relatively flat and terraced, with sandy clayish soil. The area experiences limited human disturbance, but is water logged during heavy rains. Some furrow erosion was observed in sample plot 23, and a small gully has formed in sample plot 25 where water flow to a lower terrace during heavy rains.

This sub-community is characterised by species from species group E. The vegetation is dominated by the grass *Axonopus affinis*, and the prostrate shrub *Mimosa diplotricha* (species group E), each with constancies of 100 %. The forbs *Pueraria montana*, *Verbena incompta*, and the grasses *Brachiaria mutica*, and *Setaria verticillata* (species group E) are conspicuous in this community, with constancies ranging from 75.0 % to 100 %.

The snake *A. stolata* (recorded in sample plot 21) was the only vertebrate observed in this community.

2.2. *Cynodon dactylon-Cuphea hyssopifolia* sub-community

This sub-community occurs on roadsides that are usually flat, and experience frequent disturbances in the form of grass cutting and weeding. Sample plot 50 was the only sample plot with a steep slope (34°), and a gully that has formed in this sample plot, was the only noted sign of soil erosion in this community.

This sub-community is characterised by species from species group F. The vegetation comprises a mixture of different species prominent in different localities that include the semi-woody shrubs *Cuphea hyssopifolia*, and *Eurya emarginata*, the trees *Bauhinia blakeana*, *Terminalia catappa* (species group F), and *C. camphora* (Species group A), the fern *Pteris vittata* (species group F), the forbs *C. thymifolia* (species group G), *Conyza canadensis* var. *canadensis*, and *Youngia japonica* (species group L), and the grasses *C. dactylon* (species group D), and *Eragrostis unioloides* (species group G), with constancies ranging from 20.0 % to 80.0 %.

Anolis sagrei was the only vertebrate recorded in this sub-community, and these lizards were present in every sample plot.

2.3. *Cynodon dactylon-Polygonum multiflorum* sub-community

This sub-community occurs on sandy clayish soil roadside areas that experience frequent disturbances. The areas are flat, and without aspects.

Species that characterise this sub-community are from species group H and is totally dominated by the grass *C. dactylon* (species group D). This sub-community differs from the other sub-communities with the absence and near absence of species from species groups E, F, G, and J. Locally prominent species include the forbs *Polygonum multiflorum* var. *hypoleucum* (species group H) and *Acalypha australis* (species group I), and trees *Chorisia speciosa* (species group H) and *T. catappa* (species group F).

Anolis sagrei was recorded in this sub-community in every sample plot, whilst in sample plot 138 it was sympatric with *J. swinhonis*.

2.4. *Cynodon dactylon-Acalypha australis* sub-community

This sub-community occurs in frequently disturbed areas on roadsides, neglected orchards, fallow fields, and a cemetery. The areas are usually fairly flat. Small furrows have formed in sample plot 128.

This sub-community is characterised by species from species group I. The grass *C. dactylon* (species group D), and the forb *A. australis* (species group I) co-dominate the vegetation, with constancies of 85.7 % and 57.1 % respectively. Other species locally prominent include the forb *Cleome rutidosperma* (species group L), the grasses *Eleusine indica* (species group L), and *E. unioloides* (species group G), the sedges *Fimbristylis aestivalis* var. *aestivalis* (species group J), and *K. brevifolia* (species group L), and the trees *L. chinensis* (species group C), and *Mangifera indica* (species group A), with constancies ranging from 42.9 % to 85.7 %.

Anolis sagrei was noted in every sample plot of this sub-community, except sample plot 121 (a very shady roadside area), in which *J. swinhonis* was recorded.

3. *Echinochloa colona-Eleusine indica* community

This community occurs on low-elevation foothills, and flat plain areas. The vegetation is mostly indicative of a pioneer successional stage as a result of agricultural activities in these areas. The vegetation ranged in height from short (< 0.5 m) in the cemetery, fallow fields and roadsides, to tall (> 5 m) in the orchards, plantations and park. In some of the agricultural areas and roadsides, bare ground was visible in open patches in the vegetation cover, while in the park and some fallow fields, the vegetation cover was very high (> 75 %). The occurrence of some furrow erosion was noted in sample plots 2, 26, 27, 28, 53, 54, 55, 108, 120, and 124. A gully has formed in sample plot 115, and there were signs of tunnel erosion in sample plots 6 and 8. Pedestalling was also noted at the base of a tree in sample plot 56.

The *Echinochloa colona-Eleusine indica* community is characterised by species from species group K. This herbaceous community is dominated by the forb *B. pilosa* (species group M), the grass *E. indica* (species group L), and the sedge *Cyperus iria* (species group J), with constancies ranging from 49.4 % to 87.0 %. The grass *B. mutica* (species group E) and the herbaceous perennial *M. sapientum* (species group C) are locally dominant. Other species with constancies ranging from 31.2 % to 44.2 %, and present throughout this community include the grasses *E. unioloides* (species group G), *Echinochloa colona* (species group K) and *P. maximum* (species group M). The forb *Amaranthus spinosus* (species group K), and the sedge *Fimbristylis littoralis* var. *littoralis* (species group J) are locally prominent, with constancies of 39.0 % and 33.8 % respectively.

Anolis sagrei was frequently observed in sample plots placed within orchards and plantations in this community, and often sympatrically with the lizards *E. longicaudata*, *H. frenatus*, *J. swinhonis*, and *P. elegans*, and the frogs *D. melanostictus*, *F. limnocharis*, and *M. heymonsi*. In sample plots placed within fallow fields and roadsides, *A. sagrei* was usually present, unless the vegetation cover was very high and/or there were no structures that could be utilised as perches. *Eutropis longicaudata*, *P. elegans*, and *T. formosanus* were however recorded in such habitats, although not always sympatric. In sample plots placed in areas where *A. catechu* was planted in rows along rice paddies and other agricultural fields, *A. sagrei* was usually recorded, sometimes sympatric with the snake *A. stolata*. *Anolis sagrei* was also recorded to be sympatric with *A. stolata*, and *F. limnocharis* in some agricultural fields, such as fields planted with *Luffa cylindrical* (Vietnamese luffa). In sample plot 56, placed in a park, *A. sagrei* was recorded to be sympatric with the lizards *E. longicaudata*, *J. swinhonis*, *P. elegans*, and *T. formosanus*, the frogs *D. melanostictus*, and *F. limnocharis*, and the snake *Dinodon rufozonatum rufozonatum*. The snake *X. piscator* was recorded in sample plot 2 that was placed within a fallow field that tends to be waterlogged during the rainy season.

b) The eastern study site

The results from the vegetation analysis resulted in the identification of four plant communities that can be grouped into three main communities:

1. *Turpinia ternata-Eucalyptus maculata* community
2. *Ochna kirkii-Murraya paniculata* community
3. *Cocos nucifera-Bidens pilosa* community
   - 3.1 *Cocos nucifera-Bidens pilosa-Setaria verticillata* sub-community
   - 3.2 *Cocos nucifera-Bidens pilosa-Calliandra haematocephala* sub-community

The traits of the five plant communities are summarised in Table 4.5. All references to species group in the descriptions refer to Table 4.6.

Table 4.5. The ranges of the estimated vegetation and rockiness cover of the five plant communities identified in the eastern study site. The number of species recorded, the ranges of the number of species per sample plot, the ranges of the number of species per m^2, as well as the soil types, the ranges of the slope, and the ranges of aspect recorded in each community are also given. Where applicable, the mean and standard deviation is given in parenthesis (mean ± SD).

	***Turpinia ternata-Eucalyptus maculata* community**	***Ochna kirkii-Murraya paniculata* community**	***Cocos nucifera-Bidens pilosa* community**	
			***Cocos nucifera-Bidens pilosa-Setaria verticillata* sub-community**	***Cocos nucifera-Bidens pilosa-Calliandra haematocephala* sub-community**
Tree cover *	65 – 75	10 – 75	0 – 75	0 – 80
Shrub cover *	60 – 70	10 – 70	0 – 5	0 – 90
Herb cover *	1 – 20	5 – 20	20 – 90	1 – 90
Grass cover *	0 – 2	0 – 1	0 – 75	0 – 90
Rockiness *	15 – 20	5 – 15	5 – 40	3 – 30
Number of species recorded	25	29	20	71
Number of species per sample plot	11 – 22 (16.5 ± 7.8)	7 – 14 (11.3 ± 3.8)	7 – 9 (8.0 ± 1.0)	8 – 26 (14.0 ± 6.4)
Number of species per m^2	1.1 – 2.2 (1.7 ± 0.8)	0.7 – 1.4 (1.1 ± 0.4)	0.1 – 0.9 (0.6 ± 0.5)	0.1 – 2.6 (1.0 ± 1.0)
Soil type	sandy loam	sandy loam	sandy, or sandy loam	sandy clayish, sandy loam, or sandy
Slope	20 – 35° (27.5 ± 10.6)	0 – 35° (11.7 ± 20.2)	0 – 3° (1.0 ± 1.7)	0 – 3° (0.6 ± 1.1)
Aspect	40 – 270°	0 – 270°	0 – 190°	0 – 190°

* - These values were based on visual estimates and are not accurate enough for mean and standard deviation calculations.

1. *Turpinia ternata-Eucalyptus maculata* community

This community occurs on sloped areas along a tarred road on low-elevation foothills. The vegetation comprises mostly of sub-climax species, while some pioneer species, as a result of human activities, are also present in some localities. The vegetation ranges in height from short (< 0.5 m) in the understory to tall (> 5 m) in the canopy. In some areas of the understory bare ground was visible, while the cover of the mature trees was high (> 75 %).

This community is characterised by species from species group A. The vegetation is dominated by the trees *Eucalyptus maculata*, *M. tanarius*, *Pachira macrocarpa*, *Schefflera octophylla* and *Turpinia ternata* (species group A). The trees *Mallotus paniculatus* (species group A), *Morus australis* (species group F), the fern *C. parasiticus* and the tuberous *A. odora* (species group A) are prominent throughout this community. The forbs *Boehmeria frutescens*, and *Piper kadsura*, the grass *Oplismenus compositus*, the palm *Arenga engleri*, the shrub *Zanthoxylum nitidum*, the trees *Celtis formosana*, *Lagerstroemia subcostata*, *Lasianthus obliquinervis*, *Leucaena leucocephala*, *Melanolepis multiglandulosa*, and *Tetrapanax papyriferus* (species group A), are conspicuous in parts of this community. This is a very small community and as a result only two sample plots could be placed within it.

Although during previous distribution surveys, *A. sagrei* was recorded in this area, during the data collection for the plant community study, no *A. sagrei* were observed within the sample plots placed in this community.

2. *Ochna kirkii-Murraya paniculata* community

This community occurs on flat and sloped areas along a tarred road and in urban areas on low-elevation foothills. The vegetation comprises pioneer species and cultivated ornamental species. The vegetation ranges in height from short (< 0.5 m) to a medium height (< 5 m). In some areas bare ground was visible, while the cover of the mature trees in sample plot 4 that was placed at the roadside was high (*ca*. 75 %).

This community is characterised by species from species group B. The shrub *Murraya* *paniculata* (species group B) is dominant throughout this community, with a constancy of 100 %. The vegetation is co-dominated by the shrubs *Bougainvillea spectabilis*, *Lantana camara*, and *Ochna kirkii* (species group B), all with constancies of 66.7 %. In sample plot 4, which was placed on a less disturbed foothill area, the trees *M. tanarius*, *S. octophylla* (species group A), *Dendrocnide meyeniana*, and *Ficus irisana* (species group B), and the forb *Alpinia zerumbet* are prominent. In sample plot 10, which was placed in an urban garden, the shrubs *Allamanda cathartica*, *Garcinia multiflora*, *Ixora duffii*, *Ixora* x *williamsii*, and *Polyscias fruticosa*, and the trees *P. macrocarpa* (species group A) and *Osmanthus fragrans* (species group B) are prominent.

Anolis sagrei was not observed in sample plot 4 that was placed along the tarred path, but was observed in the other two sample plots.

3. *Cocos nucifera-Bidens pilosa* community

This community occurs primarily in flat plain areas. The vegetation consists mostly of pioneer and sub-climax species that established due to human activities (primarily agriculture and gardening). The vegetation ranged in height from short (< 0.5 m) in the urban gardens and the understory of the plantations, to tall (> 5 m) in the *C. nucifera* plantations. In all the areas bare ground was visible. A total of 76 species were noted in this community, with a mean of 12 (± 6.0 SD) species per sample plot, and 0.9 (± 0.9 SD) species per m^2.

The *Cocos nucifera-Bidens pilosa* community is characterised by species from species groups C. The forb *B. pilosa*, the grasses *Axonopus compressus*, and *E. indica*, and the palm *C. nucifera* (species group C) are dominant in most localities of this community, with constancies ranging from 40.0 % to 90.0 %. The forbs *Cardiospermum halicacabum*, and *P. urinaria*, and the shrubs *C. hyssopifolia*, and *Solanum alatum* (species group C) are prominent in this community, with constancies ranging from 20.0 % to 40.0 %.

3.1 *Cocos nucifera-Bidens pilosa-Setaria verticillata* sub-community

This sub-community occurs on fairly flat areas that experience frequent disturbances as a result of gardening and agricultural activities.

This sub-community is characterised by species from species group D, and the absence of species from species group E. The vegetation is dominated by the forb *B. pilosa* (species group C), the grass *E. indica*, and the palm *C. nucifera* (species group C), with constancies ranging from 66.7 % to 100 %. Locally prominent species include the grasses *A. compressus* (species group C) and *S. verticillata* (species group D), both with constancies of 33.3 %. The forbs *Ageratum houstonianum*, *Amaranthus viridis*, *Chenopodium ambrosioides*, and the trees *Annona squamosa*, and *Artocarpus incisus* (species group D) are locally prominent in this community, all with constancies of 33.3 %.

Anolis sagrei and *H. frenatus* were the only terrestrial vertebrates recorded in this sub-community.

3.2 *Cocos nucifera-Bidens pilosa-Calliandra haematocephala* sub-community

This sub-community occurs on fairly flat areas that experience frequent disturbances due to gardening and agricultural practices.

This sub-community is characterised by species from species group E, and dominated by the forb *B. pilosa* (species group C), with a constancy of 85.7 %. The grass *E. indica*, and the palm *C. nucifera* (species group C), and the shrubs *Bougainvillea spectabilis* (species group B), and *C. haematocephala* (species group E), co-dominate in some parts of this sub-community, with constancies ranging from 28.6 % to 42.9 %. Locally prominent species include the forbs *Hydrocotyle verticillata* and *Pogostemon cablin* (species group E), the grasses *A. compressus*, *E. indica* (species group C), *Bambusa dolichoclada*, and *Nandina domestica*, and the trees *Eriobotrya japonica*, *Ficus microcarpa* var. *microcarpa*, and *Ulmus parvifolia* (species group E), with constancies ranging from 14.3 % to 42.9 %. The ferns *Christella acuminata* (species group E), and *C. parasiticus* (species group A), the forb *Crossostephium chinense* (species group E), the shrubs *M. paniculata*, *B. spectabilis*, and *L. camara* (species group B), the trees *M. tanarius*, *P. macrocarpa* (species group A), *Bischofia javanica*, *C. camphora*, *Magnolia coco*, and *Michelia compressa*, and the tuberous *Colocasia esculenta* (species group E), are prominent in parts of this sub-community, with constancies ranging from 14.3 % to 28.6 %.

Anolis sagrei was the only terrestrial vertebrate recorded in this sub-community, and these lizards were present in all the sample plots, except sample plots 2, 8 and 9.

4.3. DISCUSSION

Davis and Thompson (2000) termed the dispersal of a species over widely distant environments which are often separated by some barrier, as saltation dispersal, and short-distance dispersal to adjacent, or nearly adjacent environments, as diffusion dispersal. As the populations of *A. sagrei* in Taiwan continue to increase they can be expected to extend their distribution range by spreading into suitable neighbouring habitats, i.e. diffusion dispersal. The small size of *A. sagrei* makes it easy to hide among objects, and since *A. sagrei* is human commensal, these lizards are easily transported intentionally and/or unintentionally to new localities by humans (Campbell, 1996; Norval and Mao, 2007; Kraus, 2009). It can thus be expected that *A. sagrei* will also spread further throughout Taiwan as a result of human mediated saltation dispersal. A particularly likely agent in this regard is the nursery industry. In various parts of its distribution range where *A. sagrei* is considered to be an invasive species, the nursery industry has been implicated in the dispersal of these lizards (Kraus, 2009). Numerous small nurseries exist in the southwestern study site, where *A. sagrei* specimens have been observed among the plants cultivated at some of these nurseries (e.g. Fig. 4.3). It is thus likely that the existence of these lizards in parks and urban gardens in the southwestern and eastern study site is a result of these lizards being introduced into these localities along with plants from nurseries in *A. sagrei* invaded areas.

Since *A. sagrei* is more than likely being introduced into new localities along with nursery products, and the fact that some localities in the southwestern and eastern study site could not be surveyed because the areas belonged to religious groups that distrusted the surveys, or could not be accessed because they were military facilities or private property, the current actual distribution of *A. sagrei* in Taiwan is very likely more extensive. The distribution description herein is thus a conservative estimate and serves as a basis for future studies.

Figure 4.3. One of the numerous small nurseries located in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan, and a brown anole (*Anolis sagrei*) that was observed among the plants (the position indicated by the red arrow) at this nursery.

The results of the vegetation classification indicate considerable differences between the vegetation communities of the southwestern and eastern study site but that both sites reflect various degrees of disturbance and succession. In the southwestern study site the forbs *B. pilosa*, and *P. urinaria*, and the grass *P. maximum* are common species in all the communities whilst co-dominant in a number of them. *Bidens pilosa*, and *P. urinaria* (both exotic invasive species in Taiwan) are noxious weeds in many parts of the world, and are usually associated with disturbed habitats (Hsieh *et al*., 1993; Peng *et al*., 1998; Bromilow, 2001; Nesom, 2009; Huang *et al*., 2012). The occurance of soil erosion in most of the vegetation communities is another indication that most of the habitats in the southwestern study site are disturbed and degraded habitats, because soil erosion is usually associated with areas where the vegetation cover has been removed (Brady and

Weil, 2002). Even though single tree species occur scattered as single individuals in some of the communities, and in some communities (communities 1.1, 1.2, and 2.2) trees (native, invasive, and cultivated species in Taiwan) are prominent and co-dominant, the diagnostic species of the seven identified vegetation communities in the southwestern study site are mostly dominated by grasses and forbs, with numerous crop species. This indicates that the disturbed and degraded nature of these areas is primarily due to agricultural practices.

In the eastern study site, the forb *O. corymbosa*, and tree *M. australis* are present in all the communities, except the *Cocos nucifera-Bidens pilosa-Setaria verticillata* sub-community, most likely as a result of weeding and agricultural activities (Norval, *pers. obs*.). *Oxalis corymbosa* is a common naturalised weed in disturbed and cultivated areas in Taiwan (Huang and Liu, 1993), while *M. australis* is a common tree species occurring at low and medium altitudinal areas of Taiwan (Liao, 1996). The diagnostic species of the four identified vegetation communities are dominated by trees and shrubs, many of which are ornamental, indicating that the disturbances in this area is primarily due to gardening practices.

Anolis sagrei is a trunk-ground species, which means they usually perch within a metre and a half of the ground on broad surfaces or on the ground (Ruibal, 1961; Williams, 1969; Losos, 2009). In the southwestern and eastern study sites *A. sagrei* was only recorded in areas disturbed due to human activities. Throughout its distribution range (natural and introduced) *A. sagrei* tends to utilize areas disturbed by human activities

(Schwartz and Henderson, 1991; Rodriguez Schettino, 1999), thus the results of this study are not unique. As *A. sagrei* is an active thermo-regulator, which means it has to move between basking sites and shade to maintain its optimum body temperature (Ruibal, 1961; Lister, 1976), it therefore tends to prefer open sunny habitats (Schoener, 1968; Williams, 1969).

However, having said this, the results of this study found that not all disturbed areas in Taiwan are suitable habitats for *A. sagrei*. These lizards were not observed in habitats such as rice (*Oryza sativa*) paddies and fields planted with taro (*Colocasia esculenta*; Fig. 4.4), in which the ground was covered by water. *Anolis sagrei* was also not observed in habitats such as the artificial grassland (community 2.1) and fallow fields (Fig. 4.5) in the southwestern study site, which are open and very sunny, but lack objects that can be used by *A. sagrei* as perches. However, when concrete embankment walls, fence posts, or rows of trees, such as *A. catechu*, bordered such habitats *A. sagrei* was often observed in these marginal areas (Fig. 4.6). It thus possible for *A. sagrei* to exist in small numbers in habitats that is actually unsuitable (e.g. Fig. 4.7).

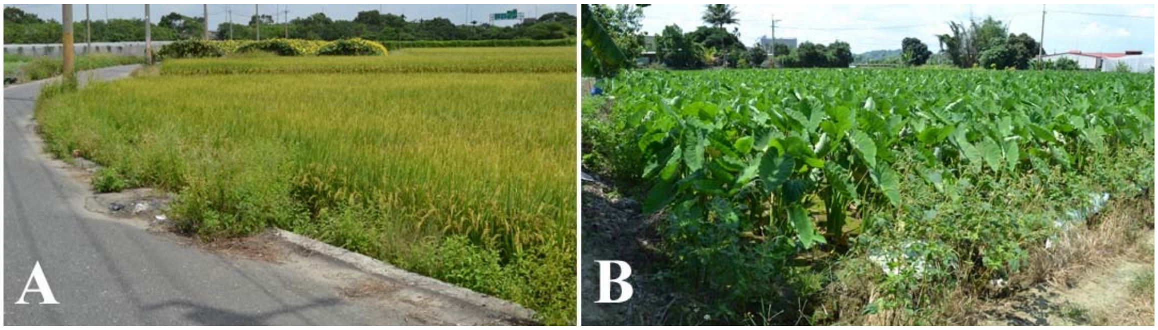


Figure 4.4. No *Anolis sagrei* was recorded in habitats such as this (A) rice paddy (sample plot 92) and (B) field planted with taro (*Colocasia esculenta*; sample plot 87) in community 3 in the southwestern study site in Chiayi County.

Figure 4.5. (A) A fallow field (sample plot 6; community 3) and (B) artificial grassland (sample plot 23; community 2.1) in the southwestern study site in Chiayi County.

Figure 4.6. *Anolis sagrei* was recorded in places such as (A) this rice paddy edge (sample plot 109) and (B) roadside bordering a drainage ditch and fallow field (sample plot 0053) in community 3 in the southwestern study site in Chiayi County.

Figure 4.7. An *Anolis sagrei* female (right) was found perching on a tree trunk of a tree (indicated by the red arrow) that was growing on the edge of two rice paddies (left) that had recently been tilled and flooded in preparation for planting in the southwestern study site in Chiayi County.

While *A. sagrei* was observed in fields planted with trees, fruit orchards, and parks (Fig. 4.8), they were also not observed in secondary forest fragments (Fig. 4.9) in the southwestern and eastern study sites. This is most probably because even though the trees

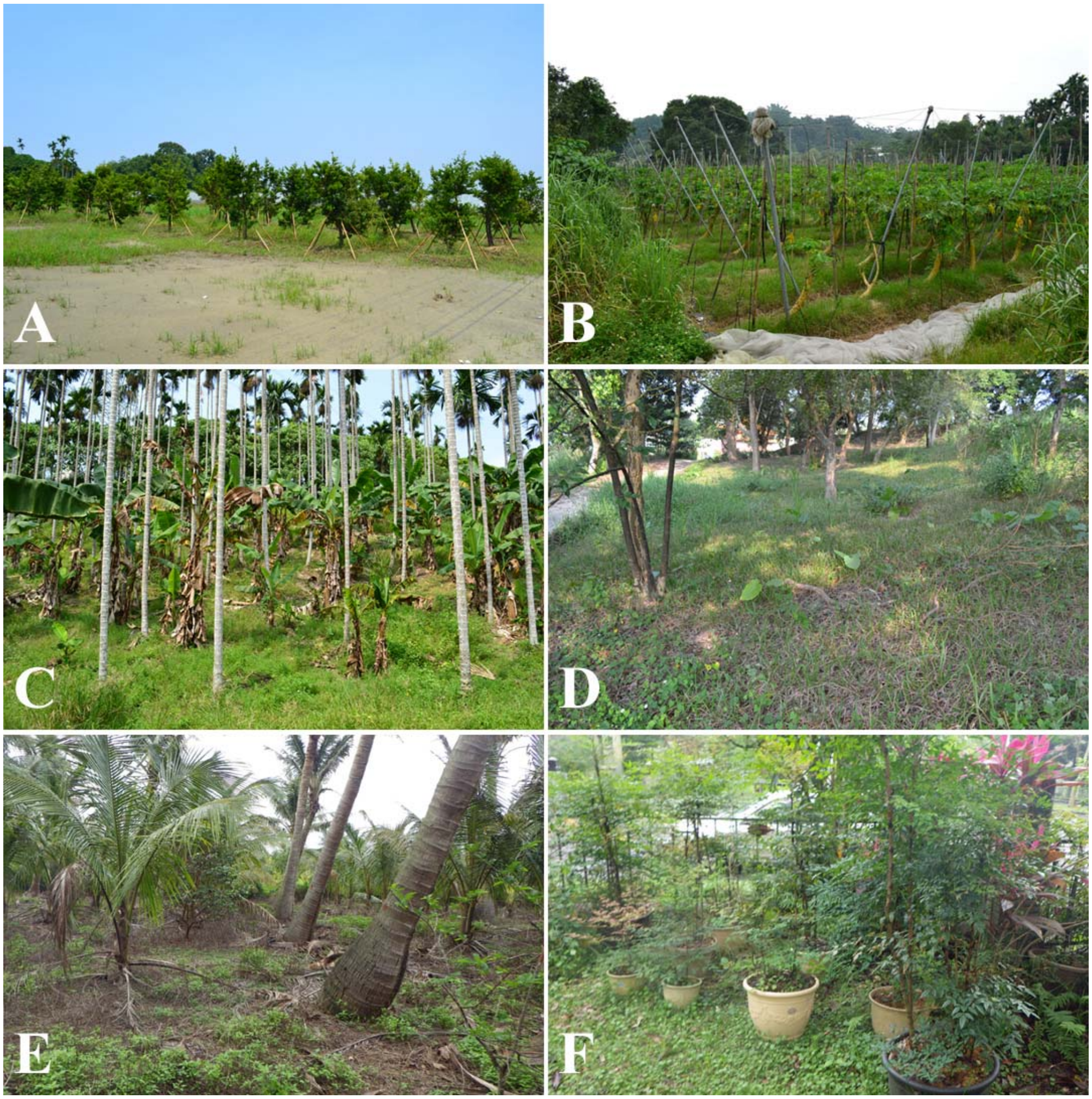


Figure 4.8. The field planted with *Podocarpus costalis* (A; sample plot 125; community 3), papaya (Carica papaya) orchard (B; sample plot 130; community 3), mixed betel nut palm (*Areca catechu*) and banana (*Musa sapientum*) plantation (C; sample plot 135; community 3), and park (D; sample plot 60; community 1.2) in the southwestern study site in Chiayi County, and the coconut palm (*Cocos nucifera*) plantation (E; sample plot 14; community 3.2), and urban garden (F; sample plot 1; community 3.2) in the eastern study site in Hualien County are typical habitats inhabited by the brown anoles (*Anolis sagrei*).

Figure 4.9. This secondary forest fragment (A; sample plot 83; community 1.2) and secondary forest (B; sample plot 144; community 1.1) in the southwestern study site, and forested roadsides (C and D; sample plots 4 and 6 respectively; communities 2 and 1 respectively) in the eastern study site in Hualien County, are habitats that brown anoles (*Anolis sagrei*) are very rarely recorded in.

in all these habitats create shady trunk-ground microhabitat (i.e. the area on the ground at the base of a tree trunk, and the *ca*. 1.5 m above the ground portion of the trunk) the herbaceous layer is dense and tall in secondary forest fragments, as opposed to in fields planted with trees, fruit orchards, and parks where the understory vegetation is usually cut short or cleared by people. The sun thus shines for at least part of the day on the trunk-ground microhabitat utilised by *A. sagrei* as basking sites and/or perches in fields planted with trees, fruit orchards, and parks. In the secondary forest fragments, the understory vegetation is denser and/or taller, obscuring the sun from shining on potential basking sites, making them unsuitable for *A. sagrei*. The more natural and less disturbed habitats are however suitable for a variety of native species.

Anolis sagrei was also rare or absent in habitats, both shady and sunny, overgrown by tall grass (usually *P. maximum*; Fig. 4.10). It was also noted in Cuba that when grass surrounded perching sites formerly utilised by *A. sagrei*, these lizards became absent from the area (Collette, 1961). This can also be attributed to the sun being obstructed from shining on basking and/or perching sites by the vegetation.

Figure 4.10. *Anolis sagrei* were not observed in this roadside (A; sample plot 112; community 3) and area of a park (B; sample plot 58; community 1.2) overgrown by grass, even though they were observed in this general area in the southwestern study site in Chiayi County.

In conclusion, the results of this study indicate that the distribution of *A. sagrei* in Taiwan is fairly extensive (≥ 245 ha) and that the habitats within which they occur are mostly disturbed and degraded (Fig. 4.11). It also indicates that as in other parts of its range *A. sagrei* inhabit open sunny habitats, created by human disturbances, and that the presence of objects that can function as perching and/or basking sites are important for determining the suitability of a habitat for *A. sagrei*. Since such habitats exist throughout the lowlands of Taiwan, and because *A. sagrei* can accidentally and intentionally be introduced into new localities by human activities, these lizards can be expected to expand their distribution range in the lowland areas of Taiwan. Since secondary forests

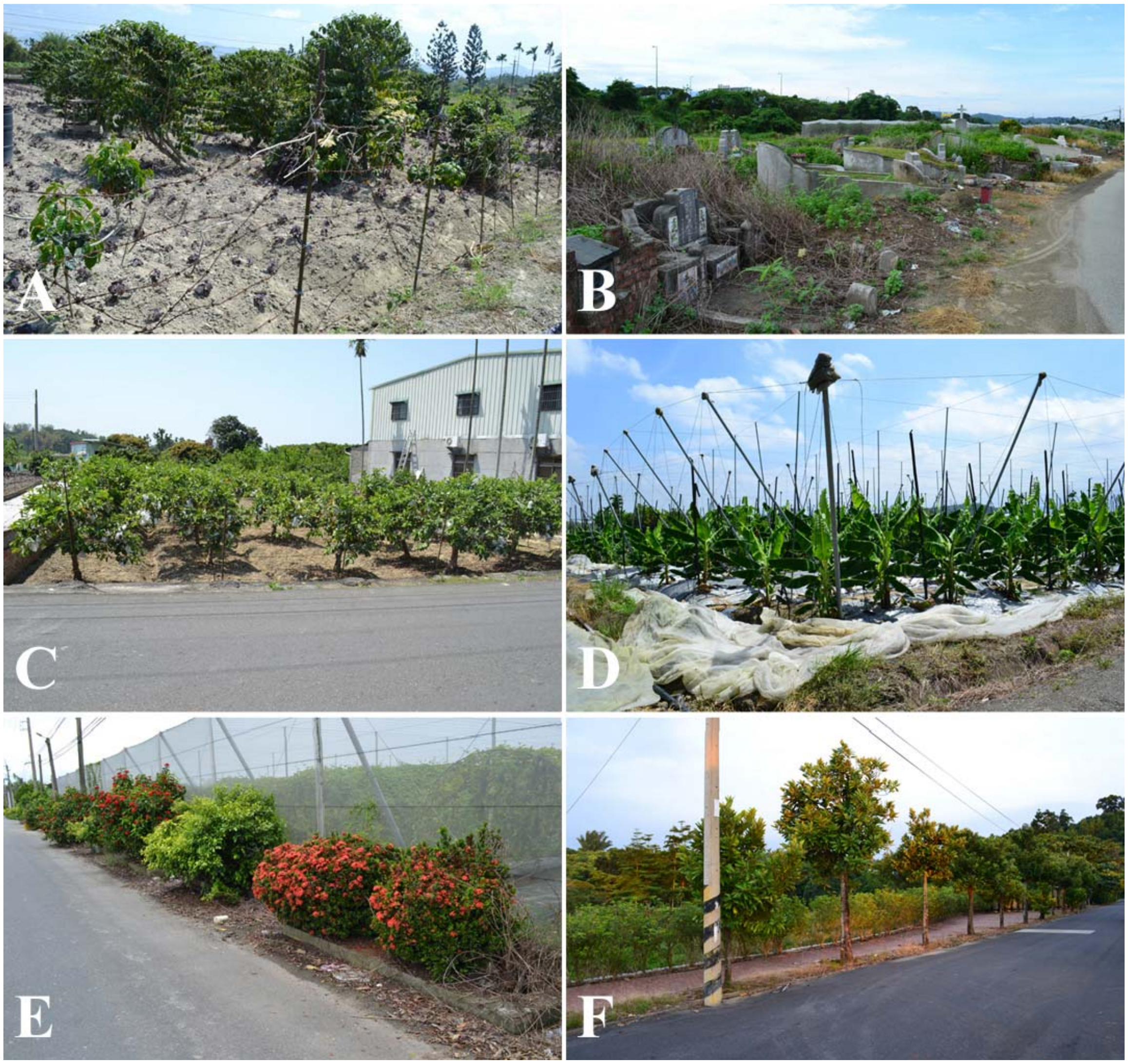


Figure 4.11. Brown anoles (*Anolis sagrei*) were often recorded in disturbed and degraded habitats such as this field planted with coffee trees (*Coffea arabica*; A; sample plot 10; community 3), cemetery (B; sample plot 91; community 3), guava (*Psidium guajava*) orchard (C; sample plot 11; community 3), banana (*Musa sapientum*) plantation (D; sample plot 98; community 3), roadside flowerbeds (E; sample plot 45; community 2.2), and roadside (F; sample plot 119; community 3) in the southwestern study site in Chiayi County.

and other dense habitats are less suitable for *A. sagrei*, the conservation, restoration, and creation of such habitats in Taiwan are crucial. These areas can impede the spread of *A. sagrei*, and at the same time create larger areas of suitable habitats for native species.

4.4. REFERENCES

Brady, N.C., and Weil, R.R. 2002. *The Nature and Properties of Soils.* 13th edition. Pearson Education Inc., New Jersey.

Bromilow, C. 2001. *Problem Plants of South Africa*. Briza Publications, Pretoria.

Campbell, T.S. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. *Herpetological Review* 27**:** 155-157.

Collette, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum of Comparative Zoology at Harvard College* 125: 137-162.

Davis, M.A., and Thompson, K. 2000. Eight ways to be a colonizer; two ways to be an invader. *Bulletin of the Ecological Society of America* 81: 226-230.

Hsieh, C.F., Chaw, S.M., Wang, J.C., Deng, M.J., and Lin, S.C. 1993. *Euphorbiaceae*. pp. 414-504. In: Huang, C.F., Li, Z.Y., Lo, H.C., Ohashi, H., Shen, C.F., Wang, J.C., Yang, K.C., and Hsieh, C.F. (eds.) 1993. *Flora of Taiwan*. Vol. 3. 2nd edition. Department of Botany, National Taiwan University, Taipei.

Huang, T.C., and Liu, T.S. 1993. *Oxalidaceae*. pp. 397-402. In: Huang, C.F., Li, Z.Y., Lo, H.C., Ohashi, H., Shen, C.F., Wang, J.C., Yang, K.C., and Hsieh, C.F. (eds.) 1993. *Flora of Taiwan*. Vol. 3. 2nd edition. Department of Botany, National Taiwan University, Taipei.

Huang, Y.L., Chen, S.J., and Kao, W.Y. 2012. Floral biology of *Bidens pilosa* var. *radiata*, an invasive plant in Taiwan. *Botanical Studies* 53: 501-507.

Kraus, F. 2009. *Alien Reptiles and Amphibians, a Scientific Compendium and Analysis*. Invading Nature: Springer Series in Invasion Biology 4. Springer, New York.

Lee, J.C. 2000. *A Field Guide to the Amphibians and Reptiles of the Maya World: the*

Lowlands of Mexico, Northern Guatemala, and Belize. Cornell University Press, New York.

Liao, J.C. 1996. *Moraceae*. pp. 136-195. In: Huang, T.C., Boufford, D.E., Ohashi, H., Yang, Y.P., and Lu, S.Y. (eds.) 1996. *Flora of Taiwan*. Vol. 2. 2nd edition. Department of Botany, National Taiwan University, Taipei.

Lister, B.C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30: 659-676.

Losos, J.B. 2009. *Lizards in an Evolutionary Tree*: *Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, California.

Meshaka, W.E. Jr., Butterfield, B.P., and Hauge, J.B. 2004. *The Exotic Amphibians and Reptiles of Florida*. Krieger Publishing Company, Florida.

Nesom, G.L. 2009. Assessment of invasiveness and ecological impact in non-native plants of Texas. *Journal of the Botanical Research Institute of Texas* 3: 971-991.

Norval, G., and Mao, J.J. 2007. Can *Anolis sagrei* be unintentionally transported to new localities in bamboo stem bundles? *Sauria* 29: 51-54.

Norval, G., Mao, J.J., Chu, H.P., and Chen, L.C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.

Peng, C.I., Chung, K.F., and Li, H.L. 1998. *Compositae*. pp. 807-1101. In: Huang, C.F., Boufford, D.E., Lowry, P.P., Ohashi, H., and Peng, C.I. (eds.) 1998. *Flora of Taiwan*. Vol. 4. 2nd edition. Department of Botany, National Taiwan University, Taipei.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of

Florida, Gainesville, Florida.

Ruibal, R. 1961. Thermal relations of five species of tropical lizards. *Evolution* 15: 98-111.

Ruibal, R. 1964. An annotated checklist and key to the anoline lizards of Cuba. *Bulletin of the Museum of Comparative Zoology* 130: 473-520.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Williams, E.E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *The Quarterly Review of Biology* 44: 345-389.

CHAPTER 5 – A MORPHOLOGICAL COMPARISON OF *ANOLIS SAGREI* SPECIMENS FROM SOUTHWESTERN AND EASTERN TAIWAN

5.1. INTRODUCTION

Meristic (scalation) and morphometric characters comparisons of *Anolis sagrei* specimens from peninsular Florida, the Florida Keys, the West Indies, and Central America, revealed that discrete phena can not be recognised based on morphological grounds (Lee, 1985; Lee, 1987; Lee, 1992). Still, interlocality and intralocality variations in some meristic characters were noted, and some of these characters changed little over time (Lee, 1985; Lee, 1992). It is thus possible to deduce that specimens from different populations originated from the same founder population, based on these meristic characters.

Eastern and southwestern populations of *A. sagrei* are known to exist in Taiwan (Norval *et al*., 2002; Chang, 2007). A study by Kolbe *et al*., (2004) found that *A. sagrei* specimens from the population in Santzepu, southwestern Taiwan (southwestern study site) is genetically similar to some populations in Florida. In addition to that, the nematode, *Cyrtosomum penneri*, which is known to infect *A. sagrei* in parts of Florida (Goldberg *et al*., 1994), has been recorded from *A. sagrei* specimens collected in both study sites in Taiwan (Norval *et al*., 2011a; Norval *et al*., 2014). These findings indicate that the population in Taiwan originated from Florida. Even though the eastern and southwestern populations are most probably from the same founder population, because it is very unlikely that *A. sagrei* was introduced from abroad into Taiwan in two localities, this still needs to be confirmed by morphological comparisons. Herein, intralocality intersexual, and interlocality intrasexual comparisons of some *A. sagrei* specimens collected from both populations in Taiwan will be made and discussed.

5.2. RESULTS

Morphological measurements and characteristics from 19 males and 19 females from the southwestern study site and 8 males and 22 females from the eastern study site were compared (Table 5.1 and 5.2).

All the males collected in the eastern study site had enlarged postanal scales (PA) scale count of two, so a statistical comparison could not be made. The males collected from the southwestern study site had a mean value close to 2 (Table 5.1). Also, none of the lizards from either locality had scales between the subocular and supralabial scales (SO/SPL), so no analysis or comparisons were necessary.

There were only a few intralocality intersexual variations and only five of the twelve compared characteristics had a statistically significant variation in at least one of the localities (Table 5.3). In both localities there were significant differences in the sizes of the sexes (i.e. snout-vent length; SVL) and the number of lamellae (Table 5.3). But only the samples from the southwestern study site had statistically significant differences in the head length (HL), left hind shank length (LHS), and ventral (Ventr. 5mm) scale count

Table 5.1. The morphometric and meristic characters of the brown anole (*Anolis sagrei*) male specimens from the eastern and southwestern study sites, used in this study. (* - data was only collected on the left lateral side of the head of the lizards)

	Eastern Study Site (*n* = 8)		**Southwestern Study Site (*n* = 19)**	
	Range	**Mean ± SD**	**Range**	**Mean ± SD**
Snout-vent length (SVL) (mm)	29.4 – 58.5	42.8 ± 10.0	47.0 – 62.1	53.7 ± 3.9
Tail length (TL) (mm) (including broken and regenerated tails)	28.0 – 76.5	61.8 ± 15.7	10.8 – 115.0	88.2 ± 27.5
Head length (HL) (mm) *	8.1 – 15.5	12.0 ± 2.5	13.0 – 17.0	14.8 ± 0.9
Left hind shank length (LHS) (mm)	7.2 – 13.9	10.6 ± 2.2	11.6 – 14.9	13.1 ± 0.8
Interorbital (IO) scale count	1 – 3	2.1 ± 0.6	1 – 2	1.2 ± 0.4
Interpariental/interorbital (IP/IO) scale count	3 – 5	3.5 ± 0.8	2 – 4	2.6 ± 0.6
Supralabials (SPL) scale count *	5 – 7	6.1 ± 0.8	5 – 6	5.2 ± 0.4
2nd row of scales between the canthal ridges (2. Canth.) scale count	5 – 10	7.1 ± 1.6	4 – 8	6.2 ± 1.0
Internasal (IN) scale count	4 – 7	5.5 ± 0.9	5 – 6	5.5 ± 0.5
Left hind foot 4th toe lamellae scale count	29 – 35	31.6 ± 1.6	29 – 35	31.3 ± 1.6
Enlarged postanal (PA) scale count	2	2 ± 0.0	2 – 5	2.5 ± 1.0
2nd loreal scale row scale count *	3 – 5	4.1 ± 0.6	4 – 5	4.9 ± 0.2
5mm. Dorsal scale count	13 – 44	23.4 ± 9.7	11 – 17	14.6 ± 1.5
5mm. Ventral scale count	10 – 19	14.8 ± 3.2	8 – 12	10.4 ± 0.9

Table 5.2. The morphometric and meristic characters of the brown anole (*Anolis sagrei*) female specimens from the eastern and southwestern study sites, used in this study. (* - data was only collected on the left lateral side of the head of the lizards)

	Eastern study aite (*n* = 22)		**Southwestern study aite (*n* = 19)**	
	Range (mm)	**Mean ± SD**	**Range (mm)**	**Mean ± SD**
Snout-vent length (SVL) (mm)	23.4 – 43.0	34.6 ± 5.0	34.9 – 44.7	38.1 ± 3.0
Tail length (TL) (mm) (including broken and regenerated tails)	29.7 – 75.5	53.3 ± 14.5	9.0 – 79.0	58.5 ± 21.8
Head length (HL) (mm) *	6.5 – 11.0	9.7 ± 1.2	10.0 – 12.5	10.9 ± 0.7
Left hind shank length (LHS) (mm)	5.5 – 10.5	8.7 ± 1.4	7.7 – 10.5	8.7 ± 0.7
Interorbital (IO) scale count	1 – 4	2.2 ± 0.6	1 – 2	1.2 ± 0.4
Interpariental/interorbital (IP/IO) scale count	2 – 4	3.2 ± 0.6	2 – 4	2.8 ± 0.6
Supralabials (SPL) scale count *	5 – 8	6.2 ± 0.8	5 – 6	5.2 ± 0.4
2nd row of scales between the canthal ridges (2. Canth.) scale count	5 – 10	6.7 ± 1.3	4 – 7	5.7 ± 1.0
Internasal (IN) scale count	3 – 6	4.6 ± 1.2	4 – 6	5.5 ± 0.7
Left hind foot 4th toe lamellae scale count	20 – 36	28.4 ± 3.7	28 – 34	30.1 ± 1.6
2nd loreal scale row scale count *	3 – 5	4.1 ± 0.6	4 – 5	4.7 ± 0.5
5mm. Dorsal scale count	18 – 40	25.7 ± 6	17 – 25	20.9 ± 2.2
5mm. Ventral scale count	11 – 34	17.8 ± 4.3	10 – 15	12.7 ± 1.3

Table 5.3. The intralocality intersexual comparisons of the brown anoles (*Anolis sagrei*) from the eastern and southwestern study sites, used in this study. (* - statistically significant)

		Male		**Female**		**Intralocality intersexual statistical result**
	Study site	**Sample size**	**Mean ± SD**	**Sample size**	**Mean ± SD**	
Snout-vent length (SVL) (mm)	Eastern	8	42.8 ± 10.0	22	34.6 ± 5.0	U = 40, p = 0.0259 *
	Southwestern	19	53.7 ± 3.9	19	38.1 ± 3.0	U = 0.0, p < 0.0001 *
Head length (HL) (mm)	Eastern	8	12 ± 2.5	22	9.7 ± 1.2	U = 84, p = 0.8696
	Southwestern	19	14.8 ± 0.9	19	10.9 ± 0.7	U = 92, p = 0.0102 *
Left hind shank length (LHS) (mm)	Eastern	8	10.6 ± 2.2	22	8.7 ± 1.4	U = 85, p = 0.9067
	Southwestern	19	13.1 ± 0.8	19	8.7 ± 0.7	U = 58, p = 0.0004 *
Interorbital (IO) scale count	Eastern	8	2.1 ± 0.6	22	2.2 ± 0.6	U = 87, p = 0.9759
	Southwestern	19	1.2 ± 0.4	19	1.2 ± 0.4	U = 180.5, p = 0.9816
Interpariental/ interorbitals (IP/IO) scale count	Eastern	8	3.2 ± 0.6	22	3.2 ± 0.6	U = 71, p = 0.3643
	Southwestern	19	2.6 ± 0.6	19	2.8 ± 0.6	U = 148, p = 0.2858
Supralabials (SPL) scale count	Eastern	8	6.1 ± 0.8	22	6.2 ± 0.8	U = 86.5, p = 0.9598
	Southwestern	19	5.2 ± 0.4	19	5.2 ± 0.4	U = 180.5, p = 0.9835
2nd row of scales between the canthal ridges (2. Canth.) scale count	Eastern	8	7.1 ± 1.6	22	6.7 ± 1.3	U = 75, p = 0.5419
	Southwestern	19	6.2 ± 1.0	19	5.7 ± 1.0	U = 131.5, p = 0.1394
Internasal (IN) scale count	Eastern	8	5.5 ± 0.9	22	4.6 ± 1.2	U = 55, p = 0.1134
	Southwestern	19	5.5 ± 0.5	19	5.5 ± 0.7	U = 180, p = 0.9999
Left hind foot 4th toe lamellae scale count	Eastern	8	31.6 ± 1.6	21	28.4 ± 3.7	U = 32, p = 0.0114 *
	Southwestern	19	31.3 ± 1.6	19	30.1 ± 1.6	U = 108, p = 0.0302 *
2nd loreal scale row scale count	Eastern	8	4.1 ± 0.6	22	4.1 ± 0.6	U = 82, p = 0.7569
	Southwestern	19	4.9 ± 0.2	19	4.7 ± 0.5	U = 142.5, p = 0.0832
5mm. Dorsal scale count	Eastern	8	23.4 ± 9.7	22	25.7 ± 6.0	U = 75, p = 0.5576
	Southwestern	19	14.6 ± 1.5	19	20.9 ± 2.2	U = 165, p = 0.6614
5mm. Ventral scale count	Eastern	8	14.8 ± 3.2	22	17.8 ± 4.3	U = 79, p = 0.696
	Southwestern	19	10.4 ± 0.9	18	12.7 ± 1.3	U = 29, p < 0.0001 *

(Table 5.3). There were several interlocality intrasexual variations and ten of the twelve compared characteristics had statistically significant variations in at least one of the sexes (Table 5.4).

In both sexes there were also significant differences in the interorbital (IO), supralabial (SPL), loreal, and ventral (Ventr. 5mm) scale counts between the two study sites. Of the other characteristics that differed significantly, the females had the most variations, and differed in LHS, the number of scales in the 2nd row of scales between the canthal ridges (2. Canth.), internasal (IN), and dorsal (Dors. 5mm) scale counts. On the other hand, only the males had a variation in the interpariental/interorbitals (IP/IO) scale count.

5.2. DISCUSSION

Anolis sagrei is visibly sexually dimorphic in build (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Butler *et al*., 2000) because in this species sexual selection favours males with a large body size (length and muscle mass), which increases the likelihood of success in territorial fights (Tokarz, 1985). A larger size also enables males to prey on relatively larger prey items than the females (Schoener, 1968; Rodriguez Schettino, 1999). In the females, sexual role selection favours the females who, once they reach a sexually mature size (*ca*. 34 mm SVL), allocate part of their acquired energy to egg production, as opposed to continued growth throughout their life as occurs in males (Schoener and Schoener, 1978; Cox *et al*., 2009). As for the males, sexual role selection, favours males that display more effectively (Losos, 2009), and as a result *A. sagrei* males tend to be more arboreal than females (Schoener, 1968; Schwartz and Henderson, 1991;

Table 5.4. The interlocality intrasexual comparisons of the male and female brown anoles (*Anolis sagrei*) from the eastern and southwestern study sites, used in this study. (* - statistically significant)

		Eastern study site		**Southwestern study site**		**Intralocality intersexual statistical result**
	Sex	**Sample size**	**Mean ± SD**	**Sample size**	**Mean ± SD**	
Snout-vent length (SVL) (mm)	Male	8	42.8 ± 10.0	19	53.7 ± 3.9	$U = 32$, $p = 0.0209$ *
	Female	22	34.6 ± 5.0	19	38.1 ± 3.0	$U = 113$, $p = 0.0125$ *
Head length (HL) (mm)	Male	8	12.0 ± 2.5	19	14.8 ± 0.9	$U = 55$, $p = 0.2763$
	Female	22	9.7 ± 1.2	19	10.9 ± 0.7	$U = 174$, $p = 0.3671$
Left hind shank length (LHS) (mm)	Male	8	10.6 ± 2.2	19	13.1 ± 0.8	$U = 62$, $p = 0.4815$
	Female	22	8.7 ± 1.4	19	8.7 ± 0.7	$U = 62$, $p = 0.0001$ *
Interorbital (IO) scale count	Male	8	2.1 ± 0.6	19	1.2 ± 0.4	$U = 18.5$, $p = 0.0004$ *
	Female	22	2.2 ± 0.6	19	1.2 ± 0.4	$U = 36.5$, $p < 0.0001$ *
Interpariental/ interorbitals (IP/IO) scale count	Male	8	3.2 ± 0.6	19	2.6 ± 0.6	$U = 31$, $p = 0.0084$ *
	Female	22	3.2 ± 0.6	19	2.8 ± 0.6	$U = 151$, $p = 0.0792$
Supralabials (SPL) scale count	Male	8	6.1 ± 0.8	19	5.2 ± 0.4	$U = 29$, $p = 0.0039$ *
	Female	22	6.2 ± 0.8	19	5.2 ± 0.4	$U = 68$, $p < 0.0001$ *
2nd row of scales between the canthal ridges (2. Canth.) scale count	Male	8	7.1 ± 1.6	19	6.2 ± 1.0	$U = 54$, $p = 0.2285$
	Female	22	6.7 ± 1.3	19	5.7 ± 1.0	$U = 121.5$, $p = 0.018$ *
Internasal (IN) scale count	Male	8	5.5 ± 0.9	19	5.5 ± 0.5	$U = 74.5$, $p = 0.9527$
	Female	22	4.6 ± 1.2	19	5.5 ± 0.7	$U = 127.5$, $p = 0.0245$ *
Left hind foot 4th toe lamellae scale count	Male	8	31.6 ± 1.6	19	31.3 ± 1.6	$U = 59.5$, $p = 0.3799$
	Female	21	28.4 ± 3.7	19	30.1 ± 1.6	$U = 140$, $p = 0.1067$
2nd loreal scale row scale count	Male	8	4.1 ± 0.6	19	4.9 ± 0.2	$U = 22.5$, $p = 0.0002$ *
	Female	22	4.1 ± 0.6	19	4.7 ± 0.5	$U = 85.5$, $p = 0.0003$ *
5mm. Dorsal scale count	Male	8	23.4 ± 9.7	19	14.6 ± 1.5	$U = 33$, $p = 0.0217$ *
	Female	22	25.7 ± 6.0	19	20.9 ± 2.2	$U = 125$, $p = 0.0290$ *
5mm. Ventral scale count	Male	8	14.8 ± 3.2	19	10.4 ± 0.9	$U = 35$, $p = 0.0315$ *
	Female	22	17.8 ± 4.3	18	12.7 ± 1.3	$U = 27$, $p < 0.0001$ *

Rodriguez Schettino, 1999). Males also usually have longer hind limbs and more subdigital lamellae than females (Collette, 1961). The structural habitat and dietary niche differences between *A. sagrei* males and females are thus most likely adaptive, rather than intersexual niche partitioning selection (Losos, 2009). However, *A. sagrei* body size and hind limb length are plastic traits (Losos *et al*., 2000; Campbell and Echternacht 2003; Kolbe *et al*., 2007), and as a result the magnitude of the sexual size dimorphism in this species varies geographically (Lee, 1987; Campbell and Echternacht 2003).

The results of the intralocality intersexual comparisons of this study are thus not out of the ordinary. In both localities there was a significant difference in the sizes of the sexes, as well as the lamellae counts. In the southwestern study site there were also significant differences in the head leghths and left hind shank lengths. All these differences can be attributed to the sexual dimorphism in this species.

Morphological comparisons of *A. sagrei* from peninsular Florida, the Florida Keys, the West Indies, and Central America, revealed interlocality and intralocality variations in Florida populations, even though all available evidence indicated that the colonisation had largely originated from Cuba (Lee, 1985; Lee, 1987; Lee, 1992). So even though statistically significant variations between the compared lizards from the two populations in Taiwan were found, it does not necessarily indicate two separate founder populations. To identify the reasons for the observed variations between the two populations in Taiwan is beyond the scope of this study. However, several hypothetical causes for the observed variations can be inferred from the available information and what is known about conspecific *A. sagrei* populations in the Americas.

It has been suggested that admixtures from different geographical locations of the native range of *A. sagrei* resulted in a large amount of genetic variation in introduced populations of this species in places like Florida, USA (Kolbe *et al*., 2004; Kolbe *et al*., 2007). Because *A. sagrei* females have the ability to store sperm (Fox, 1963; Sever and Hamlett, 2002), and because they often mate with multiple males (Calsbeek *et al*., 2007), the high genetic variation continues to exist even in some of the secondarily introduced populations, such as the one in western Taiwan (Kolbe *et al*., 2004; Calsbeek *et al*., 2007; Eales *et al*., 2008). In spite of this, and even though relatively small numbers of introduced individuals can establish a viable population (Campbell and Echternacht, 2003), genetic diversity losses can be experienced (especially when small numbers of colonisers are involved) during demographic founder events, which could result in trait means in the phenotypes in new localities, that differ from those of the source population (Kolbe *et al*., 2007; Eales and Thorpe, 2010; Kolbe *et al*., 2012). Even though it has been confirmed that such a scenario did not take place in the southwestern study site population (Kolbe *et al*., 2004), this could possibly be an explanation for the meristic variations observed in this study, and the instance of polydactyly in one of the *A. sagrei* males collected from the eastern study site for this study (Norval *et al*., 2009). However, since *A. sagrei* females are polymorphic in dorsal coloration pattern (Schoener and Schoener, 1976; Paemelaere *et al*., 2011), which is known to be heritable (Calsbeek *et al*., 2008), and because polymorphism probably requires multiple alleles, a fairly larger number of individuals should be present in the colonising founder population for female colouration polymorphism to be maintained (Paemelaere *et al*., 2011). The female colouration polymorphism (Fig. 5.1) in the populations in both study sites thus suggests that both these populations are fairly genetically diverse.

Figure 5.1. *Anolis sagrei* females are polymorphic in dorsal colouration pattern, and all three coloration patterns exist in the eastern and southwestern study sites.

It should also be noted that the nematode, *C. penneri*, which is known to infect many lizard species in North and Central America (Bursey *et al*., 2012), was recorded in *A. sagrei* collected from the southwestern study site, supporting the contention that the southwestern study site population of *A. sagrei* originated from Florida (Norval *et al*., 2011a). *Cyrtosomum penneri* was also recorded in *A. sagrei* collected from the eastern study site (Norval *et al*., 2014). These parasites are transmitted during copulation (Langford *et al*., 2013), and as a result infect sexually mature individuals (Norval *et al*., 2011a). The presence of these parasites in *A. sagrei* from both study sites in Taiwan suggest that sexually mature lizards were introduced into these localities and that they most likely have a common founder population. Some of these sexually mature individuals could have been a few females that had mated with multiple males, and thus produced sexually diverse offspring, allowing the maintenance of genetic diversity.

Microevolutionary adjustments to the novel environments in the two study sites are also plausible explanations for the variations observed in this study. Climatic variables, in particular precipitation, are a possible factor that could contribute to interlocality variations in body sizes. Because extended periods of rainfall will interfere with opportunities for the lizards to feed (Schoener and Schoener, 1978), and since the eastern study site experiences higher, although not statistically significant (*t*-test: $t = 0.8276$; df = 26.0; $p = 0.4154$), annual rainfall (the period 2000 – 2010; 2 122.6 mm ± 487.4 SD) than the southwestern study site (the period 2000 – 2010; 1 936.8 mm ± 684.0 SD) does (Taiwanese Central Weather Bureau), it is likely that *A. sagrei* in the eastern study site could experience shorter foraging periods than conpsecifics in the southwestern study site do, potentially resulting in *A. sagrei* in the eastern study site attaining smaller sizes (SVL) than those in the southwestern study site.

Climatic conditions can also provide a plausible explanation for the variations observed in some of the meristic characteristics. Except for the ventral scale count of the lizards collected in the southwestern study site, no statistically significant differences between sexes within each study site were found for any of the recorded meristic characteristics. However, when comparing each sex between study sites, all the scale counts of all the characteristics, except for the numbers of scales in the second loreal scale row and the internasal scales, were higher (although not always statistically significant) in the individuals collected in the eastern study site than those collected in the southwestern study site. Calsbeek *et al*. (2006) found that within *A. sagrei* populations, variations in scale numbers are inheritable, and that scale numbers increase with increasing precipitation and with decreasing temperatures in open arid habitats. It was suggested that this is because lizards in drier habitats are probably under intense selection pressure to maintain proper water balance, and natural selection thus favours lizards that have fewer scales to prevent water loss, since fewer numbers of scales would decrease the amount of the area between the scales exposed to the atmosphere (Calsbeek *et al*., 2006). The eastern study site experiences higher levels of rainfall than the southwestern study site, and the former is on average cooler (the period 2000 – 2010; 23.6 ºC ± 0.2 SD) than the latter (the period 2000 – 2010; 23.5 ºC ± 0.3 SD) (Taiwanese Central Weather Bureau). The differences between the annual mean temperatures of the study sites are not statistically significant (*t*-test: $t = 0.8276$; df = 26.0; $p = 0.4154$), however for the months March to October, the period in which most hatchlings would be expected to hatch (Norval *et al*., 2012), the mean monthly temperature of the eastern study site (the period 2000 – 2010; 25.5 ºC ± 0.2 SD) is significantly (*t*-test: $t = 4.1923$; df = 26.0; $p = 0.0003$) lower than that of the southwestern study site (the period 2000 – 2010; 25.9 ºC ± 0.3 SD). The variations observed in the *A. sagrei* collected from these study sites can very likely be due to small differences in climatic conditions and the selective pressures they have on the hatchlings.

Interspecies competition for resources is another possible cause for the relatively smaller sizes of *A. sagrei* from the eastern study site compared to those from the southwestern study site. Even though it has been found that anoles tend to evolve larger body sizes when released from competition (Lister, 1976), in general it has been found that on islands, due to reduced resource availability, the body sizes of vertebrates tend to decrease (Palkovacs, 2003). Schoener and Schoener (1978) speculated that observed growth in four *Anolis* species (but all different ecomorphs: *Anolis angusticeps* – twig species, *Anolis carolinensis* – trunk-crown species, *Anolis distichus* – trunk species, and *Anolis sagrei* – trunk-ground species) was limited by food supply in some localities, and that competition from three other sympatric anole species depressed the growth of *A. sagrei* males in Bimini, but not that of the females. The authors suggested that it was because the *A. sagrei* females in Bimini occupied a relatively exclusive niche (i.e. they make use of a habitat with a completely different structure) (Schoener and Schoener, 1978). In populations where ecologically similar species are sympatric, there can thus be a reduction in size dimorphism due to the competition for limited resources (Schoener and Schoener, 1978; Losos, 2009). Since a variety of diurnal lizards, which are very likely competitors, are sympatric with *A. sagrei* in the eastern study site, it is possible that this could also contribute to the observed size variations. However, this still needs to be investigated empirically.

Predation pressure and interspecies competition can also provide explanations for the other observed variations in morphological and meristic characteristics. In a study by Marnocha *et al*., (2011) it was found that *A. sagrei* from the same founder population, but collected from distinctly different habitat types, had significant differences in hind limb lengths. This is because the hind limb length of *A. sagrei* is a plastic trait that results in the development of phenotypes that are adapted to a particular environment (Losos *et al*., 2000), and as a result, individuals that utilise broad surfaces tend to have relatively longer limbs than individuals that make use of narrower surfaces (Moermond, 1979; Losos, 1990; Calsbeek and Irschick, 2007). Both the males and females from the eastern study site had left hind shank lengths that were on average longer (males = *ca*. 2.8% longer, and females = *ca*. 8.7% longer) than those of individuals of the same sex from the southwestern study site, although only the differences between the females were statistically significant. The *A. sagrei* from the eastern study site were primarily collected from a coconut palm (*Cocos nucifera*) plantation, while those from the southwestern study site were collected from roadsides, betelnut palm (*Areca catechu*) plantations, orange (*Citrus reticulata*) orchards, and some other agricultural fields. No measurements were taken, but based on visual estimates the lower portions of the trunks of mature *C. nucifera* has a diameter that is three or four times that of the trunks of *A. catechu* and *C. reticulata*. As a result, the structural habitats from which specimens of these two populations were sampled were very different, and it can be expected that there would be significant differences in their hind limb lengths as a result of that.

Anolis sagrei males tend to be more arboreal (Schoener, 1968; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999), and it is very likely that the differences in the perch diameters between these two populations resulted in the minor difference observed between the males from these two populations. As for the females, there is a possibility that the females in the eastern study site are more arboreal than conspecifics in the southwestern study site. In the presence of terrestrial predators, *A. sagrei* tend to be more arboreal (Schoener and Schoener, 1978; Schoener *et al*., 2002; Calsbeek and Cox, 2010), and it has been found that terrestrial predation pressure can induce an increase in limb length, which can increase the speed and escape success of these lizards (Schoener *et al*., 2002). To date, the only observed predators of *A. sagrei* in the wild in Taiwan are the Malay night heron (*Gorsakius melanolophus*) (Norval *et al*., 2011b), the brown shrike (*Lanius cristatus*) (Chiu *et al*., 2011), the long-tailed skink (*Eutropis longicaudata*, formerly *Mabuya longicaudata*) (Norval *et al*., 2004), the Asian king snake (*Dinodon rufozonatum rufozonatum*) (Norval and Mao, 2011), and the mountain wolf snake (*Lycodon ruhstrati ruhstrati*) (Norval *et al*., 2007; Norval and Mao, 2008), all of which occur in both study sites. However, the Chinese skink (*Plestiodon chinensis*, formerly *Eumeces chinensis*), another competitor and possible predator (Chen, and Jiang, 2006) occurs only in the eastern study site. Also, since the area in the southwestern study site from which the *A. sagrei* were sampled often experience disturbances due to agricultural activities, the known predators of *A. sagrei* are rare and more than likely have very little impact on the foraging behavior of these lizards. A dietary study of *A. sagrei* from the southwestern study site, suggested that *A. sagrei* is fairly terrestrial in this area (Norval *et al*., 2010). So it is possible that the hind limb length differences observed between *A. sagrei* from the eastern and southwestern study sites is due to a combination of interlocality structural habitat differences, and a likely predator induced more arboreal lifestyle of *A. sagrei* in the eastern study site; i.e. the longer limbs would enhance escape from terrestrial predators such as *E. longicaudata* and *P. chinensis*, and at the same time improve the utilisation of the relatively broader trunks of the coconut palms.

A correlation between the numbers of subdigital lamellae and the degree of arboreality exists not only among various *Anolis* species, but also among the sexes of some species (Losos, 2009). In *A. sagrei*, the males have more subdigital lamellae than the females (Collette, 1961). The statistically significant intralocality intersexual differences in the numbers of subdigital lamellae noted herein thus support the findings of Collette (1961) and Lee (1985) that males have significantly more subdigital lamellae than females. In the study done by Lee (1985), in the comparisons of early and recent samples of *A. sagrei* from introduced populations in Florida, the numbers of subdigital lamellae revealed the most significant differences. Therefore, in this study, the interlocality intrasexual lack of statistically significant differences in the numbers of subdigital lamellae suggests a likely common founder population.

In conclusion, even though some variations were noted in the comparisons between the *A. sagrei* collected from the eastern and southwestern study sites, there are some possible explanations for these variations. Furthermore, as noted, the nematode, *C. penneri* exist in both populations in Taiwan. Since it is very unlikely that two separate populations established independently in Taiwan, it is possible that the two populations described herein have the same founder population, and that the one is a satellite population of the other. Still, the interlocality differences recorded in this study deserve further empirical study, which is recommended should also include genetic studies.

5.3. REFERENCES

Bursey, C.R., Goldberg, S.R., Telford, S.R. Jr., and Vitt, L.J. 2012. Metazoan endoparasites of 13 species of Central American anoles (Sauria: Polychrotidae: *Anolis*) with a review of the helminth communities of Caribbean, Mexican, North American, and South American anoles. *Comparative Parasitology* 79: 75-132.

Butler, M.A., Schoener, T.W., and Losos, J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* 54: 259-272.

Calsbeek, R., Bonneaud, C., Prabhu, S., Manoukis, N., and Smith, T.B. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards. *Evolutionary Ecology Research* 09: 495-503.

Calsbeek, R., Bonneaud, C., and Smith, T.B. 2008. Differential fitness effects of immunocompetence and neighbourhood density in alternative female lizard morphs. *Journal of Animal Ecology* 77: 103-109.

Calsbeek, R., and Cox, R.M. 2010. Experimentally assessing the relative importance of predation and competition as agents of natural selection. *Nature* 465: 613-616.

Calsbeek, R., and Irschick, D.J. 2007. The quick and the dead: Correlational selection on morphology performance, and habitat use in island lizards. *Evolution* 61: 2493-2503.

Calsbeek, R., Knouft, J., and Smith, T.B. 2006. Variation in scale numbers is consistent with ecologically based natural selection acting within and between lizard species. *Evolutionary Ecology* 20: 377-394.

Campbell, T.S., and Echternacht, A.C. 2003. Introduced species as moving targets:

changes in body sizes of introduced lizards following experimental introductions and historical invasions. *Biological Invasions* 05: 193-212.

Chang, N.C. 2007. A new discovered alien lizard of Hualien – *Anolis sagrei*. *Quarterly of Natural Conservation* 57: 37-41. (In Chinese)

Chen, X., and Jiang, Y. 2006. Diet of Chinese skink, *Eumeces chinensis*: is prey size important? *Integrative Zoology* 02: 59-66.

Chiu, P.K., Norval, G., Chu, H.P., and Mao, J.J. 2011. Two records of brown shrikes (*Lanius cristatus* Linnaeus, 1758) preying on brown anoles (*Anolis sagrei* Duméril & Bibron, 1837) in Taiwan. *Herpetology Notes* 04: 87-89.

Collette, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum of Comparative Zoology at Harvard College* 125: 137-162.

Cox, R.M., Stenquist, D.S., and Calsbeek, R. 2009. Testosterone, growth and the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* 22: 1586-1598.

Eales, J., and Thorpe, R.S. 2010. Revealing the geographical origin of an invasive lizard: the problem of native population genetic diversity. *Biological Invasions* 12: 77-86.

Eales, J., Thorpe, R.S., and Malhotra, A. 2008. Weak founder effect signal in a recent introduction of Caribbean *Anolis*. *Molecular Ecology* 17: 1416-1426.

Fox, W. 1963. Special tubules for sperm storage in female lizards. *Nature* 198: 500-501.

Kolbe, J.J., Glor, R.E., Schettino, L.R., Lara, A.C., Larson, A., and Losos, J.B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature*

431: 177-181.

Kolbe, J.J., Larson, A., and Losos, J.B. 2007. Differential admixture shapes morphological variation among invasive populations of the lizard *Anolis sagrei*. *Molecular Ecology* 16: 1579-1591.

Kolbe, J.J., Leal, M., Schoener, T.W., Spiller, D.A. and Losos, J.B. 2012. Founder effects persist despite adaptive differentiation: A field experiment with lizards. *Science* 335: 1086-1089.

Langford, G.J., Willobee, B.A., and Isidoro, L.F. 2013. Transmission, host specificity, and seasonal occurrence of Cyrtosomum penneri (Nematoda: Atractidae) in lizards from Florida. *Journal of Parasitology* 99: 241-246.

Lee, J.C. 1985. *Anolis sagrei* in Florida: phenetics of a colonizing species I. Meristic characters. *Copeia* 1985: 182-194.

Lee, J.C. 1987. *Anolis sagrei* in Florida: phenetics of a colonizing species II. Morphometric characters. *Copeia* 1987: 458-469.

Lee, J.C. 1992. *Anolis sagrei* in Florida: phenetics of a colonizing species III. West Indian and Middle American comparisons. *Copeia* 1992: 942-954.

Lister, B.C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30: 659-676.

Losos, J.B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60: 369-388.

Losos, J.B. 2009. *Lizards in an Evolutionary Tree*: *Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, California.

Losos, J.B., Creer, D.A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., Haskell, N., Taylor, P., and Ettling, J. 2000. Evolution implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* 54: 301-305.

Marnocha, E., Pollinger, J., and Smith, T.B. 2011. Human-induced morphological shifts in an island lizard. *Evolutionary Applications* 04: 388-396.

Moermond, T.C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60: 152-164.

Norval, G., Bursey, C.R., Goldberg, S.R., Mao, J.J., and Slater, K. 2011a. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), in southwestern Taiwan. *Pacific Science* 65: 383-390.

Norval, G., Chiu, P.K., Chu, H.P., and Mao, J.J. 2011b. An instance of predation on the brown anole (*Anolis sagrei* Duméril & Bibron, 1837) by a Malay night heron (*Gorsakius melanolophus* Swinhoe, 1865). *Herpetology Notes* 04: 05-07.

Norval, G., Goldberg, S.R., Bursey, C.R., Mao, J.J., and Slater, K. 2014. Internal parasites of lizards from Taiwan. *Herpetological Conservation and Biology*. 9: 484-494.

Norval, G., Goldberg, S.R., and Mao, J.J. 2012. The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan. *Russian Journal of Herpetology* 19: 75-81.

Norval, G., Hsiao, W.F., Huang, S.C., and Chen, C.K. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russian Journal of Herpetology* 17: 131-138.

Norval, G., Huang, S.C., and Mao, J.J. 2007. Mountain wolf snake (*Lycodon r. ruhstrati*) predation on an exotic lizard, *Anolis sagrei*, in Chiayi County, Taiwan.

Herpetological Bulletin 101: 13-17.

Norval, G., and Mao, J.J. 2008. An instance of arboricolous predation by a mountain wolf snake (*Lycodon ruhstrati ruhstrati* [Fischer, 1886]) on a brown anole (*Norops sagrei* Duméril & Bibron, 1837). *Sauria* 30: 59-62.

Norval, G., and Mao, J.J. 2011. *Dinodon rufozonatum rufozonatum* (Cantor, 1842) attempted predation on *Anolis sagrei* Duméril & Bibron, 1837, in Chiayi County, Taiwan. *Newsletter of Wildlifers* 15: 14-16. (In Chinese)

Norval, G., Mao, J.J., Bursey, C.R., and Goldberg, S.R. 2009. A deformed hind limb of an invasive free-living brown anole (*Anolis sagrei* Duméril & Bibron, 1837) from Hualien City, Taiwan. *Herpetology Notes* 02: 219-221.

Norval, G., Mao, J.J., and Chu, H.P. 2004. *Mabuya longicaudata* (Long-tailed Skink). Predation. *Herpetological Review* 35: 393-394.

Norval, G., Mao, J.J., Chu, H.P., and Chen, L.C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Duméril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.

Paemelaere, E.D., Guyer, C., and Dobson, S.F. 2011. A phylogenetic framework for the evolution of female polymorphism in anoles. *Biological Journal of the Linnean Society* 104: 303-317.

Palkovacs, E.P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103: 37-44.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of Florida, Gainesville, Florida.

Sanger, T.J., Losos, J.B., and Gibson-Brown, J.J. 2008. A developmental staging series for the lizard genus *Anolis*: A new system for the integration of evolution, development, and ecology. *Journal of Morphology* 269: 129-137.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.

Schoener, T.W., and Schoener, A. 1976. The ecological context of female pattern polymorphism in the Lizard *Anolis sagrei*. *Evolution* 30: 650-658.

Schoener, T.W., and Schoener, A. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978: 390-405.

Schoener, T.W., Spiller, D.A., and Losos, J.B. 2002. Predation on a common Anolis lizard: Can the food-web effects of a devastating predator be reversed? *Ecological Monographs* 72: 383-407.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Sever, D.M., and Hamlett, W.C. 2002. Female sperm storage in reptiles. *Journal of Experimental Zoology* 292: 187-199.

Taiwanese Central Weather Bureau. [online]. Available at: http://www.cwb.gov.tw/V6e/index.htm (accessed 06th of August, 2013).

Tokarz, R.R. 1985. Body size as a factor determining dominance in staged agonistic encounters between males brown anoles (*Anolis sagrei*). *Animal Behaviour* 33: 746-753.

CHAPTER 6 – THE REPRODUCTIVE BIOLOGY OF *ANOLIS SAGREI* FROM SOUTHWESTERN TAIWAN

6.1. INTRODUCTION

The reproductive cycle (i.e. the period during which reproduction takes place) of *A. sagrei* has been studied in Belize (Sexton and Brown, 1977), Cuba (Rodriguez Schettino, 1999; Sanz Ochotorena and Uribe Aranzábal, 1999), Florida (Lee *et al*., 1989), Hawaii (Goldberg *et al*., 2002), Jamaica (Licht and Gorman, 1970), and southwestern Taiwan (Norval *et al*., 2012). In all these localities it was found that the reproductive period of this species is cyclic and long, and except for in Hawaii, it coincides with the rainy season (Licht and Gorman, 1970; Sexton and Brown, 1977; Lee *et al*., 1989; Rodriguez Schettino, 1999; Sanz Ochotorena and Uribe Aranzábal, 1999; Goldberg *et al*., 2002; Norval *et al*., 2012). *Anolis sagrei* females bury their eggs in soil or other suitable substrates, and even though they are inclined to choose oviposition sites randomly with respect to canopy cover (Delaney *et al*., 2013), Brown and Sexton (1973) demonstrated the importance of relative humidity for oviposition, and Warner *et al*. (2012) and Reedy *et al*. (2013) found that *A. sagrei* females prefer to select nest sites with a relatively high humidity because the nest sites selected by a female have an influence on the fitness of her offspring. Compared with the hatchlings from eggs that are deposited in relatively dry nests (≤ 50 % moisture), hatchlings from eggs that are deposited in moist nests (*ca*. 75 % moisture) have greater hatching success, tend to be larger, and have overall increased survival rates (Reedy *et al*., 2013). Still, inspite of the importance of humidity most studies to date suggest that photoperiod and the associated temperatures are the cues that regulate the reproductive cycles of *A. sagrei* (Sexton and Brown, 1977; Lee *et al*., 1989; Goldberg *et al*., 2002; Licht and Gorman, 1970).

Anolis stores most of its fat in a pair of visceral abdominal fat bodies (corpora adiposa), and measures of these abdominal fat bodies are ideal for tracking fat cycling patterns (Dessauer, 1955; Derickson, 1976). The reproductive and fat body cycles of *A. sagrei* has been described for populations in Belize (Sexton and Brown, 1977), Florida (Lee *et al*., 1989), and Jamaica (Licht and Gorman, 1970). Even though the reproductive cycle of *A. sagrei* in Taiwan has been studied (Norval *et al*., 2012), the fat body cycle has not yet been described. For the purpose of this study both the fat body and liver weight cycles of *A. sagrei* will be described, and the associations between these cycles and the reproductive cycles, as well as potential meteorological factors, will be examined. This information will contribute to the understanding of the reproductive biology of *A. sagrei* not only in Taiwan, but also as a species, since the liver weight cycle has not been described yet in any locality.

6.2. RESULTS

6.2.1. *METEOROLOGY*

The mean minimum temperature, mean temperature, and mean maximum temperature for the study period were 19.56 ºC (± 4.81 SD), 23.49 ºC (± 4.25 SD), and 28.76 ºC (± 4.39 SD) respectively. June 2002 was the hottest month and January 2003 the coldest (Fig. 6.1 A). During the same period 1 419.1 mm rain fell, of which the most fell in July 2002 (Fig. 6.1 B). The mean daily photoperiod was 790.18 minutes (± 57.79 SD), June 2002

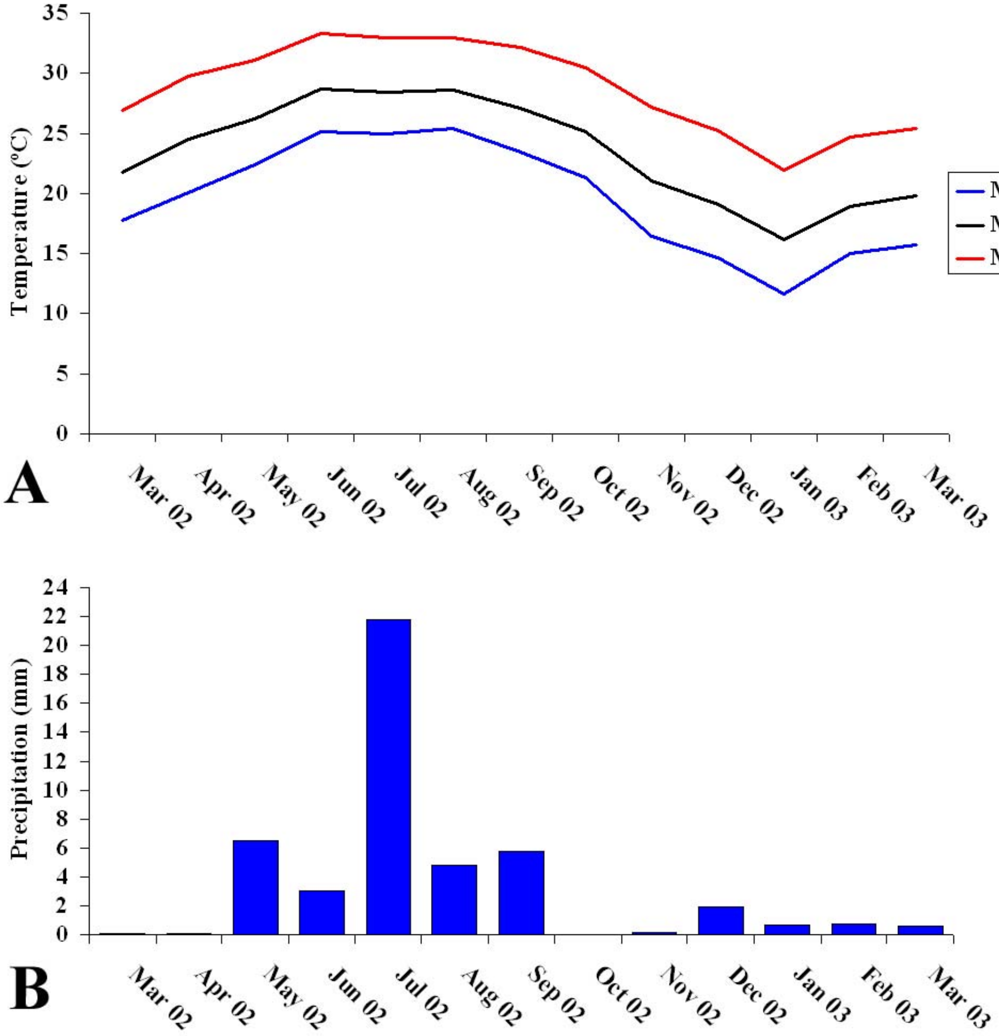


Figure 6.1. The monthly mean minimum, mean, and mean maximum temperatures (A), and monthly mean precipitation (B) of the Santzepu, southwestern Taiwan sampling area during the study period.

(867.32 minutes) being the month with the longest mean photoperiod and December 2002 (705.19 minutes) with the shortest.

6.2.2. *SAMPLED SPECIMENS*

The males ranged in snout-vent length (SVL), tail length (TL) and body mass, from 36 to 64 mm, 13 to 125 mm, and 1.3 to 6.6 g respectively, while the SVL, TL and body mass of the females ranged from 28 to 47 mm, 8 to 90 mm, and 0.6 to 3 g respectively. It was noted, that males with a SVL as small as 30 mm could be in a stage of spermiogenesis (Norval *et al*., 2012), so this was considered the size at which the males become sexually mature. Females attained a sexually mature size at a minimum SVL of 34 mm (Norval *et al*., 2012). From the specimens collected, ten females were not yet sexually mature (juveniles), one female specimen was suffering from a hepatic granuloma (Norval *et al*., 2005), one male specimen had an unidentified clinical condition affecting both testes (Norval *et al*., 2006), and seven male specimens were damaged during dissection and preparation. These specimens were thus excluded from the analysis, thereby resulting in 215 males and 204 females (Table 6.1 and 6.2) being used for the purpose of further analyses.

The mean SVL, TL and body mass of the males were 51.0 mm (± 6.07 SD), 92.03 mm (± 19.97 SD), and 3.86 g (± 1.32 SD) respectively, while that of the females were 40.82 mm (± 3.23 SD), 69.28 mm (± 14.49 SD), and 1.88 g (± 0.48 SD) respectively. The monthly sample sizes, as well as the SVL values of the *A. sagrei* specimens used in this study, are presented in Tables 6.1. and 6.2. There were some significant differences between months in the SVLs of both the males (Kruskal-Wallis test = 51.073, df = 12, $p < 0.0001$) and the females (Kruskal-Wallis test = 45.328, df = 12, $p < 0.0001$), but there were no significant differences in SVLs of the males (Mann-Whitney U-test, $U = 109.5$, $p = 0.4967$) and females (t-test, $t = 0.5854$, df = 30, $p = 0.5627$) sampled in March 2002 and March 2003.

6.2.3. *CAUDAL AUTOTOMY*

Table 6.1. The numbers (*n*) of the monthly sampled brown anole (*Anolis sagrei*) male specimens used in this study, and the monthly range, mean and standard deviation (mean ± SD) of their snout-vent lengths (SVL; in mm), abdominal fat body weight indices (AFBWI) and liver weight indices (LWI).

		SVL		AFBWI		LWI	
	Sample size	**Range (mm)**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**
Mar 2002	17	36 – 59	49.71 ± 7.5	0 – 0.25	0.1 ± 0.08	0.11 – 0.39	0.24 ± 0.07
Apr 2002	15	45 – 60	55.13 ± 4.07	0 – 0.13	0.04 ± 0.05	0.16 – 0.4	0.27 ± 0.06
May 2002	17	50 – 58	54.53 ± 2.43	0 – 0.41	0.08 ± 0.11	0.14 – 0.43	0.3 ± 0.08
Jun 2002	15	50 – 61	56.67 ± 3.64	0 – 0.32	0.16 ± 0.1	0.23 – 0.45	0.33 ± 0.06
Jul 2002	16	39 – 63	53.06 ± 7.53	0 – 0.15	0.04 ± 0.05	0.13 – 0.4	0.25 ± 0.09
Aug 2002	17	41 – 60	48.88 ± 6.84	0 – 0.34	0.1 ± 0.1	0.18 – 0.48	0.25 ± 0.08
Sep 2002	20	40 – 55	48.1 ± 3.57	0 – 0.58	0.16 ± 0.14	0.14 – 0.27	0.2 ± 0.04
Oct 2002	21	39 – 61	48.91 ± 5.4	0 – 0.5	0.19 ± 0.14	0.15 – 0.41	0.25 ± 0.06
Nov 2002	12	44 – 57	50.58 ± 4.52	0.09 – 0.65	0.39 ± 0.17	0.24 – 0.44	0.31 ± 0.07
Dec 2002	14	38 – 62	49.29 ± 5.77	0.16 – 0.56	0.31 ± 0.11	0.16 – 0.46	0.3 ± 0.1
Jan 2003	18	39 – 54	47.56 ± 4.46	0.04 – 0.42	0.22 ± 0.1	0.15 – 0.37	0.27 ± 0.07
Feb 2003	18	39 – 64	51.33 ± 7.2	0.07 – 0.47	0.27 ± 0.14	0.21 – 0.57	0.37 ± 0.1
Mar 2003	15	40 – 63	52.07 ± 6.33	0 – 0.33	0.11 ± 0.09	0.18 – 0.37	0.27 ± 0.06

Table 6.2. The numbers (*n*) of the monthly sampled brown anole (*Anolis sagrei*) female specimens used in this study, and the monthly range, mean and standard deviation (mean ± SD) of their snout-vent lengths (SVL; in mm), abdominal fat body weight indices (AFBWI) and liver weight indices (LWI).

		SVL		AFBWI		LWI	
	Sample size	**Range (mm)**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**
Mar 2002	15	35 – 46	39.73 ± 3.17	0.09 – 0.31	0.19 ± 0.08	0.15 – 0.37	0.26 ± 0.07
Apr 2002	22	34 – 44	41.14 ± 2.03	0 – 0.15	0.05 ± 0.05	0.18 – 0.34	0.26 ± 0.04
May 2002	19	36 – 47	42.42 ± 2.48	0 – 0.24	0.07 ± 0.07	0.19 – 0.5	0.33 ± 0.08
Jun 2002	19	40 – 47	43.42 ± 1.54	0 – 0.28	0.12 ± 0.09	0.23 – 0.67	0.38 ± 0.11
Jul 2002	17	38 – 47	43.24 ± 2.31	0 – 0.14	0.03 ± 0.05	0.13 – 0.46	0.31 ± 0.08
Aug 2002	15	34 – 46	39.73 ± 3.56	0 – 0.22	0.04 ± 0.07	0.15 – 0.4	0.23 ± 0.06
Sep 2002	17	35 – 45	40.35 ± 2.4	0 – 0.26	0.04 ± 0.07	0.13 – 0.33	0.22 ± 0.06
Oct 2002	16	34 – 46	39.5 ± 3.8	0 – 0.39	0.09 ± 0.12	0.12 – 0.41	0.23 ± 0.08
Nov 2002	15	34 – 46	39.67 ± 3.52	0 – 0.5	0.26 ± 0.13	0.16 – 0.38	0.23 ± 0.06
Dec 2002	11	35 – 44	39.18 ± 2.6	0 – 0.49	0.23 ± 0.13	0.13 – 0.48	0.26 ± 0.1
Jan 2003	10	34 – 45	38.7 ± 3.83	0.16 – 0.39	0.24 ± 0.07	0.15 – 0.33	0.22 ± 0.06
Feb 2003	11	34 – 47	40.55 ± 3.3	0.1 – 0.51	0.23 ± 0.12	0.18 – 0.37	0.26 ± 0.07
Mar 2003	17	34 – 47	40.47 ± 3.86	0 – 0.4	0.17 ± 0.11	0.15 – 0.49	0.3 ± 0.08

Twenty-one males and 11 females that were caught had broken tails and showed no evidence of caudal regeneration. These individuals were excluded from the analysis investigating the influence of caudal autotomy on the mean abdominal fat body weight indices (AFBWI) and mean liver weight indices (LWI), since the likelihood that the autotomy may have been caused by the capturing process could not be ruled out. No *A. sagrei* male specimens, with regenerated autotomized tails, were collected in March or August 2002. The sampled males from these months were thus also excluded from the analyses. Therefore 162 males (Table 6.3) and 193 females (Table 6.4) were used for further analyses. No statistically significant variations in the monthly mean AFBWI and monthly mean LWI of lizards that had not experienced caudal autotomy and those that had were noted (Table 6.5), and as a result the relevant data of the respective sexes were pooled for the reproductive biology study.

Table 6.3. The numbers (*n*) of the monthly sampled brown anole (*Anolis sagrei*) male specimens used in the caudal autotomy study, and the monthly range, mean and standard deviation (mean ± SD) of their mean abdominal fat body weight indices and mean liver weight indices.

	Males with an original tail			**Males with a regenerated tail**		
	Sample size	**Abdominal fat body weight index**	**Liver weight index**	**Sample size**	**Abdominal fat body weight index**	**Liver weight index**
Apr 2002	10	0.03 ± 0.04	0.25 ± 0.07	3	0.08 ± 0.07	0.32 ± 0.45
May 2002	9	0.06 ± 0.05	0.29 ± 0.08	4	0.03 ± 0.04	0.29 ± 0.07
Jun 2002	11	0.16 ± 0.11	0.33 ± 0.06	2	0.18 ± 0.03	0.39 ± 0.02
Jul 2002	9	0.05 ± 0.06	0.24 ± 0.08	6	0.03 ± 0.05	0.28 ± 0.09
Sep 2002	12	0.15 ± 0.09	0.2 ± 0.04	3	0.3 ± 0.25	0.2 ± 0.06
Oct 2002	13	0.21 ± 0.15	0.26 ± 0.06	7	0.15 ± 0.12	0.25 ± 0.08
Nov 2002	8	0.41 ± 0.16	0.32 ± 0.07	3	0.34 ± 0.24	0.3 ± 0.05
Dec 2002	12	0.32 ± 0.12	0.32 ± 0.09	2	0.29 ± 0.03	0.17 ± 0.02
Jan 2003	16	0.22 ± 0.1	0.27 ± 0.06	2	0.26 ± 0.22	0.26 ± 0.15
Feb 2003	8	0.3 ± 0.15	0.38 ± 0.08	7	0.23 ± 0.13	0.31 ± 0.1
Mar 2003	8	0.09 ± 0.08	0.28 ± 0.06	7	0.13 ± 0.1	0.26 ± 0.06

6.2.4. *MALE REPRODUCTIVE CYCLE*

Males that had seminiferous tubules in which spermatogonia and spermatocytes were present, but in which it was not possible to state when spermiogenesis would begin (stage 1: immature) were present in June to January (Fig. 6.2). Males that had seminiferous tubules that contained only spermatogonia and Sertoli cells (2: regressed) were only recorded in October (Fig. 6.2). Reproductively active males, i.e. males that had seminiferous tubules that exhibited markedly increased cellularity, with primary

Table 6.4. The numbers (*n*) of the monthly sampled brown anole (*Anolis sagrei*) female specimens used in the caudal autotomy study, and the monthly range, mean and standard deviation (mean ± SD) of their mean abdominal fat body weight indices and mean liver weight indices.

	Females with an original tail			**Females with a regenerated tail**		
	Sample size	**Abdominal fat body weight index**	**Liver weight index**	**Sample size**	**Abdominal fat body weight index**	**Liver weight index**
Mar 2002	11	0.2 ± 0.08	0.25 ± 0.07	4	0.18 ± 0.08	0.27 ± 0.08
Apr 2002	15	0.05 ± 0.05	0.26 ± 0.05	5	0.03 ± 0.03	0.24 ± 0.02
May 2002	12	0.06 ± 0.06	0.32 ± 0.08	7	0.09 ± 0.09	0.35 ± 0.1
Jun 2002	11	0.1 ± 0.08	0.38 ± 0.13	7	0.15 ± 0.09	0.36 ± 0.06
Jul 2002	5	0.03 ± 0.06	0.26 ± 0.07	12	0.03 ± 0.04	0.33 ± 0.08
Aug 2002	11	0.05 ± 0.08	0.22 ± 0.07	4	0.0	0.26 ± 0.03
Sep 2002	9	0.05 ± 0.09	0.22 ± 0.06	4	0.06 ± 0.07	0.23 ± 0.06
Oct 2002	11	0.08 ± 0.09	0.23 ± 0.09	5	0.12 ± 0.17	0.23 ± 0.07
Nov 2002	11	0.25 ± 0.11	0.23 ± 0.07	4	0.26 ± 0.21	0.23 ± 0.06
Dec 2002	2	0.27 ± 0.03	0.2 ± 0.05	8	0.24 ± 0.15	0.27 ± 0.11
Jan 2003	5	0.21 ± 0.06	0.23 ± 0.06	5	0.27 ± 0.08	0.21 ± 0.05
Feb 2003	6	0.16 ± 0.07	0.22 ± 0.04	4	0.33 ± 0.13	0.32 ± 0.06
Mar 2003	6	0.2 ± 0.14	0.34 ± 0.08	9	0.13 ± 0.1	0.27 ± 0.09

Table 6.5. The mean and standard deviation (mean ± SD) of the monthly mean abdominal fat body weight indices (AFBWI) and monthly mean liver weight indices (LWI) of the *Anolis sagrei* specimens that had not experienced caudal autotomy and those that had, and the results of their comparisons.

	Lizards with original tails	**Lizards with regenerated tails**	**Result**
AFBWI of the males	0.18 ± 0.12	0.18 ± 0.11	$U = 60, p > 0.9999$
LWI of the males	0.29 ± 0.05	0.28 ± 0.06	$U = 57, p = 0.8470$
AFBWI of the females	0.13 ± 0.09	0.15 ± 0.11	$U = 79, p = 0.8010$
LWI of the females	0.26 ± 0.05	0.28 ± 0.05	$U = 60, p = 0.2226$

spermatocytes predominating (stage 3: recrudescent; and males that had seminiferous tubules in which sperm, spermatids, and metamorphosing spermatids were abundant (stage 4: spermiogenic), were present in every month, but in various proportions (Fig. 6.2). Testicular recrudescence (stage 3) occurred from October to March, peaked from April to June, and then steadily decreased. All the males collected from April to June were in a stage of maximal spermiogenesis (stage 4), while spermatogenesis (stages 3 and 4) was minimal during September (Fig. 6.2).

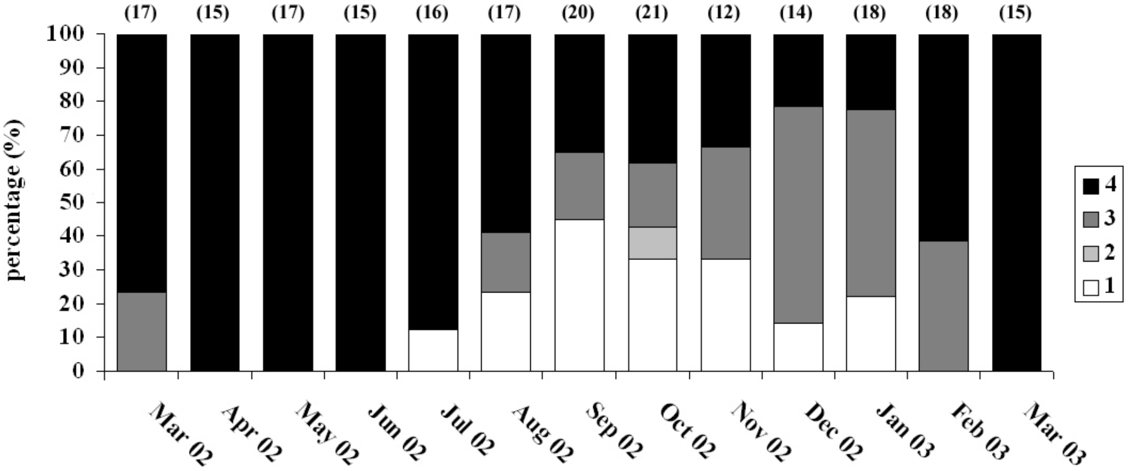


Figure 6.2. The monthly percentage of *Anolis sagrei* males in each of the four reproductive stages, 1: immature – spermatogonia and spermatocytes are present, but it is not possible to state when spermiogenesis will begin; 2: regressed – seminiferous tubules contained spermatogonia and Sertoli cells only; 3: recrudescent – seminiferous tubules exhibited markedly increased cellularity, with primary spermatocytes predominating; and 4: spermiogenic – sperm, spermatids, and metamorphosing spermatids abundant. The number of sexually mature individuals sampled in each month is given in parenthesis.

There was no correlation between the monthly mean values of the climatic variables and the monthly proportion of reproductively active males (Table 6.6). When the stages were analysed independently there were however significant negative correlations between the monthly proportion of males with testicular development stage 3 and the monthly mean photoperiod (Spearman's rank correlation coefficient $n = 13$; $r_s = -0.8534$; $p = 0.0002$)

and monthly mean temperature (Spearman's rank correlation coefficient $n = 13$; $r_s = -0.6782$; $p = 0.0108$). There was also a significant positive correlation between the monthly proportion of males with testicular development stage 4 and the monthly mean photoperiod (Spearman's rank correlation coefficient $n = 13$; $r_s = 0.7494$; $p = 0.0032$).

Table 6.6. The results of the Spearman's rank correlation coefficient examination of the relationships between the monthly percentage of reproductive *Anolis sagrei* specimens (Repro.), monthly mean abdominal fat body weight index (AFBWI), monthly mean liver weight index (LWI), monthly mean precipitation (Prec.), monthly mean temperature (Temp.), and monthly mean photoperiod (Photo.) (*n* = number of points; * - statistically significant).

Variable	**Males**			**Females**	
	n	r_s	***p***	r_s	***p***
Repro. and AFBWI	13	-0.3699	0.2135	-0.6371	0.0192*
Repro. and LWI	13	0.5895	0.0340*	0.5707	0.0417*
Repro. and Photo.	13	0.3179	0.2899	0.8504	0.0002*
Repro. and Prec.	13	-0.02312	0.9402	0.2161	0.4783
Repro. and Temp.	13	-0.1011	0.7423	0.6898	0.0091*
AFBWI and LWI	13	0.3571	0.2309	-0.1264	0.6808
AFBWI and Photo.	13	-0.7802	0.0017*	-0.7912	0.0013*
AFBWI and Prec.	13	-0.2473	0.4154	-0.4670	0.1076
AFBWI and Temp.	13	-0.5495	0.0518	-0.7912	0.0013*
LWI and Photo.	13	-0.1813	0.5533	0.5055	0.0780
LWI and Prec.	13	-0.2198	0.4706	0.2967	0.3249
LWI and Temp.	13	-0.3626	0.2233	0.2582	0.3943

6.2.5. *MALE ABDOMINAL FAT-BODY WEIGHT CYCLE*

Males with no dissectible abdominal fat bodies were present in the months March to October, and were highest in July (Fig. 6.3). The AFBWI of the males within any monthly sample were very variable and there were significant differences between the monthly samples (Kruskal-Wallis test = 97.880, df = 12, $p < 0.0001$), but overall, the monthly mean AFBWI appeared to follow a cycle (Fig. 6.4) that started with a decrease with the marked increase of spermatogenesis (stage 3; March to April). During the later part of the peak period of spermatogenesis (May and June) the monthly mean AFBWI

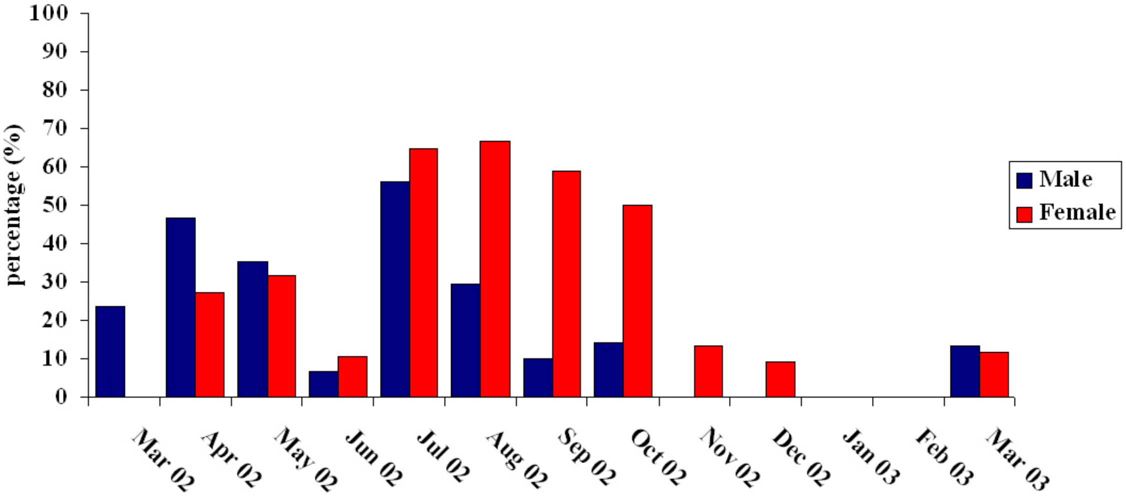


Figure 6.3. The percentage of *Anolis sagrei* specimens from every monthly sample that had no dissectible abdominal fat bodies.

increased, but declined again in July. As the proportion of reproductively active males decreased the monthly mean AFBWI increased until just before the period of shortest monthly mean photoperiods (December), at which point the monthly mean AFBWI again started to decrease (February to March) after an initial increase as the monthly mean photoperiod started to increase (January). The monthly mean AFBWI of the males sampled in March 2002 and March 2003 did not differ significantly (*t*-test, $t = 0.5031$, df = 30, $p = 0.6185$). The monthly mean AFBWI was lowest in July and highest in November, and in general, it had an inverse relationship with the proportion of reproductively active males in each monthly sample, but the correlation was not statistically significant (Table 6.6). Even when the monthly mean AFBWI and the proportions of males in the different testicular development stages were analysed individually, there was only a significant negative correlation between the monthly proportion of males in testicular development stage 4 and their monthly mean AFBWI

(Spearman's rank correlation coefficient $n = 13$; $r_s = -0.6129$; $p = 0.0259$). There was however a negative correlation between the overall monthly mean AFBWI and the monthly mean photoperiod (Table 6.6).

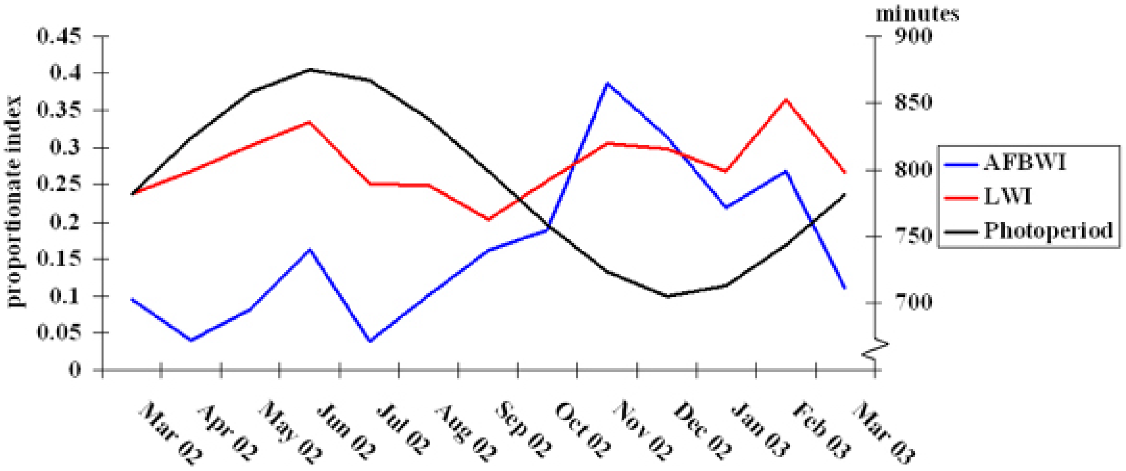


Figure 6.4. The monthly mean photoperiod for the study period, and the monthly mean abdominal fat body weight index (AFWI) and monthly mean liver weight index (LWI) of the *Anolis sagrei* males used in this study.

6.2.6. *MALE LIVER WEIGHT CYCLE*

The LWI of the male specimens within any monthly sample were also variable and there were significant differences between the monthly samples (Kruskal-Wallis test = 55.944, df = 12, $p < 0.0001$). The monthly mean LWI increased prior to, and during the period of maximal spermatogenesis (stage 4; March to June). As the monthly mean photoperiod and the number of reproductively active individuals decreased, the monthly mean LWI also decreased (July to September). The monthly mean LWI was at its lowest at the same period (September) when spermatogenesis was at its lowest, and as spermatogenesis increased, so did the LWI until just before the period of shortest monthly mean photoperiod (December), during which the LWI slightly decreased. After this initial decrease as the monthly mean photoperiods started to increase (January), the monthly mean LWI first increased (February, when it was at its highest), and then decreased again (March). The monthly mean LWI of the males sampled in March 2002 and March 2003 did not differ significantly (*t*-test, $t = 1.2594$, df = 30, $p = 0.2176$). The monthly mean LWI (Fig. 6.4) cycle resembles the reproductive cycle, and there was a positive correlation between the monthly mean LWI and the monthly proportion of reproductively active males (Table 6.6).

6.2.7. *FEMALE REPRODUCTIVE CYCLE*

Non-reproductive females, i.e. females in which no yolk deposition was noted in any of the ovarian follicles (stage 1: inactive), were recorded in every month, except April and June (Fig. 6.5). Reproductive females, i.e. females in which there was yolk deposition in one or more ovarian follicles (stage 2); females in which there was yolk deposition in one or more ovarian follicles and oviductal eggs were present (stage 3); and females in which no yolk deposition was noted in any of the ovarian follicles, but oviductal eggs were

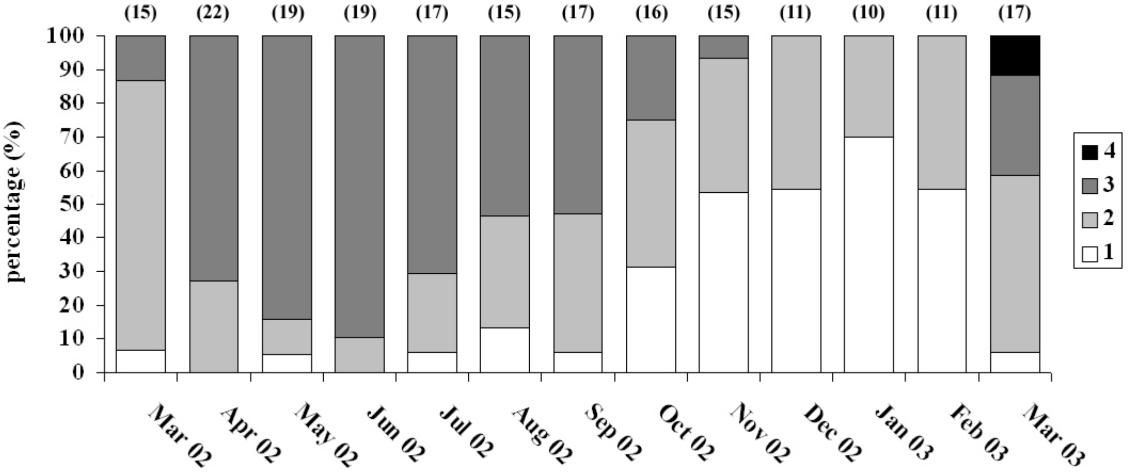


Figure 6.5. The monthly percentage of *Anolis sagrei* females in each of the four reproductive stages, 1: inactive – no yolk deposition; 2: yolk deposition in one or more ovarian follicles; 3: oviductal eggs present and yolk deposition in one or more ovarian follicles; and 4: oviductal eggs present, and no yolk deposition in ovarian follicles. The number of sexually mature individuals sampled in each month is given in parenthesis.

present (stage 4), were present in every month (Fig. 6.5). Females with oviductal eggs were present from March and comprised the majority of specimens in the samples from April to September (Fig. 6.5), after which the monthly proportion of reproductive individuals decreased. Female reproductive activity was lowest during January, and ovarian recrudescence occurred from February to March (Fig. 6.5). There were significant positive correlations between the monthly proportion of reproductively active females and the monthly mean photoperiod and monthly mean temperature (Table 6.6).

6.2.8. *FEMALE ABDOMINAL FAT-BODY WEIGHT CYCLE*

Females with no dissectible abdominal fat bodies were present in the months March to December 2002 and March 2003, but tended to be more common in the months July to October (Fig. 6.3). The AFBWI of the females within any monthly sample were also variable and there were significant differences between the monthly samples (Kruskal-Wallis test = 95.355, df = 12, $p < 0.0001$). In general, the monthly mean AFBWI varied inversely with the monthly proportion of ovigerous females in each monthly sample, and was highest (November) shortly before the period of shortest day lengths (December). The monthly mean AFBWI decreased at the onset of ovarian recrudescence (stage 2) and the start of the peak period of reproductive activity (March to April). As in the males, during the peak reproductive period (May and June) the monthly mean AFBWI increased, after which it decreased to its lowest value (July) and remained relatively low until a marked decrease in the proportion of ovigerous females (July to September). The monthly mean AFBWI then sharply increased (October and November) as reproduction decreased prior to the onset of the next cycle, at which it started to decrease again

(January to March). The monthly mean AFBWI of the females sampled in March 2002 and March 2003 did not differ significantly (Mann-Whitney *U*-test, $U = 110.0$, $p = 0.5087$). The monthly mean LWI (Fig. 6.6) cycle inversely resembled the reproductive cycle, and there was a strong negative correlation between the monthly mean LWI and the monthly proportion of reproductively active females (Table 6.6).

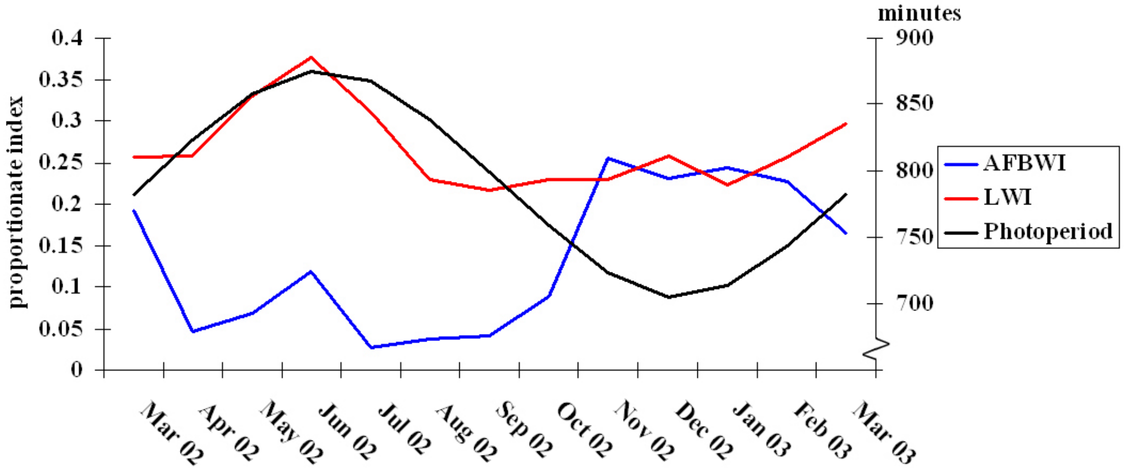


Figure 6.6. The monthly mean photoperiod for the study period, and the monthly mean abdominal fat body weight index (AFWI) and monthly mean liver weight index (LWI) of the *Anolis sagrei* females used in this study.

6.2.9. *FEMALE LIVER WEIGHT CYCLE*

The LWI of the female specimens within any monthly sample were also variable and there were significant differences between the monthly samples (Kruskal-Wallis test = 59.614, df = 12, $p < 0.0001$). In general, the monthly mean LWI varied little (Fig. 6.6), except for a three-month (April to June) increase to its highest level (June), followed by a three-month decrease to its lowest level (September), after which it increased slightly as day lengths decreased (October to December). As day lengths started to increase (January), the monthly mean LWI decreased slightly, but increased again slightly as the proportion of ovigerous females started to increase (February and March). The monthly mean LWI of the females sampled in March 2002 and March 2003 did not differ significantly (*t*-test, t = 1.4364, df = 30, p = 0.1612). There was a weak positive correlation between the monthly mean LWI and the monthly proportion of reproductively active females (Table 6.6).

6.3. DISCUSSION

The results of this study indicate that in southwestern Taiwan, *A. sagrei* males and females have annual reproductive cycles, but they are not completely synchronized. That of the males is initiated earlier than that of the females, whose end later than that of the males. The observed timing differences are most likely related to the respective reproductive roles of the sexes and their different responses to the environmental cues that regulate reproduction.

As in Cuba (Sanz Ochotorena and Uribe Aranzábal, 1999), Florida (Lee *et al*., 1989), and Jamaica (Licht and Gorman, 1970), the period of high reproductive activity of the *A. sagrei* males in southwestern Taiwan is from March to August. The reproductive season of *Anolis carolinensis* males from Louisiana, U.S.A., is also from March to August (Licht, 1967a). Studies on *A. carolinensis* males from this locality found that these lizards become photoperiod sensitive towards the end of the reproductive cycle at the end of summer, and as day lengths decrease a regression of their testicular activity is triggered (Licht, 1971). After a brief period of quiescence, during which testicular development is most likely photoperiodically inhibited (Licht, 1969), testicular recrudence is initiated in autumn, most likely by some endogenous trigger, and the lizards become thermal sensitive (Licht, 1967a). The testes develop during autumn and winter, but the cool temperatures prior to spring prevent the completion of the testicular development (Licht, 1967b). In spring, shortly before the onset of the breeding season, the higher temperatures allow these lizards to complete the spermatogenesis process, enabling them to breed (Licht, 1967b; Licht, 1969).

Although the reproductive cycle of *A. sagrei* males from the study described herein resemble the same pattern, there are differences. Unlike in *A. carolinensis*, there was no period in which all the males were quiescent. The mean testis weight of the *A. sagrei* males from this study was at its lowest in October 2003 (Norval *et al.*, 2012), and it could be argued that based on the relative small sizes (volume, range = 1.1 – 54.8 mm^3, mean ± SD = 12.3 mm^3 ± 13.24) of the testes at this time, that the males with spermatogenesis stage 4 had seminiferous tubules that contained abundant spermatids and spermatozoa, but the epididymides were hypertrophied and empty (stage 5 in Licht, 1967a). However, this is not necessarily the case, because the epididymis can be hypertrophied with the presence of sperm in the epididymis even when the testes are almost completely regressed (Licht and Pearson, 1969). Also, even though the epididymis of the specimens in this study were not examined, the results of the testes cyles of this study are very similar to the results from the studies done in Belize (Sexton and Brown, 1977) and Jamaica (Licht and Gorman, 1970), in which it was confirmed that irrespective of the time of year, large *A. sagrei* males had testes in which spermatids and spermatozoa were abundant in the seminiferous tubules, and the epididymides were hypertrophied and contained many sperm (stage 6 in Licht, 1967a).

This suggests that at least the largest *A. sagrei* males (SVL > 50 mm) in spermatogenesis stage 4 in this study were also in a maximal stage of spermatogenesis. Even though a few specimens, collected in October 2003, had regressed testes (stage 2), indicating that testicular regression does occur in some specimens, it is unlikely that the sexually mature specimens in stages 1 and 3, from August to December, were the result of testicular regression. Rather, they were specimens that became sexually mature at the end of the reproductive cycle.

The strong negative correlations between monthly proportion of sexually mature males in stage 3 of the testicular development and the monthly mean photoperiod and monthly mean temperature indicate that males that reach sexual maturity at the end of the reproductive period (March to August) are photoperiod and/or thermal sensitive and that the decreasing photoperiod and/or associated cooling temperatures inhibit the complete development of the testes. However, as photoperiods and temperatures increase, testicular development is completed so that most of the sexually mature males are in a maximal stage of spermatogenesis (stage 4) at the onset (March) of the high reproductive period (March to August).

Once the males reach the maximal stage of spermatogenesis they usually remain in this state (Licht and Gorman, 1970; Sexton and Brown, 1977). Considering that the life expectancy of *A. sagrei* males is about one year (Schoener, and Schoener, 1982b;

Schwartz and Henderson, 1991), males have to maximize their likelihood to reproduce, and remaining in an advanced stage of spermiogenesis enables them to mate whenever mature receptive females are present. *Anolis sagrei* females, on the other hand, have the ability to store sperm (Fox, 1963; Sever and Hamlett, 2002; Calsbeek *et al*., 2007), and have a longer life expectancy than the males (ca. 1.8 years; Schoener, and Schoener, 1982b; Schwartz and Henderson, 1991). Mating by males who remain in the maximal stage of spermatogenesis can therefore take place very late in the females' reproductive cycle. Males can therefore very likely still fertilize some of the eggs that would be laid at the start of the following high reproductive period. The decline in the proportion of males in the maximal stage of spermatogenesis during the period August to December is very likely due to mortality among the large males reaching the end of their life expectancy.

The monthly proportion of reproductively active females had a significant positive correlation with the mean monthly temperature and photoperiod (Table 6.6). Similar results were noted in reproductive cycle studies involving *A. sagrei* females in Belize (Sexton and Brown, 1977), Florida (Lee *et al*., 1989), Hawaii (Goldberg *et al*., 2002), and Jamaica (Licht and Gorman, 1970). A study involving *A. carolinensis* from Louisiana found that a combination of photoperiodic and thermal cues initiated reproduction in spring and regression in autumn (Licht, 1973). The results of the study described herein suggest that this is also the case in *A. sagrei* females. Temperature plays an important role in the development of reptilian eggs, which tend to develop faster at higher temperatures within an acceptable temperature range wherein successful development can take place (Birchard, 2004). Considering that higher temperatures are associated with longer photoperiods, it is not surprising that there was a strong positive correlation between the photoperiod and the reproductive cycle of the *A. sagrei* females in this study. Timing reproduction to coincide with a period of longer day lengths also has other advantages. *Anolis sagrei* usually becomes active by mid morning and stays active until in the afternoon (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999). Longer daylight hours would therefore mean a longer period for foraging. As in the females of other *Anolis* species, *A. sagrei* females produce multiple clutches, consisting of a single egg, throughout the breeding season (Andrews and Rand, 1974), and the frequency at which these eggs are produced and deposited depends on both the available energy (Licht, 1974; Stamps, 1977; Stamps, 1984; Stamps and Tanaka, 1981; Guyer 1988; Warner *et al*., 2015) and the appropriate environment for oviposition (Brown and Sexton, 1973; Sanger *et al*., 2008). Even though these lizards evolved to produce a single-egg clutch size in order to reduce the female's reproductive burdon (Kratochvíl and Kubička, 2007), reproduction remains energy demanding for *A. sagrei* females (Cox and Calsbeek, 2010; Cox *et al*., 2010). Furthermore, as a short-lived species they need to maximize potential fecundity by allocating acquired energy mainly to reproduction (Vitt *et al*., 1977). Longer periods for foraging would make this possible for *A. sagrei* females.

Longer periods for foraging would also benefit immature *A. sagrei* males and females. Hatchlings and juveniles of this species have a faster growth rate than that of the adults (Schoener and Schoener, 1978; Cox *et al*., 2009; Wright *et al*., 2013; Norval *et al*., 2014), and longer periods available for foraging enables them to obtain enough prey (nutrition) to sustain their growth. Timing reproduction to coincide with a period of longer day lengths would thus also likely increase the likelihood of offspring to grow fast enough to become sexually mature within the fastest time possible.

The biochemical mechanism of storing energy (which can be utilised for growth, maintenance and or reproduction) as lipids, enable animals to accumulate and reserve large amounts of energy in a relatively small space (Derickson, 1976). Although lizards of the genus *Anolis* store lipids in various parts of their body, lipid contents of the abdominal fat bodies (corpora adiposa) and the liver undergo the most seasonal changes (Dessauer, 1955). The study by Dessauer (1955) found that in *A. carolinensis*, changes in glycogen, lipids, protein and water caused the seasonal variations in liver sizes, and of these, lipids caused the greatest change. This is most likely also the case in the livers of the *A. sagrei* specimens used in this study. The reptilian liver plays a vital role in the metabolism of bile acids, bile pigments, carbohydrates, hormones, lipids and proteins (Schaffner, 1998). In females, the liver is stimulated by estrogen to convert lipids from the abdominal fat bodies into vitellogin, which is then selectively absorbed from the bloodstream by the ovarian follicles during vitellogenesis (Schaffner, 1998; DeNardo, 1999; Zug *et al.*, 2001). As a result, the liver enlarges dramatically during the reproductive period (DeNardo, 1999), thus, during the storage and utilisation of lipids, the liver likely functions as an intermediary organ (Dessauer, 1955; Derickson, 1976; Cheng and Lin, 1987). The study described herein supports this since not just the females, but also the males, experienced a decrease in abdominal fat body weights and increase in the liver weights during the period of high reproductive activity, when the animals are expected to have a greater energetic demand. Additional support for this is the positive correlation between the monthly mean LWI and the monthly proportion of reproductively active lizards noted in both sexes.

From the dietary study involving the same specimens used in this study (Norval *et al*., 2010), it is apparent that foraging takes place throughout the year, and even though it is highly unlikely that the lizards could feed to satiation, it still suggests that prey availability does not appear to be a limiting factor for *A. sagrei* in southwestern Taiwan. Anoles (species belonging to the genera *Anolis* and *Norops*) in general tend to be opportunistic feeders (Losos, 2009), and are capable of rapid fattening at any time of the year if the opportunity exists (Licht, 1974). Still, it was observed that various proportions (7 – 67%) of specimens used in this study had no dissectible abdominal fat bodies during the period of high reproductive activity (Fig. 6.3). It has been noted that most anoles tend to be relatively lean during the high reproductive period, and fatter during the low reproductive period (Licht and Gorman, 1970). This indicates that the fat from the abdominal fat bodies, one of the two main fat storage depots in anoles (Dessauer, 1955), is an important source of energy for reproduction, suggesting that these lizards are capital breeders. However, if the abdominal fat bodies were the only source of energy during reproduction, it would be expected that they would gradually decrease and/or remain low in weight. As can be seen in the study described herein, as well as in other studies (Licht and Gorman, 1970; Sexton *et al*., 1971), this is not the case, indicating that *A. sagrei* and most (if not all) other anoles are to a certain extent also income breeders, i.e. they expend parts of their acquired energy from foraging for reproduction soon after that energy is acquired (Jönsson, 1997). A study by Warner and Lovern (2014), found that females provided with a large amount of food produced larger eggs and offspring than females that received a lesser amount of food, providing additional support for this conclusion. It can thus be concluded that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction.

Not all acquired energy is however allocated to reproduction, and in both sexes some of this energy is utilised for growth. As adults, body sizes in both sexes are important, and smaller-sized sexually mature *A. sagrei* can be expected to continue growing during the high reproductive period, but to a different extent. *Anolis sagrei* is a very territorial polygynous species (Evans, 1938; Schoener and Schoener, 1980; Schoener and Schoener, 1982a; Scott, 1984; Les, 2013), and in the males body size is crucial since larger males tend to be more successful in establishing and defending territories (Tokarz, 1985). A study involving *Anolis cristatellus* found that when supplementary food was provided towards the end of the breeding season males shunted the extra energy into growth and the depositing of lipids in the abdominal fat bodies (Guyer, 1988), while a similar study involving *Norops humilis* during the breeding season also found that additional energy was shunted into growth (Licht, 1974). This suggests that irrespective of when the food is available, once the demands for reproduction have been met the additional energy is shunted into growth. In *A. sagrei*, it was found that either in the absence of competition or with an overabundance of prey, males also grew larger as a result of more available food (Schoener and Schoener, 1978; Campbell, 1999). This suggests that once the demands for reproduction have been met, *A. sagrei* males can be expected to direct available energy towards growth, which continues throughout the life of the animal

(Schoener and Schoener, 1978; Cox *et al*., 2009).

However, the reduction in stored abdominal fat-body mass that reproductively active *A. sagrei* males undergo at the onset of the high reproductive period can not only be due to growth. Rather than having a pure dominance hierarchy, *A. sagrei* males tend to occupy territories that overlap with the territories of one or more females, which in turn have relatively overlapping territories themselves, and sometimes overlap the territories of more than a single male (Schoener and Schoener, 1980; Schoener and Schoener, 1982a). At the onset of the high reproductive period males experience a reduction in stored abdominal fat-body mass (Licht and Gorman, 1970; Sexton and Brown, 1977; Lee *et al*., 1989; Tokarz *et al*., 1998; Sanz Ochotorena and Uribe Aranzábal, 1999), indicating that in addition to spermatogenesis, the expenditure of energy during territorial conflicts and territorial displays, combined by the loss of possible foraging opportunities during these activities, are energetically costly for the males. In many *Anolis* species males spend less time foraging and more time displaying during the breeding season (Losos, 2009). The high proportions of males with no dissectible abdominal fat bodies during the period of high reproductive activity (March to August) (Fig. 6.3) suggest this is more than likely also the case in *A. sagrei*.

The lack of a correlation between the monthly mean AFBWI and the monthly proportion of reproductively active males is thus more than likely due to the fact that lipids are not only utilised for reproduction and that aspects such as growth also greatly contribute to the depletion of energy reserves. The correlation between the monthly mean AFBWI of the males and the monthly mean photoperiod is very likely because during the periods of relatively long photoperiods the lizards are in a high reproductive activity period, during which males expend most energy on growth, spermatogenesis, territorial conflicts, and territorial displays.

Although *A. sagrei* females are also territorial (Evans, 1938; Scott, 1984), growth in smaller-sized adults is to increase reproductive output rather than for establishing and defending territories as in the males. A female lizard's body volume constrains the available space for developing eggs (Du *et al*., 2005). *Anolis sagrei* females produce multiple clutches, each consisting of a single egg, which are produced at one to two week intervals, depending on the body size of the female and environmental factors such as food availability and rainfall (Cox and Calsbeek, 2010). Due to the relatively more available capacity, larger females are able to produce eggs in quicker succession under favourable conditions. As a result, after the requirements for maintenance and reproduction have been met, smaller females can be expected to allocate energy towards growth, but as females reach a size at which egg production rates can be increased, reproduction becomes a priority and growth rates decline dramatically as more energy is allocated to reproduction (Schoener and Schoener, 1978; Cox *et al*., 2009; Norval *et al*., 2014).

In *A. sagrei* females energy is evidently primarily allocated to reproduction, so it is not surprising that significant negative correlations were noted between the monthly mean AFBWI and the monthly proportion of reproductively active females, as well as between the monthly mean AFBWI and the monthly mean photoperiods and monthly mean temperatures, which determine the period of high reproductive activity.

Although no correlation was found between the monthly proportion of reproductive lizards, monthly AFBWI, or monthly LWI of both sexes, the importance of precipitation should not be ignored. As in Belize (Sexton and Brown, 1977), Florida (Lee *et al*., 1989), and Jamaica (Licht and Gorman, 1970), the period of maximal reproductive activity in the females in this study coincided with the rainy season. And even though the study in Hawaii (Goldberg *et al*., 2002), has found that the period of maximumal reproductive activity in that locality is during the dry season, it must be noted that *A. sagrei* females prefer nest sites with a relatively high humidity, and that compared to the hatchlings from eggs that are deposited in relatively dry nests (≤ 50 % moisture), hatchlings from eggs that are deposited in moist nests (*ca*. 75 % moisture) have greater hatching success, tend to be larger, and have overall increased survival rates (Warner *et al*., 2012; Reedy *et al*., 2013). Also, Brown and Sexton (1973) found that females tend to deposit their eggs in an environment that has a relatively high humidity. A study involving *Anolis aeneus* also found that moisture was crucial for juvenile growth, and that even when food was in abundance they can not grow rapidly when water is limited (Stamps and Tanaka, 1981). Moisture is also important for many insects (i.e. potential prey), since in dry periods their eggs become quiescent, while at optimum moisture levels the larvae develop quickly (Smith, 1996). It has also been found that in tropical areas, during the dryer seasons, insect abundance tends to be higher in moist localities (Janzen and Schoener, 1968; Janzen, 1973), and many ant species are relatively intolerant of desiccation and therefore prefer moister environments and usually increase in abundance during the rainy season (Kaspari and Weiser, 2000). Therefore, although it does not regulate the reproductive cycles of *A. sagrei*, precipitation plays direct (e.g. nest environment) and indirect roles (e.g. abundence of potential prey) in the reproduction of this species.

Precepitation may also impact reproduction in a negative way. The abdominal fat body weights of both sexes in this study were minimal in July, after a period (May to June) in which the fat bodies were increasing in weight (Fig. 6.4 and 6.6). As opposed to most years, in which August is the month with the highest recorded rainfall, during the study period July was the month with the highest recorded monthly mean rainfall, which was a result of typhoons Rammasun and Nakri that passed and affected Taiwan. This indicates that during the period of high reproductive activity, environmental conditions such as prolonged periods of rainfall, which for *A. sagrei* is unfavourable for foraging (Schoener, 1968), can cause rapid decreases in the abdominal fat body weights (i.e. energy reserves), and thus potentially influence the reproductive output.

Because reproduction is energetically demanding for both *A. sagrei* males and females, and since in short-lived species like *A. sagrei* energy is only diverted away from reproduction and towards other bodily functions once the demands for reproduction has been met (Vitt *et al.*, 1977), it is surprising that in this study no significant differences were found in the monthly mean AFBWI and monthly mean LWI of lizards that had not experienced tail autotomy and those that had. The regeneration of an autotomized tail would require energy and material, diverted from other bodily functions, or from increased food intake (Ballinger and Tinkle, 1979; Althoff and Thompson, 1994). In a study by Norval *et al*. (2014), it was found that *A. sagrei* males and females that had experienced tail autotomy had a lower monthly growth rate, which suggests that energy was being diverted away from growth for the regeneration of an autotomized tail. Still, the differences in growth rates were not statistically significant (Norval *et al*., 2014). An important limitation in this study is that the specific timing of tail regeneration is mostly unknown and that tail regeneration did not always coincide with that of the different captured lizards. This in it self could be why the effects of tail regeneration are not that apparent in this stufy. Still, it is unlikely that the energy for tail regeneration is only from energy diverted away from growth. Since it has been found that when enough food is available, in some lizards the reduced body growth rate during tail regeneration can be minimized (Ballinger and Tinkle, 1979), it is very likely that the results of this study is the result of a combination of energy diverted away from growth and an increase in foraging in the *A. sagrei* specimens that experienced tail autotomy and tail regeneration.

The reproductive strategies of lizards usually entail either maturing early, having relatively short lives, and being highly fecund (often as a result of producing multiple clutches per breeding season); or maturing later, having relatively long lives as reproductive adults, reproducing less often during the reproductive season, and producing few offspring per reproductive bout (Tinkle, 1969; Tinkle *et al*., 1970). Both sexes of *A. sagrei* have a life expectancy of less than two years (Schoener, and Schoener, 1982b; Schwartz and Henderson, 1991), and although the females produce clutches consisting of a single egg, under favourable conditions they are able to produce a clutch at one to two week intervals (Cox and Calsbeek, 2010), which means these lizards can be potentially highly fecund. So in conclusion, this study not only provides additional support for the conclusion that photoperiods and the associated temperatures determine the reproductive cycles in *A. sagrei*, but also that *A. sagrei* is a typical short-lived species. This study also demonstrated that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction, which is energetically demanding for both sexes of this species.

6.4. REFERENCES

Althoff, D.M., and Thompson, J.M. 1994. The effects of tail autotomy on survivorship and body growth of *Uta stansburiana* under conditions of high mortality. *Oecologia* 100: 250-255.

Andrews, R., and Rand, A.S. 1974. Reproductive effort in anoline lizards. *Ecology* 55: 1317-1327.

Ballinger, R.E., and Tinkle, D.W. 1979. On the cost of tail regeneration to body growth in lizards. *Journal of Herpetology* 13: 374-375.

Birchard, G.F. 2004. *Effects of incubation temperature*. pp. 103-123. In: Deeming, D.C. (ed.) 2004. *Reptilian Incubation: Environment, Evolution, and Behaviour*. Nottingham University Press, Nottingham.

Brown, K.M., and Sexton, O.J. 1973. Stimulation of reproductive activity of female *Anolis sagrei* by moisture. *Physiological Zoology* 46: 168-172.

Calsbeek, R., Bonneaud, C., Prabhu, S., Manoukis, N., and Smith, T.B. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards.

Evolutionary Ecology Research 09: 495-503.

Campbell, T. 1999. Consequences of the Cuban brown anole invasion in Florida: it's not easy being green. *Anolis Newsletter* 05: 12-21.

Cheng, H.Y., and Lin, J.Y. 1987. Annual ovarian, fat body and liver cycles of the grass lizard *Takydromus stejnegeri* in Taiwan. *Zoological Science* 04: 557-561.

Cox, R.M., and Calsbeek, R. 2010. Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution* 64: 1321-1330.

Cox, R.M., Parker, E.U., Cheney, D.M., Liebl, A.L., Martin, L.B., and Calsbeek, R. 2010. Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Functional Ecology* 24: 1262-1269.

Cox, R.M., Stenquist, D.S., and Calsbeek, R. 2009. Testosterone, growth and the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* 22: 1586-1598.

Delaney, D.M., Reedy, A.M., Mitchell, T.S., Durso, A.M., Durso, K.P., Morrison, E.J., and Warner, D.A. 2013. *Anolis sagrei* (Brown anole). Nest-site choice. *Herpetological Review* 44: 314.

DeNardo, D. 1999. *Reproductive biology*. pp. 212-224. In: Mader D.R. (ed.) 1999. *Reptile Medicine and Surgery*. Saunders, Philadelphia.

Derickson, W.K. 1976. Lipid storage and utilization in reptiles. *American Zoologist* 16: 711-723.

Dessauer, H.C. 1955. Seasonal changes in the gross organ composition of the lizard, *Anolis carolinensis*. *Journal of Experimental Zoology* 128: 1-12.

Du, W., Ji, X., and Shine, R. 2005. Does body volume constrain reproductive output in lizards? *Biology Letters* 1: 98-100.

Evans, L.T. 1938. Cuban field studies on territoriality of the lizard, *Anolis sagrei*. *Journal of Comparative Psychology* 26: 97-125.

Fox, W. 1963. Special tubules for sperm storage in female lizards. *Nature* 198: 500-501.

Goldberg, S.R., Kraus, F., and Bursey, C.R. 2002. Reproduction in an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawaii. *Pacific Science* 56: 163-168.

Guyer, C. 1988. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* 69: 362-369.

Janzen, D.H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54: 687-708.

Janzen, D.H., and Schoener, T.W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96-110.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78: 57-66.

Kaspari, M., and Weiser, M.D. 2000. Ant activity along moisture gradients in a neotropical forest. *Biotropica* 32: 703-711.

Kratochvíl, L., and Kubička, L. 2007. Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. *Functional Ecology* 21: 171-177.

Lee, J.C., Clayton, D., Eisenstein, S., and Perez, I. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989: 930-937.

Les, A.M. 2013. *Anolis sagrei* (Cuban brown anole). Aggressive behavior.

Herpetological Review 44: 137-138.

Licht, P. 1967a. Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. I. Interaction of light and temperature in the initiation of testicular recrudescence. *Journal of Experimental Zoology* 165: 505-516.

Licht, P. 1967b. Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. II. Seasonal variations in the effects of photoperiod and temperature on testicular recrudescence. *Journal of Experimental Zoology* 166: 243-253.

Licht, P. 1969. Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. III. Temperature thresholds for photoperiodism. *Journal of Experimental Zoology* 172: 311-322.

Licht, P. 1971. Regulation of the annual testis cycle by photoperiod and temperature in the lizard *Anolis carolinensis*. *Ecology* 52: 240-252.

Licht, P. 1973. Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* 1973: 465-472.

Licht, P. 1974. Response of *Anolis* lizards to food supplementation in nature. *Copeia* 1974: 215-221.

Licht, P. and Gorman, G.C. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *University of California Publications in Zoology* 95: 1-52.

Licht, P. and Pearson, A.K. 1969. Effects of mammalian gonadotropins (FSH and LH) on the testes of the lizard *Anolis carolinensis*. *General and Comparative Endocrinology* 13: 367-381.

Losos, J.B. 2009. *Lizards in an Evolutionary Tree*: *Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, California.

Norval, G., Goldberg, S.R., and Mao, J.J. 2012. The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan. *Russian Journal of Herpetology* 19: 75-81.

Norval, G., Hsiao, W.F., Huang, S.C., and Chen, C.K. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russian Journal of Herpetology* 17: 131-138.

Norval, G., Huang, S.C., and Mao, J.J. 2014. Notes on the growth rates of *Anolis sagrei* Duméril & Bibron, 1837, from a small betelnut palm (*Areca catecha*, L) plantation in southwestern Taiwan. *IRCF Reptiles & Amphibians* 21: 9-15.

Norval, G., Tung, C.L., and Cooper, J.E. 2005. A report of hepatic granuloma in free-living brown anoles (*Anolis sagrei*) in Taiwan: two cases. *Herpetological Bulletin* 93: 9-13.

Norval, G., Tung, C.L., and Cooper, J.E. 2006. *Anolis sagrei* (Brown anole). Testicular pathology. *Herpetological Review* 37: 219-220.

Reedy, A.M., Zaragoza, D., and Warner, D.A. 2013. Maternally chosen nest sites positively affect multiple components of offspring fitness in a lizard. *Behavioral Ecology* 24: 39-46.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of Florida, Gainesville, Florida.

Sanger, T.J., Hime, P.M., Johnson, M.A., Diani, J., and Losos, J.B. 2008. Laboratory protocols for husbandry and embryo collection of *Anolis* lizards. *Herpetological Review* 39: 58-63.

Sanz Ochotorena, A., and Uribe Aranzábal, M.C. 1999. Ciclo gonadal y de los cuerpos grasos de *Anolis sagrei* (Sauria: Iguanidae) en Ciudad de La Habana. *Revista de Biología* 13: 26-32. (In Spanish)

Schaffner, F. 1998. *The liver*. pp. 485-531. In: Gans, C., and Gaunt, A.S. (eds.) 1998. *Biology of the Reptilia*. Vol. 19. Society for the Study of Amphibians and Reptiles, New York.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.

Schoener, T.W., and Schoener, A. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978: 390-405.

Schoener, T.W., and Schoener, A. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *Journal of Animal Ecology* 49: 19-53.

Schoener, T.W., and Schoener, A. 1982a. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* 63: 809-823.

Schoener, T.W., and Schoener, A. 1982b. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* 39: 1-16.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Scott, M.P. 1984. Agonistic and courtship displays of male *Anolis sagrei*. *Breviora* 479: 1-22.

Sever, D.M., and Hamlett, W.C. 2002. Female sperm storage in reptiles. *Journal of Experimental Zoology* 292: 187-199.

Sexton, O.J., and Brown, K.M. 1977. The reproductive cycle of an iguanid lizard *Anolis* *sagrei*, from Belize. *Journal of Natural History* 11: 241-250.

Sexton, O.J., Ortleb, E.P., Hathaway, L.M., Ballinger, R.E., and Licht, P. 1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. *Ecology* 52: 201-215.

Smith, R.L. 1996. *Ecology and Field Biology. 5th Edition*. Addison-Wesley Educational Publishers, Inc., New York.

Stamps, J., and Tanaka, S. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). *Ecology* 62: 33-40.

Stamps, J.A. 1977. Rainfall, moisture and dry season growth rates in *Anolis aeneus*. *Copeia* 1977: 415-419.

Stamps, J.A. 1984. Growth costs of territorial overlap: experiments with juvenile lizards (*Anolis aeneus*). *Behavioral Ecology and Sociobiology* 15:115-119.

Tinkle, D.W. 1969. The concept of reproductive effort and its relation to the evolution of life histories in lizards. *American Naturalist* 103: 501-516.

Tinkle, D.W., Wilbur, H.M., and Tilley, S.G. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24: 55-74.

Tokarz, R.R. 1985. Body size as a factor determining dominance in staged agonistic encounters between males brown anoles (*Anolis sagrei*). *Animal Behaviour* 33: 746-753.

Tokarz, R.R., McMann, S., Seitz, L., and John-Adler, H. 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*). Physiological Zoology 71: 139-146.

Vitt, L.J., Congdon, J.D., and Dickson, N.A. 1977. Adaptive strategies and energetics of tail autonomy in lizards. *Ecology* 58: 326-337.

Warner, D.A., Buckelew, A.M., Pearson, P.R., and Dhawan, A. 2015. The effect of prey availability on offspring survival depends on maternal food resources. *Biological Journal of the Linnean Society* 115: 437-447.

Warner, D.A., and Lovern, M.B. 2014. The maternal environment affects offspring viability via an indirect effect of yolk investment on offspring size. *Physiological and Biochemical Zoology* 87: 276-287.

Warner, D.A., Moody, M.A., Telemeco, R.S., and Kolbe, J.J. 2012. Egg environment have large effects on embryonic development, but have minimal consequences for hatchling phenotypes in an invasive lizard. *Biological Journal of the Linnean Society* 105: 25-41.

Wright, A.N., Piovia-Scott, J., Spiller, D.A., Takimoto, G., Yang, L.H., and Schoener, T.W. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. *Oikos* 122: 1496-1504.

Zug, G.R., Vitt, L.J., and Caldwell, J.P. 2001. *Herpetology. An Introductory Biology of Amphibians and Reptiles. 2nd Edition*. Academic Press, San Diego.

CHAPTER 7 – GENERAL DISCUSSION AND CONCLUSION

7.1. DISCUSSION

Both native and exotic species colonise new habitats, and when such species are able to disperse without significant human assistance and have a large impact on the new environments, they are considered to be invasive species (Davis and Thompson, 2000). Human mediated introductions of exotic species into new habitats can be accidental and/or intentional. Accidental introductions usually involve the unintentional release of invertebrates and pathogens (Levin, 1989). Intentional introductions normally involve species that are imported for a limited purpose, but which then escape, or organisms (usually plants and vertebrates) that are deliberately introduced into the natural landscape for a particular reason (Levin, 1989). Since the introduction and spread of animals, pathogens, and plants into non-native environments is believed to pose a significant threat to biodiversity (Sala *et al*., 2000), the introduction of non-native species into areas where they do not naturally occur should be avoided and discouraged as far as possible.

Anolis sagrei, which is believed to have originated in Cuba, is a very successful coloniser, and has dispersed to various islands around Cuba and in the Bahamas, as well as the Atlantic coast of México to Belize (Williams, 1969; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999). This species is a habitat generalist that tends to favour open sunny habitats and areas disturbed by human activities, such as agricultural practices and urbanisation (Ruibal, 1964; Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Lee, 2000; Meshaka *et al*., 2004). Being a habitat generalist and human commensal, are characteristics of many invasive vertebrates (Meshaka *et al*., 2004). Being human commensal often results in a species being accidentally and/or intentionally introduced into new localities, and a habitat generalist has an increased probability of surviving when it is introduced into such localities (Meshaka *et al*., 2004). In addition to this, since human activities alter natural habitats in such a way that they often become unsuitable for native species, such activities result in a subsequent reduction in the potential competitors and/or predators of invasive species that are being introduced into and/or are living in areas disturbed by human activities (Meshaka *et al*., 2004). It is thus not surprising that A. sagrei is a well-documented example of a very successful invasive vertebrate, and introduced populations have been recorded in parts of the Americas, and even the Pacific islands of Hawaii, Singapore, and Taiwan (Kraus, 2009; Tan and Lim, 2012).

The study discussed herein found that in Taiwan *A. sagrei* occurs primarily in areas disturbed by human activities in urban and rural agricultural areas, and that these lizards are rare in areas overgrown by vegetation and absent in secondary forests. In urban areas, the lizards were primarily found in parks and some gardens, while in rural agricultural areas, they tend to inhabit habitats, such as betel nut palm (*Areca catechu*) plantations, which are fairly open and has some structures (trunks of the palms) that can be used as perches. A study pertaining to the dispersal patterns of *A. sagrei* in the southwestern study site also found the occurance of these lizards is limited to disturbed habitats (Wang, 2013). The study also found that the dispersal of *A. sagrei* is north-westwards, towards the neigbouring urban areas of Chiayi City (Wang, 2013). Due to severe human population pressure, the lowland areas of Taiwan have been extensively developed, and currently no pristine lowland forests remain, with patches of secondary forests being restricted to the foothills (Lee *et al*., 2004). Many parts of the lowland areas of Taiwan are thus potenial habitats that *A. sagrei* can colonise. As a result, it is possible that *A. sagrei* occurs in some unrecorded localities in Taiwan and that the distribution of this species thus extends beyond the estimated 237 hectares in the southwestern study site and eight hectares in the eastern study site.

Anolis sagrei is a sit-and-wait (ambush) predator, with a catholic diet, which primarily includes a variety of invertebrates, but may also occasionally include smaller lizards, fruit, and sap (Schoener, 1968; Rodriguez Schettino, 1999; Norval *et al*., 2010; Holbrook, 2012; Norval and Mao, 2013). There are also spatial variations in the diet composition of *A. sagrei* (Schoener, 1968; Huang *et al*., 2008b; Norval *et al*., 2010), indicating that this lizard is an opportunistic switching predator that preys primarily on whichever prey types are the most abundant in a particular habitat. Being a dietary generalist is one of the main characteristics of successful invasive vertebrates (Ehrlich, 1989; Pullin, 2002), and the presence of adequate food in the area where an introduced species has been introduced into increases the ability of the species to survive, even if it has no particular competitive advantage over local similar species (Van Driesche and Van Driesche, 2000). In *A. sagrei* an abundance of prey can lead to increased growth rates (Schoener and Schoener, 1978a; Cox *et al*., 2010; Norval *et al*., 2014b) and in females greater fecundity (Wright *et al*., 2013).

A very successful predator could severely impact local ecosystems (Zug *et al*., 2001), because they reduce the population sizes of certain prey species and alter ecological traits of prey individuals, and may increase the risks of extinction of certain prey species (Schoener *et al*., 2001; Schoener *et al*., 2002). In studies done in the Bahamas, it was found that through predation, *A. sagrei* impacted terrestrial ecosystems by reducing spider abundances (Spiller and Schoener, 1990; Spiller and Schoener, 1995; Schoener and Spiller, 1999a; Spiller and Schoener 2001) and excluding (i.e. local extinction) rare spider species (Schoener and Spiller, 1996; Spiller and Schoener, 1998). These lizards also increased the abundence of certain arthropods by reducing the spiders that prey on them (Spiller and Schoener, 1994). The effects of *A. sagrei* on the spiders and arthropod communities in these studies were however often weak or variable (Schoener and Spiller, 1999b; Spiller and Schoener 2001). It was also found that arthropod communities on smaller islands were impacted more than those on larger islands (Schoener and Spiller, 1999b). Similarly, in studies done in the southwestern study site, in which *A. sagrei* was either present (at natural densities) in or exluded from enclosures, it was also found that through predation *A. sagrei* impacted ant and ground-living spider communities by reducing the abundence of certain species (Huang *et al*., 2008a; Huang *et al*., 2008b). In spite of these impacts on the ant and ground-living spider communities, no significant effect was noted on collembola communities or leaf litter decomposition rates (i.e. nutrient cycling) (Huang, 2007a). The effects of *A. sagrei* on terrestrial food webs in Taiwan are thus also likely weak.

Some exotic invaders can be so competitive that they may persist by taking over the habitats of resident species through direct competition (Shigesada and Kawasaki, 1997). Studies conducted in the Bahamas found that where some spiders are sympatric with *A. sagrei*, the adult females of these spiders had a reduced cephalothorax width (i.e. have a reduced body size) and they were less fecund, which indicates that in addition to direct predation, the lizards also impacted the spiders by competing with them for prey (Spiller and Schoener, 1988; Spiller and Schoener, 1990). Such competition is not limited to only spiders. Studies involving *A. sagrei* and other anole species in the Americas have found that some species, such as the green anole (*Anolis carolinensis*) and Cayman blue-throated anole (*Anolis conspersus*), become more arboreal in habitats that are being invaded by *A. sagrei* (Collette, 1961; Losos *et al*., 1993; Campbell, 1999). This indicates that *A. sagrei* is an aggressive competitor, which may force some other species of lizards from their habitats. In the study discussed herein, *Eutropis longicaudata*, *Japalura swinhonis*, and *Plestiodon elegans* were also found to occur in areas disturbed by human activities in both study sites, and in the southwestern study site *Sphenomorphus indicus* was observed in the edges (ecotones) of the secondary forest fragments and other shady habitats. Since many of the prey types reported from studies pertaining to the diets of these lizards were also recorded as prey types of *A. sagrei* (Schoener, 1968; Shieh *et al*., 1986; Zhang and Ji, 2004; Huang, 2006; Huang, 2007b; Kuo *et al*., 2007; Huang *et al*., 2008b; Norval *et al*., 2010; Norval *et al*., 2012b; Norval *et al*., 2012c), it is likely that in the habitats in Taiwan where these lizards are sympatric, there is possibly competition for at least some prey types. In particular, there is a substantial dietary niche overlap, and therefore likely competition, between *A. sagrei* and the endemic trunk-ground species, *J. swinhonis* (Norval *et al*., 2012c).

However, because some exotic invasive species may persist by coexisting with the resident species after establishment, and/or by moving into open spaces (vacant niches) that arise either occasionally or periodically (Shigesada and Kawasaki, 1997), not all exotic invasive species represent a serious extinction threat to most native species (Davis *et al.*, 2011). *Anolis cristatellus* and *A. sagrei* adults are similar in size (Lee, 2000) and both species utilise the same structural habitat (Schoener and Schoener, 1971a; Schoener and Schoener, 1971b). In southern Florida (U.S.A.) where both species are exotic invasive species, in habitats where *A. cristatellus* and *A. sagrei* are sympatric, *A. sagrei* is more terrestrial as a result of competition for basking sites (Salzburg, 1984). Studies done in the Bahamas found that when the northern curly-tailed lizard (*Leiocephalus carinatus*), a competitor and predator of *A. sagrei* (Schoener *et al.*, 1982), was released into habitats in which *A. sagrei* occurs, *A. sagrei* became more arboreal (Schoener *et al.*, 2001; Schoener *et al.*, 2002). In Bimini it was also found that in the presence of competition from sympatric anole species (but all different ecomorphs: *Anolis angusticeps* – twig species, *Anolis carolinensis* – trunk-crown species, *Anolis distichus* – trunk species, and *A. sagrei* – trunk-ground species), *A. sagrei* tends to be more arboreal, which results in reduced foraging opportunities and a subsequent reduction in the sizes of these lizards (Schoener and Schoener, 1978a). This indicates that *A. sagrei* is not always able to out-compete other lizard species.

A variety of frog and lizard species (excluding *A. sagrei*) have been recorded in the southwestern (frogs = 10 species; lizards = 9 species) and eastern study site (frogs = 4 species; lizards = 8 species), so some competition for prey between *A. sagrei* and these native species in habitats where they co-occur is very likely. Although many of the frogs, especially microhylids (family: Microhylidae) and froglets of *Duttaphrynus melanostictus* and *Fejervarya limnocharis* (Norval *et al*., 2014c), prey on many of the same prey types as *A. sagrei*, the frogs are usually nocturnal so competition between them and *A. sagrei* is likely very limited. Since the gecko (family: Gekkonidae) species recorded in the study sites are also primarily nocturnal, competition between them and *A. sagrei* is also likely limited. Some diurnal lizard species, such as *S. indicus* and the grass lizards (*Takydromus* spp.) tend to inhabit habitats in which *A. sagrei* is usually rare or absent, so there is also likely limited competition between them and *A. sagrei*. All the other lizard species usually grow to larger sizes than *A. sagrei* and are aggressive territorial species (Shang and Lin, 2001). In the few instances in which *A. sagrei* was observed being approached by *E. longicaudata*, *J. swinhonis*, and *P. elegans*, *A. sagrei* was the species that retreated (Norval *et al*. 2004; Norval *et al*. 2012c; Norval *et al*. 2012d), which suggests that it is unlikely that *A. sagrei* can outcompete these species.

One of the main characteristics of the majority of successful invasive vertebrates is that they have a relatively high reproductive rate, which enables them to build up a large population under favourable conditions (Pullin, 2002). Throughout its distribution range (native and introduced), the reproductive biology of *A. sagrei* is very similar (Licht and Gorman, 1970; Sexton and Brown, 1977; Lee *et al*., 1989; Rodriguez Schettino, 1999; Sanz Ochotorena and Uribe Aranzábal, 1999; Goldberg *et al*., 2002b; Norval *et al*., 2012a). *Anolis sagrei* males and females rarely live for more than two years (Schoener and Schoener, 1982; Schwartz, and Henderson, 1991), and under favourable conditions they can reach sexual maturity within a year after hatching (Wright *et al*., 2013). Because *A. sagrei* females have the ability to store sperm for several weeks (Fox, 1963; Sever and Hamlett, 2002; Norval *et al*., 2012a), and since they often mate with multiple males (Calsbeek *et al*., 2007), the eggs can be fertilised by different males and as a result the offspring are usually genetically diverse. Although the clutch size of *A. sagrei* is fixed and always consists of a single egg, multiple clutches are produced at frequent intervals (*ca*. 1 to 2 weeks) throughout a fairly long reproductive period (Andrews and Rand, 1974; Cox and Calsbeek, 2011; Norval *et al*., 2012a), making this species highly fecund. For example, in the study done by Campbell (1999), 40 *A. sagrei* were released onto a small island and by 1998 the population had grown to more than 400 individuals. The high fecundity of *A. sagrei* makes it possible for them to build up large populations in a relatively short period of time, and the multiple paternity and sperm storage enables them to minimize genetic diversity losses during demographic founder events (Eales *et al.*, 2008). These characteristics contribute to the high success of *A. sagrei* as an invasive species, since in suitable habitats even relatively small numbers of introduced individuals can establish a founder population.

As can be expected, the high fecundity of *A. sagrei* comes at a cost. The changes in the abdominal fat bodies and liver weights during the reproductive cycle indicate that both these lipid storage depots provide energy during reproduction. Since *A. sagrei* adults tend to be fatter during the low reproductive period and leaner during the high reproductive period (Licht and Gorman, 1970; Sexton *et al*., 1977; this study), it is evident that reproduction is energetically demanding. However, *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction, which therefore enables this species to maintain high fecundity even when the stored energy reserves (lipids in the abdominal fat bodies and liver) become depleted.

Another direct and/or indirect factor that can contribute to the success of a species as an exotic invader is parasites. Parasites potentially play a role in the establishment and success of exotic invasive species, because due to a reduced probability of the introduction of parasites with exotic species or early extinction after the establishment of the host due to the absence of other required hosts in the new location (Torchin *et al*., 2003), introduced species tend to be liberated from many parasites (i.e. enemy release hypothesis) from their native range (Torchin *et al*., 2003; Prenter *et al*., 2004; Horwitz and Wilcox, 2005; Miura *et al*., 2006) when they are introduced into new localities. The liberation of an introduced species from many parasites from its native range may allow it to grow to larger sizes than in its native range (e.g. Torchin *et al*., 2001), and thus enable them to be more competitive. When considering that 43 species of parasites have been reported from *A. sagrei* throughout its native and introduced range (Schwartz and Henderson, 1991; Rodriguez Schettino, 1999; Norval *et al*., 2011a), but only four parasite species were recorded from *A. sagrei* in Taiwan (Norval *et al*., 2011a; Norval *et al*., 2014a), it is clear that these lizards have been liberated from many of their parasites. Campbell and Echternacht (2003) found that *A. sagrei* from the population in the southwestern study site grow to larger sizes than in its native range. *Anolis sagrei* in both study sites of the study described herein are infected by the same common parasite species (Norval *et al*., 2014a). The study described herein found that the specimens from the eastern study site were significantly smaller than those collected in the southwestern study site, which suggests that the larger sizes of the specimens from the southwestern study site is thus likely due to reduced competition rather than a liberation from parasites.

Exotic invasive species can have an advantage over local species since there may also be an absence of transmission routes that could be specific to native hosts and thus protect introduced species from native parasites (Prenter *et al*., 2004; Horwitz and Wilcox, 2005), or the host-specific limitations of native parasites adapting to new hosts (Torchin *et al*., 2003), which could prevent them from infecting the introduced species. A very likely example of this is the nematodes, *Pseudabbreviata yambarensis* and *Strongyluris calotis*, which are very common in *J. swinhonis*, a species that is very often sympatric with *A. sagrei* in the southwestern study site and which also has a very similar diet as *A. sagrei*, but has not been found in any of the *A. sagrei* examined to date (Norval *et al*., 2014a).

Still, parasites may be introduced into new localities along with introduced species, and when naïve host populations are infected by a new parasite, transported along with introduced hosts, the invasive host species may acquire an advantage over the local species, which would contribute to the success of the invasion process (Prenter *et al*., 2004; Horwitz and Wilcox, 2005). Some helminths have been reported to have been introduced along with *A. sagrei* into Grand Cayman Island, Hawaii and Taiwan (Goldberg *et al*., 1995; Goldberg and Bursey, 2000; Goldberg *et al*., 2002a; Norval *et al*., 2011a). The nematode, *Cyrtosomum penneri*, which was introduced into Taiwan along with *A. sagrei* (Norval *et al.*, 2011a), however is transmitted from one host to another during copulation (Norval *et al.*, 2011a; Langford *et al.*, 2013) and appears to have a fair degree of host specificity (Langford *et al.*, 2013), so the spread of *C. penneri* to native lizard species in Taiwan is thus suggested to be unlikely (Norval *et al.*, 2014a). Because *C. penneri* most likely only reach their greatest intensity (i.e. the number of individuals infecting a host) just before the natural death of the *A. sagrei* host (Norval *et al.*, 2011a), and since there is a possibility that they are commensal rather than parasitic (Baer, 1951), they are unlikely to have any negative impact on the population size of *A. sagrei* in Taiwan.

Under some conditions exotic invasive species can acquire non-host-specific parasites from the new locality into which they have been introduced (e.g. Rolbiecki, 2006). An example of such instances is the digenean, *Mesocoelium sociale*, and the pentastome, *Kiricephalus pattoni* that have been recorded as acquired parasites of *A. sagrei* in the southwestern study site (Norval *et al.*, 2009a; Norval *et al.*, 2011a; Norval *et al.*, 2014a). Although infections by *K. pattoni* can be expected to be detrimental to the *A. sagrei* host due to the damage the parasite causes to internal organs as it migrates through the host's body (e.g. Norval *et al.*, 2009a), these parasites have not yet been recorded from *A. sagrei* in the eastern study site. Their infection frequencies are relatively low in the *A. sagrei* population in the southwestern study site, and thus have no observed significant impact on the *A. sagrei* populations in Taiwan (Norval *et al.*, 2011a; Norval *et al.*, 2014a; Norval, *pers. obs.*).

In dealing with invasive species, eradication is generally considered to be the favoured approach (Zavaleta *et al*., 2001), but considering that most successful eradications of invasive species have been confined to small islands (Zavaleta *et al*., 2001), and that the largest proportion of invasive species are those that exist in vacant niches and/or that coexist with native species (Williamson, 1999; Davis *et al*., 2011), it has been argued that eradication efforts should be directed at those species that cause serious ecological and/or financial losses (Davis *et al*., 2011). Since late 2007 actions have been in place to attempt to eradicate *A. sagrei* in Taiwan by capturing them. For example, in the southwestern study site, during the period 2009 to 2011, the local authorities paid a bounty to members of the general public for every *A. sagrei* they collected. During this three-year period, the authorities spent N.T.$ 4 825 050 (*ca*. R 1 500 000) on eradication efforts, and 418 299 *A. sagrei* were collected. Although ambitious, such actions are unrealistic because it would be impossible to remove every existing specimen. Some religious groups are against the killing of animals and do not permit the capturing of these lizards on their properties (Norval, *pers. obs*.). Even in areas where the capturing of the lizards is permitted it is difficult to collect all the individuals present. *Anolis sagrei* that have escaped after being captured tend to flee from a perceived threat at greater distances (Regalado, 1998), which means that such individuals could persist in an area without the collectors being aware of them. These lizards are also opportunistic and can utilise a variety of natural and man-made structures (such as embankment drainage pipes) as shelters, many of which would hinder the capturing of lizards. In addition to that, some agricultural practices such as the use of greenhouses can act as reservoirs for these lizards

(Norval *et al*. 2013). It is also possible for *A. sagrei* to exist in small numbers in habitats that may seem unsuitable. It is thus not surprising that in spite of the large numbers of lizards removed, to date, *A. sagrei* still exists in the southwestern and eastern study site and seems to be expanding its distribution range in Taiwan (Wang, 2013).

When dealing with invasive species, management approaches should be based on a scientific basis and not necessarily on the origin of a species (Davis *et al*. 2011), because where multiple invasive species coexist at different trophic levels, the eradication of one invasive species can lead to net negative impacts on populations of native species (Zavaleta *et al*., 2001). It must also be noted that some invasive species benefit some native species (e.g. Somaweera *et al*., 2012), and the eradication of these invaders may therefore negatively affect the native species (Davis *et al*., 2011). To date, under natural conditions in Taiwan, *A. sagrei* has been recorded as a prey item of two reptile species (a lizard and a snake; Norval *et al*., 2004; Norval *et al*., 2007; Norval and Mao, 2008), and two bird species (Chiu *et al*., 2011; Norval *et al*., 2011b). In addition to that, various other native birds (such as *Dicrurus macrocercus* and *Egretta garzetta*) and snakes (such as *Dinodon rufozonatum rufozonatum* and *Sibynophis chinensis chinensis*) are also potential predators of *A. sagrei* in Taiwan. Due to their high abundance (*A. sagrei* has been determined to reach densities of up to 29 individuals per 100m^2, with an mean of about 21.91 [SD=6.47] in *A. catechu* plantations; Huang *et al*., 2008b), *A. sagrei* can be a readily available food resource for these, and other potential predators in Taiwan. It should also be noted that in the study by Huang *et al*. (2008a), *A. sagrei* preyed primarily on the most abundant ant species, and although predation by *A. sagrei* impacted the ant community, it did not influence the overall abundance of ants, indicating that these lizards benefited rarer and/or less competitive ant species by reducing their competitors. It has also been found that *A. sagrei* can have a positive effect on vegetation by preying on herbivorous arthropods (Spiller and Schoener, 1994; Spiller and Schoener, 1997). Considering that most of the areas in which *A. sagrei* occurs in Taiwan are agricultural fields and plantations, and since many of their prey in these areas are agricultural pests, such as the larvae (caterpillars) of some lepidopterans and flea beetles (Coleoptera; Chrysomelidae) (Norval, *pers. obs.*), it is possible that these lizards may be beneficial to farmers.

Based on what is known about *A. sagrei* in Taiwan, there is little idication that this species poses a significant threat to native wildlife. Since the distribution of *A. sagrei* in Taiwan is fairly extensive and the species disperses very easily, the eradication of *A. sagrei* through capturing techniques in Taiwan is considred impractical. Efforts should thus rather focus on managing this species.

An important aspect of the proposed management of *A. sagrei* is the manipulation of habitats to make them unsuitable for *A. sagrei* to inhabit, which in turn can hinder the spread of this species in Taiwan and limit its population growth. The cultivation of crops such as rice (*Oryza sativa*) and taro (*Colocasia esculenta*), which are unsuitable habitats for *A. sagrei* and native lizards, but are suitable habitats for native frogs and some snakes, should be encouraged in agricultural areas where *A. sagrei* is known to occur. Also, since the understory vegetation of lowland secondary forests (i.e. remnants of broadleaf forests) in Taiwan is usually dense and/or tall, it obscures the sun from shining on potential basking sites, thus making this type of habitat unsuitable for *A. sagrei* (Wang, 2013; Norval *et al.*, *in prep*.), greater efforts should be made to re-establish and conserve large areas of these forests in disturbed lowland areas of Taiwan. This would not only contribute to the conservation of native forest species, but such areas will also function as reservoirs for species like *J. swinhonis* that can compete with *A. sagrei*, as well as being barriers for its spread.

Predation and competition can also play an important role in the management of *A. sagrei* populations in Taiwan. A study in the Bahamas found that predation by rats (*Rattus* sp.) reduced the genetic diversity and population sizes of *A. sagrei* on some small islands (Gasc *et al*., 2010). It has also been found that predation and/or competition from birds, other lizards, and snakes cause *A. sagrei* to shift from being fairly terrestrial to being more arboreal, which results in these lizards attaining smaller (length) body sizes due to reduced growth rates (Schoener and Schoener, 1978b; Schoener and Schoener, 1982; Schoener *et al*., 2001; Schoener *et al*., 2002; Calsbeek and Cox, 2010). The conservation of native birds, lizards, and snakes in urban and rural areas in Taiwan thus require special attention, because bird species such as *Gorsakius melanolophus*, and *Lanius cristatus*, and lizard species such as *E. longicaudata*, *J. swinhonis*, and *P. elegans*, which can be human commensal, can be instrumental in mitigating the impact of *A. sagrei* on native ecosystems by competing with and preying on these invasive lizards (Norval *et al*., 2004; Chiu *et al*., 2011; Norval *et al*., 2011b; Norval *et al*., 2012b; Norval *et al*., 2012c).

An important part in the conservation efforts of native urban wildlife is to develop a better appreciation among the general public of native birds and lizards in urban gardens and parks, and to reduce the impact on these animals by their pets, especially domestic cats (*Felis catus*), which may prey on them (Lee, 2007). People should also be encouraged to be more tolerant towards snakes, in particular non-venomous species such as *D. r. rufozonatum*, *L. r. ruhstrati*, and *S. c. chinensis*. Also, in agricultural areas the hatchlings and neonates of native lizard species should be protected to enable them to grow large enough that they are no longer potential prey of large *A. sagrei* males. In order to do so, in *A. catechu* plantations and other similar habitats, the understory vegetation should not be cleared, because in habitats devoid of ground cover, large *A. sagrei* males can be saurophagous (Norval, 2007).

In view of its great potential to spread to new territories, and to prevent future introductions of *A. sagrei* into new localities, drastic steps, including the quarantining of newly imported cargos originating from areas where this lizard is known to occur are recommended. Ports and harbours, such as Hualien harbour, should regularly be surveyed, and if *A. sagrei* specimens are noted in this locality, actions, such as intensive capturing and exclusion barriers, like those constructed to prevent the spread of the green anole (*Anolis carolinensis*) in the Ogasawara Islands of Japan (Toda *et al*., 2010), should be taken to minimize the risk of these lizards dispersing to new localities from this point.

7.2. CONCLUSION

This study set out to contribute to the understanding of the *A. sagrei* populations in Taiwan and their natural history by addressing the following key questions:

- What is the current known distribution of *A. sagrei* in Taiwan?
- What are the characteristics of the habitat types that *A. sagrei* are mostly observed in in Taiwan?
- What intersexual intralocality, and interlocality intrasexual morphological variations exist among the *A. sagrei* specimens from the two study sites?
- What are the abdominal fat body and liver weight cycles of *A. sagrei* in Taiwan, and what associations are there between these cycles and the reproductive cycles and meteorological factors that may regulate them?

In summary, it was determined that the population in the southwestern study site in Chiayi County, southwestern Taiwan has an estimated distribution of about 237 hectares, while that of the population in the eastern study site in Hualien County, eastern Taiwan is about 8 hectares. Since not all areas could be surveyed and because it is possible that these lizards may also exist elsewhere in Taiwan, these were conservative minimum distribution estimates. In both study sites *A. sagrei* favours open sunny habitats disturbed by human activities, and it was found that secondary forest fragments and areas overgrown by tall grass are unsuitable for *A. sagrei* due to a possible lack of suitable basking sites. It was also found that structures that can be utilised as perches are essential for making a habitat suitable for *A. sagrei*.

Some morphological differences were found in the comparison of specimens from both study sites. However, since some possible explanations for these variations were presented, and due to the interlocality intrasexual lack of statistically significant differences in the numbers of subdigital lamellae it was concluded that the two populations described herein most likely had the same founder population, and that the one is a satellite population of the other. It was also stated that the interlocality differences recorded in this study deserve further empirical study, and it was recommended that future studies should also include genetic studies.

This study found that both the abdominal fat bodies and liver have roles to play in reproduction in the reproductive cycles in *A. sagrei,* and provides additional support for the conclusion that photoperiods and the associated temperatures determine the reproductive cycles in this species. It also demonstrated that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction, and that reproduction is energetically demanding for both sexes of *A. sagrei*.

7.3. REFERENCES

Andrews, R., and Rand, A.S. 1974. Reproductive effort in anoline lizards. *Ecology* 55: 1317-1327.

Baer, K.G. 1951. *Ecology of Animal Parasites.* University of Illinois Press, Urbana, Illinois.

Calsbeek, R., Bonneaud, C., Prabhu, S., Manoukis, N., and Smith, T.B. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards. *Evolutionary Ecology Research* 09: 495-503.

Calsbeek, R., and Cox, R.M. 2010. Experimentally assessing the relative importance of predation and competition as agents of selection. *Nature* 465: 613-616.

Campbell, T.S. 1999. Consequences of the Cuban brown anole invasion in Florida: it's not easy being green. *Anolis Newsletter* 5: 12-21.

Campbell, T.S., and Echternacht, A.C. 2003. Introduced species as moving targets: changes in body sizes of introduced lizards following experimental introductions and historical invasions. *Biological Invasions* 5: 193-212.

Chiu, P.K., Norval, G., Chu, H.P., and Mao, J.J. 2011. Two records of brown shrikes (*Lanius cristatus* Linnaeus, 1758) preying on brown anoles (*Anolis sagrei* Duméril & Bibron, 1837) in Taiwan. *Herpetology Notes* 04: 87-89.

Collette, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum of Comparative Zoology at Harvard College* 125: 137-162.

Cox, R.M., and Calsbeek, R. 2011. An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. *Journal of Evolutionary Biology* 24: 343-353.

Cox, R.M., Parker, E.U., Cheney, D.M., Liebl, A.L., Martin, L.B., and Calsbeek, R. 2010. Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Functional Ecology* 24: 1262-1269.

Davis, M.A., and Thompson, K. 2000. Eight ways to be a colonizer; two ways to be an invader. *Bulletin of the Ecological Society of America* 81: 226-230.

Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Del Tredici, P., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., and Briggs, J.C. 2011. Don't judge species on their origins. *Nature* 474: 153-154.

Eales, J., Thorpe, R.S., and Malhotra, A. 2008. Weak founder effect signal in a recent introduction of Caribbean *Anolis*. *Molecular Ecology* 17: 1416-1426.

Ehrlich, P.R. 1989. *Attributes of invaders and the invading process: vertebrates*. pp. 315-328. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., and Williamson, M. (eds.) 1999. *Biological Invasions. A Global Perspective*. John Wiley & Sons, New York.

Fox, W. 1963. Special tubules for sperm storage in female lizards. *Nature* 198: 500-501.

Gasc, A., Duryea, M.C., Cox, R.M., Kern, A., and Calsbeek, R. 2010. Invasive predators deplete genetic diversity of island lizards. *PLoS ONE* 5: e12061. doi:10.1371/journal.pone.0012061.

Goldberg, S.R., and Bursey, C.R. 2000. Transport of helminths to Hawaii via the brown anole, *Anolis sagrei* (Polychrotidae). *Journal of Parasitology* 86: 750-755.

Goldberg, S.R., Bursey, C.R., and Cheam, H. 1995. Helminth parasites of three sympatric lizards from Grand Cayman Island, *Anolis conspersus*, *Anolis sagrei* (Polychridae) and *Leiocephalus carinatus* (Tropiduridae). *Caribbean Journal of Science* 31: 339-340.

Goldberg, S.R., Bursey, C.R., and Kraus, F. 2002a. Seasonal variation in the helminth community of the brown anole, *Anolis sagrei* (Sauria: Polychrotidae), from Oahu, Hawaii. *American Midland Naturalist* 148: 409-415.

Goldberg, S.R., Kraus, F., and Bursey, C.R. 2002b. Reproduction in an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawaii. *Pacific Science* 56: 163-168.

Holbrook, J.D. 2012. *Anolis sagrei* (Brown anole). Prey. *Herpetological Review* 43: 641.

Horwitz, P., and Wilcox, B.A. 2005. Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *International Journal of Parasitology* 35: 725-732.

Huang, S.C. 2007a. *The Effects of Anolis sagrei, an Exotic Lizard, on Arthropod Diversity and Ecosystem Functioning in a Betelnut Plantation in Southern Taiwan*. M.Sc. thesis. Tunghai University, Taichung, Taiwan, R.O.C.

Huang, S.C., Norval, G., and Tso, I.M. 2008a. Predation by an exotic lizard, *Anolis sagrei*, alters the ant community structure in betelnut palm plantations in southern Taiwan. *Ecological Entomology* 33: 569-576.

Huang, S.C., Norval, G., Wei, C.S., and Tso, I.M. 2008b. Effects of the brown anole invasion and betelnut palm planting on arthropod diversity in southern Taiwan. *Zoological Science* 25: 1121-1129.

Huang, W.S. 2006. Ecological characteristics of the skink, *Mabuya longicaudata*, on a tropical East Asian Island. *Copeia* 2006**:** 293-300.

Huang, W.S. 2007b. Ecology and reproductive patterns of the agamid lizard *Japalura swinhonis* on an East Asian island, with comments on the small clutch sizes of island lizards. *Zoological Science* 24: 181-188.

Kraus, F. 2009. *Alien Reptiles and Amphibians, a Scientific Compendium and Analysis*. Invading Nature: Springer Series in Invasion Biology 4. Springer, New York.

Kuo, C.Y., Lin, Y.S., and Lin, Y.K. 2007. Resource use and morphology of two sympatric *Japalura* lizards (Iguania: Agamidae). *Journal of Herpetology* 41: 713-723.

Langford, G.J., Willobee, B.A., and Isidoro, L.F. 2013. Transmission, host specificity, and seasonal occurrence of *Cyrtosomum penneri* (Nematoda: Atractidae) in lizards from Florida. *Journal of Parasitology* 99: 241-246.

Lee, F.R. 2007. Natural killer. *Notes and Newsletter of Wildlifers (NOW)* 11: 31-37. (In Chinese)

Lee, J.C. 2000. *A Field Guide to the Amphibians and Reptiles of the Maya World: the Lowlands of Mexico, Northern Guatemala, and Belize*. Cornell University Press, New York.

Lee, J.C., Clayton, D., Eisenstein, S., and Perez, I. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989: 930-937.

Lee, P.F., Ding, T.S., Hsu, F.H., and Geng, S. 2004. Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. *Journal of Biogeography* 31: 307-314.

Levin, S.A. 1989. *Analysis of risk for invasions and control programs*. pp. 425-435. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., and Williamson, M. (eds.) 1989. *Biological Invasions*. *A Global Perspective*. SCOPE 37. John Wiley & Sons, New York.

Licht, P. and Gorman, G.C. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *University of California Publications in Zoology* 95: 1-52.

Losos, J.B., Marks, J.C., and Schoener, T.W. 1993. Habitat use and ecological interaction of an introduced and native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes on anole introductions. *Oecologia* 95: 525-532.

Meshaka, W.E. Jr., Butterfield, B.P., and Hauge, J.B. 2004. *The Exotic Amphibians and Reptiles of Florida*. Krieger Publishing Company, Florida.

Miura, O., Torchin, M.E., Kuris, A.M., Hechinger, R.F., and Chiba, S. 2006. Introduced cryptic species of parasites exhibit different invasion pathways. *Proceedings of the National Academy of Sciences* 103: 19818-19823.

Norval, G. 2007. A report on male *Anolis sagrei* saurophagy in Chiayi County, Taiwan. *Herpetological Bulletin* 102: 34-37.

Norval, G., Bursey, C.R., Goldberg, S.R., Mao, J.J., and Slater, K. 2011a. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), in southwestern Taiwan. *Pacific Science* 65: 383-390.

Norval, G., Bursey, C.R., Goldberg, S.R., Tung, C.L., and Mao, J.J. 2009a. *Norops sagrei* (Brown anole) pathology and endoparasite. *Herpetological Bulletin* 107: 42-44.

Norval, G., Chiu, P.K., Chu, H.P., and Mao, J.J. 2011b. An instance of predation on the brown anole (*Anolis sagrei* Duméril & Bibron, 1837) by a Malay night heron (*Gorsakius melanolophus* Swinhoe, 1865). *Herpetology Notes* 04: 05-07.

Norval, G., Goldberg, S.R., and Mao, J.J. 2012a. The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan. *Russian Journal of Herpetology* 19: 75-81.

Norval, G., Goldberg, S.R., Bursey, C.R., Mao, J.J., and Slater, K. 2014a. Internal parasites of lizards from Taiwan. *Herpetological Conservation and Biology*. 9: 484-494.

Norval, G., Hsiao, W.F., Huang, S.C., and Chen, C.K. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. *Russian Journal of Herpetology* 17: 131-138.

Norval, G., Huang, S.C., and Mao, J.J. 2007. Mountain wolf snake (*Lycodon r. ruhstrati*) predation on an exotic lizard, *Anolis sagrei*, in Chiayi County, Taiwan. *Herpetological Bulletin* 101: 13-17.

Norval, G., Huang, S.C., and Mao, J.J. 2014b. Notes on the growth rates of *Anolis sagrei* Duméril & Bibron, 1837, from a small betelnut palm (*Areca catecha*, L) plantation in southwestern Taiwan. *IRCF Reptiles & Amphibians* 21: 9-15.

Norval, G., Huang, S.C., Mao, J.J., and Goldberg, S.R. 2012b. Notes on some dietary items of *Eutropis longicaudata* (Hallowell, 1857), *Japalura polygonata xanthostoma* Ota, 1991, *Plestiodon elegans* (Boulenger, 1887), and *Sphenomorphus indicus* (Gray, 1853) from Taiwan. *Herpetology Notes* 5: 453-456.

Norval, G., Huang, S.C., Mao, J.J., Goldberg, S.R., and Slater, K. 2012c. Additional notes on the diet of *Japalura swinhonis* (Agamidae), from southwestern Taiwan, with comments about its dietary overlap with that of sympatric *Anolis sagrei* (Polychrotidae). *Basic and Applied Herpetology* 26: 87-97.

Norval, G., Huang, S.C., Mao, J.J., Goldberg, S.R., and Yang, Y.J. 2014c. Notes on the diets of five amphibian species from southwestern Taiwan. *Alytes* 30: 69-77.

Norval, G., Ivanova, L.V., and Mao, J.J. 2013. Greenhouses as potential reservoirs for the brown anole (*Anolis sagrei* Duméril & Bibron, 1837), an exotic invasive lizard in southwestern Taiwan. *IRCF Reptiles & Amphibians* 20: 199-202.

Norval, G., and Mao, J.J. 2008. An instance of arboricolous predation by a mountain wolf snake (*Lycodon ruhstrati ruhstrati* [Fischer, 1886]) on a brown anole (*Norops sagrei* Duméril & Bibron, 1837). *Sauria* 30: 59-62.

Norval, G., and Mao, J.J. 2013a. An instance of a brown anole (*Anolis sagrei* Duméril & Bibron, 1837) feeding on the sap of a banana plant (*Musa sapientum* L.). *Herpetology Notes* 6: 501-502.

Norval, G., Mao, J.J., and Chu, H.P. 2004. *Mabuya longicaudata* (Long-tailed skink). Predation. *Herpetological Review* 35: 393-394.

Norval, G., Mao, J.J., and Slater, K. 2012d. A description of an observed interaction between an elegant skink (*Plestiodon elegans* [Boulenger, 1887]) and a brown anoles (*Anolis sagrei* Duméril & Bibron, 1837) in southwestern Taiwan. *Herpetology Notes* 5: 189-192.

Norval, G., Mao, J.J., Chen, T.I., and Brown, L.R. (*in preperation*) Is a biodiverse environment reducing the invasibility of the brown anole (*Anolis sagrei*) in Taiwan?

Prenter, J., MacNeil, C., Dick, J.T.A., and Dunn, A.M. 2004. Roles of parasites in animal invasions. *Trends in Ecology and Evolution* 19: 385-390.

Pullin, A.S. 2002. *Conservation Biology*. 1st edition. Cambridge University Press, Cambridge.

Regalado, R. 1998. Approach distance and escape behavior of three species of Cuban *Anolis* (Squamata, Polychrotidae). Caribbean Journal of Science 34: 211-217.

Rodriguez Schettino, L.R. 1999. *The Iguanid Lizards of Cuba*. University Press of Florida, Gainesville, Florida.

Rolbiecki, L. 2006. Parasites of the round goby, *Neogobius melanostomus* (Pallas, 1811), an invasive species in the Polish fauna of the Vistula Lagoon ecosystem. *Oceanologia* 48: 545-561.

Ruibal, R. 1964. An annotated checklist and key to the anoline lizards of Cuba. *Bulletin of the Museum of Comparative Zoology* 130: 473-520.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Salzburg, M.A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. *Ecology* 65: 14-19.

Sanz Ochotorena, A., and Uribe Aranzábal, M.C. 1999. Ciclo gonadal y de los cuerpos grasos de *Anolis sagrei* (Sauria: Iguanidae) en Ciudad de La Habana. *Revista de Biología* 13: 26-32. (In Spanish)

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.

Schoener, T.W., and Schoener, A. 1971a. Structural habitats of West Indian *Anolis* lizards I. Lowland Jamaica. *Breviora* 368: 1-53.

Schoener, T.W., and Schoener, A. 1971b. Structural habitats of West Indian *Anolis* lizards II. Puerto Rican uplands. *Breviora* 375: 1-39.

Schoener, T.W., and Schoener, A. 1978a. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978: 390-405.

Schoener, T.W., and Schoener, A. 1978b. Inverse relation of survival of lizards with island size and avifaunal richness. *Nature* 274: 685-687.

Schoener, T.W., and Schoener, A. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* 39: 1-16.

Schoener, T.W., and Spiller, D.A. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381: 691-694.

Schoener, T.W., and Spiller, D.A. 1999a. Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist* 153: 347-358.

Schoener, T.W., and Spiller, D.A. 1999b. Variation in the magnitude of a predator's effect from small to large islands. Ecologia de les illes. *Monografies de la Societat d'Història Natural de les Balears* 6: 35-66.

Schoener, T.W., Slade, J.B., and Stinson, C.H. 1982. Diet and sexual dimorphism in the very catholic lizard genus *Leiocephalus* of the Bahamas. *Oecologia* 53: 160-169.

Schoener, T.W., Spiller, D.A., and Losos, J.B. 2001. Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412: 183-186.

Schoener, T.W., Spiller, D.A., and Losos, J.B. 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? *Ecological Monographs* 72: 383-407.

Schwartz, A., and Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History*. University Press of Florida, Florida.

Sever, D.M., and Hamlett, W.C. 2002. Female sperm storage in reptiles. *Journal of Experimental Zoology* 292: 187-199.

Sexton, O.J. and Brown, K.M. 1977. The reproductive cycle of an iguanid lizard *Anolis* *sagrei*, from Belize. *Journal of Natural History* 11: 241-250.

Shang, G.S., and Lin, S.L. 2001. *Natural Portraits of the Lizards of Taiwan*. Big Trees Publishers, Taipei. (In Chinese)

Shieh, C.J., Juan, L.Y., and Lue, K.Y. 1986. The study of the feeding habit of *Sphenomorphus indicus* in Ha-Pen area, Taipei County. Biological Bulletin of National Taiwan Normal University 21: 73-84. (In Chinese)

Shigesada, N. and Kawasaki, K. 1997. *Biological Invasions: Theory and Practice*. Oxford University Press, New York.

Somaweera, R., Wijayathilaka, N., and Bowatte, G. 2012. Does the invasive shrub *Ulex europaeus* benefit an endemic Sri Lankan lizard? *Herpetological Conservation and Biology* 7: 219-226.

Spiller, D.A., and Schoener, T.W. 1988. An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs* 58: 57-77.

Spiller, D.A., and Schoener, T.W. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83: 150-161.

Spiller, D.A., and Schoener, T.W. 1994. Effects of top and intermediated predators in a terrestrial food web. *Ecology* 75: 182-196.

Spiller, D.A., and Schoener, T.W. 1995. Long-term variation in the effect of lizards on spider density is linked to rainfall. *Oecologia* 103: 133-139.

Spiller, D.A., and Schoener, T.W. 1997. Folivory on islands with and without insectivorous lizards: an eight-year study. *Oikos* 78: 15-22.

Spiller, D.A., and Schoener, T.W. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* 79: 503-516.

Spiller, D.A., and Schoener, T.W. 2001. An experimental test for predator-mediated interactions among spider species. *Ecology* 82: 1560-1570.

Tan, H.H., and Lim, K.K.P. 2012. Recent introduction of the brown anole *Norops sagrei* (Reptilia: Squamata: Dactyloidae) to Singapore. *Nature in Singapore* 5: 359-362.

Toda, M., Takahashi, H., Nakagawa, N., and Sukigara, N. 2010. Ecology and control of the green anole (*Anolis carolinensis*), an invasive alien species on the Ogasawara Islands. pp. 145-152. In: Kawakami, K., and Okochi, I. (eds.) 2010. *Restoring the Oceanic Island Ecosystem*. *Impact and Management of Invasive Alien Species in the Bonin Islands*. Springer-Verlag Tokyo, Springer Japan, Tokyo.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., and Kuris, A.M. 2003. Introduced species and their missing parasites. *Nature* 421: 628-630.

Torchin, M.E., Lafferty, K.D., and Kuris, A.M. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3: 333-345.

Van Driesche, J., and Van Driesche, R. 2000. *Nature Out of Place*: *Biological Invasions in the Global Age*. Island Press, Washington D.C.

Wang, G.Q. 2013. *Modeling the Dispersal Pattern of Brown Anole (Anolis sagrei) Population in Samtzepu, Chiayi County, Taiwan*. M.Sc. dissertation. National Cheng Kung University, Tainan, Taiwan, R.O.C.

Williams, E.E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *The Quarterly Review of Biology* 44: 345-389.

Williamson, M. 1999. Invasions. *Ecography* 22: 5-12.

Wright, A.N., Piovia-Scott, J., Spiller, D.A., Takimoto, G., Yang, L.H., and Schoener, T.W. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. *Oikos* 122: 1496-1504.

Zavaleta E.S., Hobbs, R.J., and Mooney, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16: 454-459.

Zhang, Y.P., and Ji, X. 2004. Sexual dimorphism in head size and food habits in the blue-tailed skink *Eumeces elegans*. *Acta Zoologica Sinica* 50: 745-752. (In Chinese)

Zug, G.R., Vitt, L.J., and Caldwell, J.P. 2001. *Herpetology*. *An Introductory Biology of Amphibians and Reptiles*. *2nd Edition*. Academic Press, San Diego.

Appendices

Appendix 4.1.

A list of the plant species recorded in the southwestern study site in Chiayi County.

Family	Species	Family	Species
Dicotyledoneae		Boraginaceae	*Cordia dichotoma*
Acanthaceae	*Rhinacanthus nasutus*		*Ehretia acuminata*
Altingiaceae	*Liquidambar formosana*		*Ehretia dicksonii*
Amaranthaceae	*Alternanthera sessilis*	Brassicaceae	*Lepidium virginicum*
	Amaranthus spinosus	Buddlejaceae	*Buddleja asiatica*
	Celosia argentea	Cactaceae	*Hylocereus undatus*
Anacardiaceae	*Aleurites montana*	Capparidaceae	*Cleome rutidosperma*
	Mangifera indica	Caricaceae	*Carica papaya*
Apocynaceae	*Alstonia scholaris*	Caryophyllaceae	*Drymaria diandra*
	Trachelospermum gracilipes	Chenopodiaceae	*Chenopodium serotinum*
	Trachelospermum jasminoides	Combretaceae	*Terminalia catappa*
Aristolochiaceae	*Aristolochia shimadai*	Convolvulaceae	*Ipomoea batatas*
Asteraceae	*Ageratum conyzoides*		*Ipomoea cairica*
	Artemisia indica		*Ipomoea indica*
	Aster subulatus var. *subulatus*		*Ipomoea obscura*
	Bidens pilosa		*Ipomoea triloba*
	Blumea balsamifera var. *microcephala*	Crassulaceae	*Kalanchoe pinnata*
	Blumea riparia var. *megacephala*	Cucurbitaceae	*Momordica charantia* var. *abbreviata*
	Chromolaena odorata		*Luffa cylindrica*
	Cichorium intybus	Ebenaceae	*Diospyros oldhamii*
	Conyza canadensis var. *canadensis*	Euphorbiaceae	*Acalypha australis*
	Conyza sumatrensis		*Breynia officinalis*
	Crassocephalum crepidioides		*Bridelia balansae*
	Eclipta prostrata		*Bridelia tomentosa*
	Elephantopus mollis		*Chamaesyce hypericifolia*
	Emilia praetermissa		*Chamaesyce thymifolia*
	Emilia sonchifolia var. *javanica*		*Codiaeum variegatum*
	Gnaphalium luteoalbum affine		*Codiaeum variegatum* var. *variegatum*
	Ixeris chinensis		*Euphorbia heterophylla*
	Mikania micrantha		*Euphorbia hirta*
	Pterocypsela indica		*Flueggea suffruticosa*
	Sonchus oleraceus		*Flueggea virosa*
	Tridax procumbens		*Glochidion acuminatum*
	Vernonia cinerea var. *parviflora*		*Glochidion rubrum*
	Wedelia trilobata		*Macaranga denticulata*
	Youngia japonica		*Macaranga tanarius*
Basellaceae	*Basella alba*		*Mallotus japonicus*
Bignoniaceae	*Pyrostegia venusta*		*Melanolepis multiglandulosa*
Bombacaceae	*Pachira macrocarpa*		*Phyllanthus tenellus*
Boraginaceae	*Bothriospermum zeylanicum*		*Phyllanthus urinaria*

Appendix 4.1. (*continued*)

Family	Species	Family	Species
Labiatae	*Orthosiphon aristatus*	Moraceae	*Ficus nervosa*
Lamiaceae	*Mesona chinensis*		*Morus australis*
Lamiaceae	*Perilla frutescens*	Myristicaceae	*Myristica ceylanica* var. *cagayanensis*
Lauraceae	*Cinnamomum camphora*	Myrsinaceae	*Ardisia squamulosa*
Lauraceae	*Cinnamomum zeylanicum*	Myrsinaceae	*Maesa perlaria* var. *perlaria*
	Machilus thunbergii	Myrtaceae	*Melaleuca leucadendra*
Lauraceae	*Machilus zuihoensis* var. *zuihoensis*	Myrtaceae	*Myrciaria cauliflora*
Leguminosae	*Acacia confusa*		*Psidium guajava*
	Alysicarpus vaginalis var. *vaginalis*		*Syzygium cumini*
	Arachis duranensis	Myrtaceae	*Syzygium samarangense*
	Bauhinia × *blakeana*	Oleaceae	*Fraxinus griffithii*
	Callerya reticulata		*Jasminum nervosum*
	Crotalaria juncia		*Osmanthus fragrans*
	Desmodium heterocarpum var. *strigosum*	Onagraceae	*Ludwigia decurrens*
	Desmodium triflorum		*Ludwigia hyssopifolia*
	Glycine max		*Ludwigia octovalvis*
	Leucaena leucocephala	Oxalidaceae	*Averrhoa carambola*
	Milletia reticulata		*Oxalis corniculata*
	Mimosa diplotricha		*Oxalis corymbosa*
	Pueraria montana	Papilionaceae	*Lablab purpureus*
	Senna occidentalis		*Neonotonia wightii*
	Sesbania sesban		*Uraria crinita*
	Vigna radiata var. *radiata*	Passifloraceae	*Passiflora foetida* var. *hispida*
	Vigna reflexopilosa		*Passiflora suberosa*
Lythraceae	*Ammannia baccifera*	Plantaginaceae	*Mecardonia procumbens*
	Cuphea hyssopifolia	Plumbaginaceae	*Plumbago zeylanica*
	Lagerstroemia speciosa	Polygonaceae	*Muehlenbeckia platyclada*
	Cuphea carthagenensis		*Polygonum barbatum*
Malvaceae	*Abelmoschus moschatus*		*Polygonum chinense*
	Chorisia speciosa		*Polygonum multiflorum* var. *hypoleucum*
	Hibiscus cannabinus	Portulacaceae	*Portulacea oleracea*
	Hibiscus sabdariffa	Rosaceae	*Rubus croceacanthus*
	Pachira aquatica	Rubiaceae	*Coffea arabica*
	Sida alnifolia		*Hedyotis diffusa*
	Sida rhombifolia var. *maderensis*		*Ixora duffii* cv.
	Urena lobata		*Ixora* x *williamsii* cv.
Melastomataceae	*Melastoma candidum*		*Morinda parvifolia*
Meliaceae	*Swietenia macrophylla*		*Mussaenda pubescens*
Menispermaceae	*Stephania japonica*		*Paederia foetida*
	Cocculus orbiculatus		*Psychotria rubra*
Moraceae	*Artocarpus heterophyllus*		*Spermacoce latifolia*
	Ficus ampelas		*Hedyotis angustifolia*
	Ficus erecta var. beecheyana		*Hedyotis corymbosa*
	Ficus microcarpa var. *microcarpa*	Rutaceae	*Citrus* × *sinensis*

Appendix 4.1. (*continued*)

Family	Species	Family	Species
Rutaceae	*Citrus aurantifolia*	Araceae	*Epipremnum aureum*
	Citrus reticulata cv.		*Syngonium podophyllum*
	Clausena excavata		*Typhonium blumei*
	Murraya paniculata var. *paniculata*	Arecaceae	*Areca catechu*
Sapindaceae	*Cardiospermum halicacabum*	Arecaceae	*Cocos nucifera*
	Dimocarpus longan		*Phoenix hanceana*
	Litchi chinensis	Asparagaceae	*Asparagus officinalis*
	Koelreuteria henryi	Bromeliaceae	*Ananas comosus*
Sapotaceae	*Lucuma nervosa*	Commelinaceae	*Commelina communis*
	Planchonella obovata		*Commelina diffusa*
Scrophulariaceae	*Lindernia crustacea*	Cyperaceae	*Bulbostylis barbata*
	Scoparia dulcis		*Carex cruciata*
	Torenia concolor		*Cyperus compressus*
Solanaceae	*Physalis angulata*		*Cyperus cyperinus*
	Capsicum annuum		*Cyperus cyperoides*
	Solanum diphyllum		*Cyperus distans*
	Solanum erianthum		*Cyperus involucratus*
	Solanum nigrum		*Cyperus iria*
	Solanum torvum		*Cyperus rotundus*
Sphenocleaceae	*Sphenoclea zeylanica*		*Fimbristylis aestivalis* var. *aestivalis*
Symplocaceae	*Symplocos chinensis*		*Fimbristylis cymosa*
Theaceae	*Camellia brevistyla*		*Fimbristylis dichotoma*
	Eurya chinensis		*Fimbristylis littoralis* var. *littoralis*
	Eurya emarginata		*Kyllinga brevifolia*
Thymelaeaceae	*Aquilaria sinensis*		*Kyllinga nemoralis*
Tiliaceae	*Triumfetta tomentosa*		*Schoenoplectus validus*
Ulmaceae	*Trema orientalis*		*Scirpus ternatanus*
Umbelliferae	*Centella asiatica*		*Scleria terrestris*
Urticaceae	*Pilea microphylla*	Dioscoreaceae	*Dioscorea alata*
	Pouzolzia zeylanica	Liliaceae	*Dianella ensifolia*
Verbenaceae	*Clerodendrum inerme*	Musaceae	*Musa sapientum*
	Clerodendrum paniculatum	Poaceae	*Arundo donax*
	Clerodendrum quadriloculare		*Axonopus affinis*
	Clerodendrum calamitosum		*Axonopus compressus*
	Lantana camara		*Bambusa dolichomerithalla*
	Verbena incompta		*Brachiaria mutica*
Vitaceae	*Ampelopsis brevipedunculata*		*Cenchrus echinatus*
	Ampelopsis glandulosa		*Chloris barbata*
	Cissus kerrii		*Chloris gayana*
	Tetrastigma formosanum		*Cynodon dactylon*
Monocotyledoneae			*Cynodon plectostachyus*
Agavaceae	*Sansevieria trifasciata*		*Cyrtococcum accrescens*
Araceae	*Alocasia odora*		*Dactyloctenium aegyptium*
	Colocasia esculenta		*Dendrocalamus latiflorus*

Appendix 4.1. (*continued*)

Family	Species	Family	Species
Poaceae	*Dichanthium annulatum*	Poaceae	*Saccharum spontaneum*
	Digitaria ciliaris		*Setaria geniculata*
	Digitaria radicosa var. *radicosa*		*Setaria verticillata*
	Digitaria sanguinalis		*Setaria viridis*
	Digitaria setigera		*Sorghum bicolor*
	Echinochloa colona		*Sporobolus indicus*
	Eleusine indica		*Sporobolus virginicus*
	Eragrostis multicaulis	Smilacaceae	*Smilax bracteata*
	Eragrostis unioloides		*Smilax ocreata*
	Eriochloa procera		*Heterosmilax japonica*
	Hemarthria compressa	Typhaceae	*Typha orientalis*
	Imperata cylindrica var. *major*	Zingiberaceae	*Alpinia zerumbet*
	Leersia hexandra		*Costus speciosus*
	Leptochloa chinensis		*Zingiber officinale*
	Leptochloa panicea	**Pteridophyta**	
	Melinis repens	Cupressaceae	*Juniperus chinensis*
	Microstegium glaberrimum	Cycadaceae	*Cycas taitungensis*
	Miscanthus floridulus	Equisetaceae	*Equisetum ramosissimum debile*
	Oplismenus hirtellus	Podocarpaceae	*Podocarpus costalis*
	Oryza sativa	Pteridaceae	*Pteris kidoi*
	Panicum maximum		*Pteris semipinnata*
	Paspalum conjugatum		*Onychium japonicum*
	Paspalum orbiculare		*Pteris vittata*
	Paspalum urvillei	Schizaeaceae	*Lygodium japonicum*
	Pennisetum americanum	Thelypteridaceae	*Christella acuminata*
	Pennisetum purpureum		*Cyclosorus parasiticus*

Appendix 4.2.

A list of the plant species recorded in the eastern study site in Hualien County.

Family	Species	Family	Species
Dicotyledoneae		Moraceae	*Morus australis*
Amaranthaceae	*Amaranthus viridis*	Myrsinaceae	*Ardisia crenata*
Annonaceae	*Annona squamosa*	Myrtaceae	*Psidium guajava*
Apocynaceae	*Allamanda cathartica*		*Eucalyptus maculata* var. *citriodora*
Araliaceae	*Schefflera octophylla*	Nyctaginaceae	*Bougainvillea spectabilis*
	Tetrapanax papyriferus	Ochnaceae	*Ochna kirkii*
	Hydrocotyle verticillata	Oleaceae	*Jasminum sambac*
	Polyscias fruticosa var. *deleauana*		*Osmanthus fragrans*
Asteraceae	*Ageratum houstonianum*	Onagraceae	*Oenothera laciniata*
	Aster subulatus var. *subulatus*	Oxalidaceae	*Oxalis corniculata*
	Bidens pilosa		*Oxalis corymbosa*
	Chromolaena odorata		*Oxalis triangularis* var. *purpurea*
	Conyza sumatrensis	Phyllanthaceae	*Bischofia javanica*
	Crossostephium chinense	Phytolaccaceae	*Rivina humilis*
	Ixeris chinensis	Piperaceae	*Piper kadsura*
	Veronica peregrina var. *xalapens*	Ranunculaceae	*Clematis grata*
	Youngia japonica	Rosaceae	*Eriobotrya japonica*
Balsaminaceae	*Impatiens walleriana*		*Potentilla indica*
Berberidaceae	*Nandina domestica*	Rubiaceae	*Ixora duffii* cv.
Bombacaceae	*Pachira macrocarpa*		*Ixora* x *williamsii* cv.
Chenopodiaceae	*Chenopodium ambrosioides*		*Lasianthus obliquinervis*
Clusiaceae	*Garcinia multiflora*	Rutaceae	*Murraya paniculata* var. *paniculata*
Elaeagnaceae	*Elaeagnus oldhamii*		*Zanthoxylum nitidum*
Euphorbiaceae	*Mallotus paniculatus*	Sapindaceae	*Cardiospermum halicacabum*
	Phyllanthus urinaria		*Koelreuteria henryi*
	Macaranga tanarius	Solanaceae	*Solanum alatum*
	Melanolepis multiglandulosa		*Solanum capsicastrum*
Lamiaceae	*Pogostemon cablin*		*Solanum diphyllum*
Lauraceae	*Cinnamomum burmannii*		*Sonchus arvensis*
	Cinnamomum camphora	Staphyleaceae	*Turpinia ternata*
Leguminosae	*Calliandra haematocephala*	Theaceae	*Camellia japonica*
	Desmodium triflorum	Tiliaceae	Grewia rhombifolia
	Leucaena leucocephala	Ulmaceae	*Celtis formosana*
Lythraceae	*Cuphea hyssopifolia*		*Ulmus parvifolia*
	Lagerstroemia subcostata	Umbelliferae	*Centella asiatica*
Magnoliaceae	*Magnolia coco*	Urticaceae	*Boehmeria frutescens*
	Michelia compressa		*Boehmeria nivea* var. *tenacissima*
	Michelia figo		*Dendrocnide meyeniana*
Melastomataceae	*Melastoma candidum*		*Pilea peploides* var. *major*
Moraceae	*Artocarpus incisus*	Verbenaceae	*Clerodendrum thomsoniae*
	Ficus irisana		*Lantana camara*
	Ficus microcarpa var. *microcarpa*		*Duranta repens*

Appendix 4.2. (*continued*)

Family	Species	Family	Species
Verbenaceae	*Phyla nodiflora*		*Digitaria ciliaris*
Vitaceae	*Cayratia japonica*	Poaceae	*Eleusine indica*
Monocotyledoneae			
Araceae	*Alocasia odora*		*Miscanthus floridulus*
	Colocasia esculenta		*Oplismenus compositus*
	Epipremnum aureum		*Panicum repens*
Arecaceae	*Arenga engleri*		*Setaria palmifolia*
	Cocos nucifera		*Setaria verticillata*
	Phoenix hanceana	Smilacaceae	*Smilax china*
Asparagaceae	*Asparagus cochinchinensis*	Zingiberaceae	*Alpinia speciosa*
Commelinaceae	*Pollia japonica*		*Alpinia zerumbet*
Laxmanniaceae	*Cordyline fruticosa*	**Pteridophyta**	
Liliaceae	*Lilium longiflorum* var. *scabrum*	Podocarpaceae	*Podocarpus macrophyllus* var. *maki*
Poaceae	*Axonopus compressus*	Thelypteridaceae	*Christella acuminata*
	Bambusa dolichoclada		*Cyclosorus parasiticus*