

Additional notes on the diet of *Japalura swinhonis* (Agamidae) from southwestern Taiwan, with comments about its dietary overlap with the sympatric *Anolis sagrei* (Polychrotidae)

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Received: 9 September 2012; received in revised form: 28 October 2012; accepted: 31 October 2012.

Japalura swinhonis is an endemic agamid lizard in Taiwan, and although its diet has been examined in northern Taiwan and Orchid Island, it has not been investigated in other parts of its range. Investigating the diet of a species from different parts of its range is crucial due to temporal and spatial variations in it. This study examined the dietary items of 47 *J. swinhonis* from Santzepu and Yunlin, southwestern Taiwan. We also reviewed the diet of *J. swinhonis* and compared it with that of *Anolis sagrei* from Santzepu, where these species are sympatric in anthropogenically created habitats such as *Areca catechu* plantations and fruit orchards. The diet of *J. swinhonis* from Santzepu was dominated by hymenopterans, followed by coleopterans, lepidopterans and trichopterans, while that of the *J. swinhonis* from Yunlin was dominated by isopterans, followed by hymenopterans, lepidopterans and coleopterans. The diet of *A. sagrei* from Santzepu was mainly dominated by hymenopterans, lepidopterans, araneids, hemipterans, coleopterans, dipterans, isopterans and orthopterans, in that order of frequency. From the results of this study it is evident that in areas where *J. swinhonis* and *A. sagrei* are sympatric there is a substantial dietary niche overlap, and competition for prey is very likely.

Key words: arboreal; competition; invasive species; sit-and-wait forager.

Notas adicionales sobre la dieta de *Japalura swinhonis* (Agamidae) en el suroeste de Taiwán, con comentarios acerca de su solapamiento trófico con la especie simpátrica *Anolis sagrei* (Polychrotidae). *Japalura swinhonis* es un agámido endémico en Taiwán, y aunque su dieta se ha examinado en el norte de Taiwán y la isla de Orchid, no se ha estudiado en otras partes de su rango de distribución. Investigar la dieta de una especie en diferentes partes de su rango geográfico es crucial debido a la existencia de variaciones temporales y espaciales. Este estudio examina la dieta de 47 *J. swinhonis* de Santzepu y Yunlin, en el suroeste de Taiwan. También revisamos la dieta de *J. swinhonis* y la comparamos con la de *Anolis sagrei* en Santzepu, donde estas especies aparecen en simpatría en hábitats creados por el hombre, tales como las plantaciones de *Areca catechu* y frutales. La dieta de *J. swinhonis* de Santzepu estuvo dominada por himenópteros, seguidos de coleópteros, lepidópteros y tricópteros, mientras que la de *J. swinhonis* de Yunlin estuvo dominada por isópteros, seguidos de himenópteros, lepidópteros y coleópteros. La dieta de *A. sagrei* de Santzepu consistió principalmente de himenópteros, lepidópteros, araneidos, hemípteros, coleópteros, dípteros, isópteros y ortópteros, en este orden de frecuencia. A partir de los resultados de este estudio parece evidente que en áreas en las que *J. swinhonis* y *A. sagrei* aparecen en simpatría existe un solapamiento sustancial de la dieta, con una probable competencia por las presas.

Key words: arbórea; competencia; especies invasoras; predador sit-and-wait.

A crucial part of the natural history of an animal is its diet, because not only does it reveal the source of the animal's energy for growth, maintenance, and/or reproduction (DUNHAM *et al.*, 1989; ZUG *et al.*, 2001), but it also provides information on the ecological roles of the animal. Diets are thus often used in intraspecific (e.g. ROCHA & ANJOS, 2007; BULTÉ *et al.*, 2008) and interspecific (e.g. ORTEGA-RUBIO *et al.*, 1995; VIEIRA & PORT, 2007) niche-overlap studies. Since there may be temporal and spatial variations in the diet of a species (e.g. RODRÍGUEZ *et al.*, 2008; HAWLENA & PÉREZ-MELLADO, 2009; GOODYEAR & PIANKA, 2011), information on diet from different localities is useful in elucidating the ecological niche of an animal.

The Swinhoe's tree lizard (*Japalura swinhonis* Günther, 1864) is an endemic agamid lizard in Taiwan and occurs throughout the island, and on the offshore Orchid Island at elevations below 1500 m (OTA, 1991). It is diurnal and occurs in various habitat types, ranging from forests to areas extensively altered by anthropogenic activities, provided there is sufficient sunlight (KUO *et al.*, 2007). Dietary descriptions have only been made for *J. swinhonis* from northern Taiwan (KUO *et al.*, 2007) and Orchid Island (HUANG, 2007). There is thus still a need for dietary descriptions from other parts of its range.

The brown anole (*Anolis sagrei* Duméril & Bibron, 1837), also known as *Norops sagrei* (KÖHLER, 2000; LEE, 2000), is an exotic invasive lizard species in Taiwan (NORVAL *et al.*, 2002, 2009; CHANG, 2007). It is a diurnal trunk-ground species that favours a variety of sunny habitat types and areas disturbed by anthropogenic activities (SCHWARTZ & HENDERSON, 1991). *Anolis sagrei* is an aggres-

sive competitor that has been shown to displace other species of lizards from their habitats (SALZBURG, 1984; TOKARZ & BECK, 1987; LOSOS *et al.*, 1993; LOSOS & SPILLER, 1999). Ongoing research on this species in Taiwan indicates that in areas disturbed by anthropogenic activities, it is increasingly becoming part of local ecosystems, both as predator (HUANG *et al.*, 2008a; NORVAL *et al.*, 2010) and prey (NORVAL *et al.*, 2004, 2007, 2011; NORVAL & MAO, 2008; CHIU *et al.*, 2011).

This study aims to identify the dietary items of *J. swinhonis*, using individuals that were collected on an *ad hoc* basis from southwestern Taiwan, to contribute to the overall understanding of the diet of this species. Furthermore, the current knowledge on the diet of *J. swinhonis* is reviewed and compared with that of *A. sagrei* from Taiwan.

MATERIALS AND METHODS

On the 28th of June, 2002, a *J. swinhonis* male was found dead on a road (DOR) in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan (23° 25' 46" N, 120° 28' 55" E; datum WGS84). During July and September 2004, and on the 5th of October, 2007, live *J. swinhonis* were also collected from a small betel nut palm (*Areca catechu* L.) plantation in Santzepu (23° 25' 42" N, 120° 29' 06" E; datum WGS84), where *J. swinhonis* is sympatric with *A. sagrei*. Between the 24th of May and the 1st of June, 2008, additional specimens were collected from two localities (23° 36' 34" N, 120° 34' 13" E and 23° 35' 44" N, 120° 35' 47" E) in Yunlin County, southwestern Taiwan.

The snout-vent length (SVL) and tail length (TL) were measured to the nearest mm with a transparent plastic ruler, and the ani-

imals were weighed (body mass) to the nearest 0.1 g with a digital scale. The DOR lizard was dissected by making a mid-ventral incision and the stomach was removed and slit longitudinally, after which the stomach contents were removed. In order to determine the diet of the living *J. swinhonis* in a non-lethal manner in the field, the mouth of each collected individual was held open by placing a hard plastic tube (diameter = 10 mm; length = 30 mm) in the oral cavity of the lizard when it opened its mouth as a threat display in response to handling. The stomach contents were then obtained by inserting a no. 4 catheter, lubricated with sunflower cooking oil, into the throat

and stomach of the lizard, and then flushing the stomach contents out by holding the lizard facing downwards over a plastic container while injecting 15 ml clean drinking water through the catheter into the stomach (Fig. 1). A similar method was employed by KUO *et al.* (2007), and in a preliminary study we found that typically more than 80% (often nearly 100%) of the stomach contents were flushed from the stomachs of the lizards (S.C. Huang & G. Norval, unpublished data), so we considered the method reliable enough for our investigation. After the lizards were stomach-flushed they were released back into the wild at the same locality where they had been collected.

In the laboratory, the stomach contents were spread in a petri dish and examined under a dissection microscope, and all the prey items were identified to the order level (samples from the year 2004) and, if possible, to the family level (samples from years other than 2004).

The dietary descriptions for *J. swinhonis* from Orchid Island (HUANG, 2007), and northern (KUO *et al.*, 2007) and southwestern (this study) Taiwan were incorporated for comparison with the dietary descriptions for *A. sagrei* from Santzepu, southwestern Taiwan (HUANG *et al.*, 2008a; NORVAL *et al.*, 2010). Because not all the dietary items were identified to the family level, the order level was used in the analysis as the resource category. We used the software Ecological Methodology Version 6.1.1. (Exeter software, Setauket, New York, USA) to analyze and compare the diets of *J. swinhonis* and *A. sagrei* as follows. The diet diversity index of each species was measured with the Shannon-Wiener function, using the original (H') and the natural logarithm-transformed (N_1) indexes; however, since HUANG (2007) and KUO *et al.* (2007) did



Figure 1: Stomach flushing methodology. (top) Equipment used for performing stomach flushing. (bottom) A *Japalura swinhonis* male undergoing stomach flushing.

not indicate the numbers of prey items, the results from their studies were not used for the diet diversity index calculations. Niche breadths of *J. swinhonis* and *A. sagrei* were estimated using the Levin's measure of niche breadth (B) and the Levin's standardized niche breadth (B_A) (KREBS, 1999). Only studies indicating the numbers of lizards that preyed on each prey type (i.e. frequency of occurrence: F) were used for these analyses, being therefore excluded the results of HUANG *et al.* (2008a) and part of the results described herein. The dietary niche overlap was measured with the Pianka's measure, and the percentage overlap (Schoener Overlap Index) was used to examine the extent of the dietary niche overlap (KREBS, 1999). Again, due to a lack of the required information, the results of the studies by HUANG (2007) and KUO *et al.* (2007) were excluded from the analysis of dietary niche overlap.

RESULTS

Thirty-nine *J. swinhonis* (20 males and 19 females) were collected from Santzepu (Table 1), with SVL ranging from 51 to 77 mm (mean \pm

SD = 65.6 \pm 7.0), TL from 123 to 196 mm (mean \pm SD = 160.5 \pm 21.0), and body mass from 3.9 to 13 g (mean \pm SD = 7.7 \pm 2.6). Eight *J. swinhonis* (seven males and one female) were collected from Yunlin (Table 1), with SVL ranging from 68 to 78 mm (mean \pm SD = 73.0 \pm 3.2), TL from 168 to 202 mm (mean \pm SD = 183.4 \pm 9.8), and body mass from 8.7 to 14.9 g (mean \pm SD = 11.0 \pm 1.9).

For description and analysis, we pooled all the dietary data of both sexes from each locality. We recorded 1277 prey items, belonging to 13 orders from three classes, from the Santzepu individuals, and 47 prey items, belonging to six orders from two classes, from the Yunlin ones (Table 2). In the stomachs of the *J. swinhonis* from Santzepu, the most numerous prey items were hymenopterans, more than 90% of which were ants (Formicidae), followed by coleopterans, lepidopterans and trichopterans, respectively (Table 2). For the *J. swinhonis* from Yunlin, the most numerous prey items were termites (Isoptera), followed by hymenopterans (all Formicidae), lepidopterans (all caterpillars) and coleopterans, respectively (Table 2). Cumulatively, the most numerous prey items in the diet of *J. swinhonis* from southwestern

Table 1: Range and mean (\pm SD) snout-vent length (SVL), tail length (TL) and body mass of the *Japalura swinhonis* from Santzepu and Yunlin used in this study.

Locality	Collection period	Sex	N	SVL (mm)	TL (mm)	Mass (g)
Santzepu	2002	♂	1	72	178	8.7
	2004	♂	18	58-77 (70.4 \pm 4.6)	148-196 (177.8 \pm 15.0)	5.9-13 (9.7 \pm 2.2)
		♀	19	51-73 (61.4 \pm 5.6)	129-167 (146.0 \pm 6.0)	3.9-9.3 (6.0 \pm 1.2)
	2007	♂	1	54	123	4.2
Yunlin	2008	♂	7	68-78 (73.4 \pm 3.2)	168-202 (184.3 \pm 10.2)	8.7-14.9 (11.1 \pm 2.0)
		♀	1	70	177	10.1

Table 2: Percentage of each type of dietary item (% items) in *Japalura swinhonis* from two sites in southwestern Taiwan, and cumulated values considering both sites altogether. For the Yunlin population, the occurrence frequency (F) of each prey is also shown.

Class	Order	Santzepu	Yunlin		Cumulated
		% items (N = 1277)	% items (N = 47)	F (N = 8)	% items (N = 1324)
Insecta	Blattaria	0.31	0.00	0	0.30
	Coleoptera	1.88	4.26	2	3.25
	Dermaptera	0.08	0.00	0	0.08
	Diptera	0.63	0.00	0	0.60
	Hemiptera	0.71	0.00	0	0.68
	Hymenoptera	93.50	14.89	3	90.71
	Isoptera	0.08	59.57	4	2.19
	Lepidoptera	1.18	12.77	5	1.59
	Orthoptera	0.08	2.13	1	0.15
	Phasmatodea	0.08	0.00	0	0.08
Arachnida	Trichoptera	1.10	0.00	0	1.06
	Aranea	0.31	0.00	0	0.30
Crustacea	Isopoda	0.00	2.13	1	0.08
Magnoliopsida	Asterales	0.08	0.00	0	0.08
Unknown		0.00	4.26	2	0.15

Taiwan were hymenopterans (primarily Formicidae), followed by coleopterans, isopterans, lepidopterans and trichopterans, in that order of frequency (Table 2), while the prey items from the remaining orders made up ca. 3%.

The diet of *A. sagrei* from Taiwan (based on the studies done in Santzepu), consisted mostly of hymenopterans (primarily Formicidae), followed by lepidopterans, araneids, hemipterans, coleopterans, dipterans, isopterans and orthopterans, respectively (Table 3). Prey items from the remaining orders made up ca. 5% of the diet of *A. sagrei* from Taiwan.

The Shannon-Wiener function resulted in $H' = 0.7135$ ($N_1 = 0.6099$) for *J. swinhonis* and $H' = 2.6238$ ($N_1 = 0.1622$) for *A. sagrei*. Niche breadth measures were $B = 0.6644$ and $B_A = 0.0129$ for *J. swinhonis*, and $B = 1.6149$ and $B_A = 0.0237$ for *A. sagrei*. The Pianka's

measure and the percentage dietary niche overlap between *J. swinhonis* and *A. sagrei* were 0.945 and 65.7%, respectively.

DISCUSSION

Based on what is understood about the diet of *J. swinhonis* (HUANG, 2007; KUO *et al.*, 2007), this species can be regarded as a dietary generalist, preying upon a variety of prey types although, according to the calculated Shannon-Wiener function and Levin's measures, depending to a large extent on large numbers of a relatively few prey types. The occurrence in the diet of *J. swinhonis* of prey primarily active, mobile, moving on the surface, and visually conspicuous (e.g. ants, termites, and lepidopterans and their larvae) suggests that this species is an opportunistic sit-and-wait (ambush) foraging species (HUEY & PIANKA, 1981;

Table 3: Percentage of each type of dietary item (% items) in *Anolis sagrei* from Santzepu, southwestern Taiwan, according to the studies of HUANG *et al.* (2008a) and NORVAL *et al.* (2010), and cumulated values considering both studies altogether. Using the data from NORVAL *et al.* (2010), the occurrence frequency (F) of each prey is calculated.

Class	Order	HUANG <i>et al.</i> (2008a)	NORVAL <i>et al.</i> (2010)		Cumulated
		% items (N = 2355)	% items (N = 2984)	F (N = 502)	% items (N = 5339)
Insecta	Blattaria	0.72	0.50	13	0.60
	Coleoptera	5.99	6.94	113	6.52
	Collembola	0.17	0.34	7	0.26
	Dermaptera	0.04	0.24	6	0.15
	Diptera	3.65	7.86	101	6.01
	Hemiptera	4.76	4.26	100	4.48
	Homoptera	2.72	2.01	50	2.32
	Hymenoptera	49.51	49.93	260	49.75
	Isoptera	1.66	3.02	25	2.42
	Lepidoptera	20.72	6.10	140	12.55
	Mantodea	0.04	0.00	0	0.02
	Neuroptera	0.76	0.24	7	0.47
	Odonata	0.00	0.27	6	0.15
	Orthoptera	0.47	2.68	67	1.70
	Plecoptera	0.00	0.24	7	0.13
	Psocoptera	0.89	0.03	1	0.41
	Thysanoptera	0.09	0.10	3	0.09
Trichoptera	0.43	0.07	1	0.23	
Chilopoda	Scolopendromorpha	0.00	1.58	40	0.88
Diplopoda	Spirobolida	0.00	0.17	5	0.09
Arachnida	Acarina	0.00	0.03	1	0.02
	Aranea	7.39	9.99	166	8.84
Crustacea	Isopoda	0.00	0.91	16	0.51
Gastropoda	Stylommatophora	0.00	1.07	30	0.60
Reptilia	Squamata	0.00	0.17	5	0.09
Unknown		0.00	1.27	25	0.71

PIANKA & VITT, 2003). Prey such as millipedes (Diplopoda) are known to produce toxins, and it is suggested that actively foraging lizards can presumably detect the toxic compounds released by these prey and therefore avoid them, whereas sit-and-wait foragers generally do not (VITT & COOPER, 1986). Seeing as *J. swinhonis* does feed on millipedes, this further supports the suggestion that this species utilizes a sit-and-wait foraging strategy.

Most of the prey items of the *J. swinhonis* from southwestern Taiwan belonged to orders described as prey of *J. swinhonis* in the studies done in other parts of Taiwan. Dietary studies from northern Taiwan (KUO *et al.*, 2007) and Orchid Island (HUANG, 2007) found that hymenopterans (primarily Formicidae) were the most frequently preyed upon items, and although these prey were not as large as some of the other common prey orders, either volumetrically or by mass, they still tended to have

a high index of relative importance (*IRI*; Table 4). As in those studies, hymenopterans comprised a large part of the diet of *J. swinhonis* from southwestern Taiwan.

HUANG (2007) did not record isopterans in the diet of *J. swinhonis* from Orchid Island, while KUO *et al.* (2007) infrequently recorded isopterans in the diet of *J. swinhonis* from northern Taiwan. Although isopterans were the most numerous dietary items in the diet of *J. swinhonis* samples from Yunlin, it is highly unlikely that this is due to a regional dietary variation. Rather, the isopterans recorded were winged sexuals, which would illustrate the opportunistic feeding behaviour of *J. swinhonis*, and how these lizards make use of a temporarily available dietary resource. None of the *J. swinhonis* dietary studies exa-

mined the seasonal utilization of prey or examined the diet of these lizards systematically for a whole year, and thus there is not enough information to comment on the seasonality of prey. However, seasonal differences could exist and deserve further empirical studies. It should also be noted that even though the diet of *J. swinhonis* consist primarily of numerous, relatively common, small prey, such as ants and lepidopteran larvae, these lizards may also eat relatively large prey (Fig. 2).

Since *J. swinhonis* usually perches a short distance above the ground on tree trunks and other objects, but forages readily on the ground (JUN-YI & KAU-HUNG, 1982; KUO *et al.*, 2007), it can be described as a trunk-ground species (WILLIAMS, 1972). This means that the exotic invasive lizard, *A. sagrei*, occu-

Table 4: Occurrence frequency (F), mean percent weight (W) or mean percent volume (V), and index of relative importance (*IRI*) of each type of dietary item in male and female *Japalura swinhonis* from northern Taiwan (data retrieved from KUO *et al.*, 2007) and in adult *J. swinhonis* from Orchid Island (data retrieved from HUANG, 2007). The *IRI* for the Orchid Island population is calculated following BJORN DAL *et al.* (1997) with data from the original publication. The *IRI* for the northern Taiwan population is retrieved from the original publication.

Class	Order	Northern Taiwan						Orchid Island		
		Males (N = 29)			Females (N = 27)			(N = 20)		
		F	W	<i>IRI</i>	F	W	<i>IRI</i>	F	V	<i>IRI</i>
Insecta	Coleoptera	6	5.65	2.52	10	7.15	5.23	1	11.79	2.62
	Hemiptera	5	6.92	2.57	7	5.75	2.94			
	Homoptera	5	11.06	4.11	4	5.62	1.64	2	11.85	5.26
	Hymenoptera	24	28.45	50.7	25	22.45	41.04	16	7.31	25.97
	Isoptera	2	1.80	0.27	0	0	0			
	Lepidoptera	15	32.17	35.83	15	38.55	42.29			
	Orthoptera	4	3.04	0.9	6	0.54	0.24	5	55.05	61.11
	Psocoptera	3	0	0	2	0	0			
	Insect larvae							3	1.97	1.31
Chilopoda	Scolopendromorpha	3	1.53	0.34	3	1.51	0.33	1	7.25	1.61
Diplopoda	Spirobolida	2	0	0	2	4.02	0.59			
Arachnida	Aranea	10	3.18	2.36	15	3.13	3.43	2	4.79	2.13
Crustacea	Isopoda	2	0.77	0.11	5	1.35	0.49			
Gastropoda	Stylommatophora	3	1.30	0.29	3	8.06	1.77			



Figure 2: *Japalura swinhonis* feeding on large prey. (top) A male in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan, preying on a relatively large moth (Sphingidae). (bottom) A female from the same area consuming a stag beetle (Lucanidae) grub.

pies the same niche as *J. swinhonis*, and both species have the same foraging mode. The Levin's measures also indicate that the niche breadth of *A. sagrei* is broader than that of *J. swinhonis*. From the results of this study it is also clear that in areas where these two lizard species are sympatric there is a substantial dietary niche overlap, and therefore competition for prey is very likely. However, *J. swinhonis* males and females have SVLs that range from 22 to 82 mm ($N = 104$; mean \pm SD = 70.5 ± 8.4) and 22 to 74 mm ($N = 59$; mean \pm SD = 58.2 ± 13.9) respectively (G. Norval, personal observation; from a sample of animals larger than what was used for the present study), and are thus substantially larger than *A. sagrei* from populations in Taiwan,

where males and females have SVLs that range from 16 to 64 mm ($N = 522$; mean \pm SD = 46.2 ± 9.1) and 17 to 48 mm ($N = 538$; mean \pm SD = 38.2 ± 5.5), respectively (G. Norval, personal observation). This means that adults of *J. swinhonis* should be able to feed on larger prey than *A. sagrei*. It is also worth pointing out that in interactions in the wild, *A. sagrei* usually gives way to *J. swinhonis* (G. Norval, personal observation). So, even though there is a substantial dietary overlap between these species, it is unlikely to have a negative effect on *J. swinhonis*.

Lister (1976) found that in the presence of competition from sympatric anole species, *A. sagrei* tends to occupy lower perches. However, in the presence of terrestrial predators, *A. sagrei* tends to be more arboreal (SCHOENER *et al.*, 2002; LOSOS, 2009). Both the competition for prey and the microhabitat shift to higher perches result in reduced foraging opportunities and a subsequent reduction in body sizes of these lizards (LISTER, 1976; SCHOENER & SCHOENER, 1978; SCHOENER *et al.*, 2002; LOSOS, 2009). So, competition between *J. swinhonis* and *A. sagrei*, especially in habitats where terrestrial predators such as *Eutropis longicaudata* occur, could reduce the ability of *A. sagrei* to compete with other sympatric saurian species in Taiwan.

It must be noted that, through predation, *A. sagrei* impacts arthropod populations (SPILLER & SCHOENER, 1994; SCHOENER & SPILLER, 1996; SCHOENER *et al.*, 2002; HUANG *et al.*, 2008a,b). Because sympatric *J. swinhonis* and *A. sagrei* prey on many of the same types of prey, it can be expected that they can thus exert substantial pressure on arthropods. How such combined pressures would affect arthropod communities warrants empirical studies.

There does not seem to be an apparent decline in *J. swinhonis* or *A. sagrei* in areas where these lizards are sympatric (G. Norval, personal observation). In highly disturbed and open habitats, such as in *A. catechu* plantations, *A. sagrei* tends to be more abundant than *J. swinhonis* (HUANG *et al.*, 2008a). However, in less disturbed areas, such as parks with large trees, even though *A. sagrei* is present, *J. swinhonis* tends to be more abundant (G. Norval, personal observation). Thus, the differences in the densities of these lizards most likely depend on the habitat structure. *Japalura swinhonis* is more shady-habitat tolerant than *A. sagrei* (HUANG *et al.*, 2008a), which does not occur in closed habitats (LOSOS *et al.*, 1993), so the re-establishment of large areas of broadleaf forests in disturbed lowland areas of Taiwan will contribute to the conservation of *J. swinhonis* and other native forest species. Such areas will also function as reservoirs of species like *J. swinhonis* that can compete with *A. sagrei*, as well as being barriers for its spread.

Acknowledgement

The authors thank Jin-Hsiang Wu for his assistance with the collection of lizards from Yunlin County. The research presented here adhered to the Guidelines for the Use of Live Amphibians and Reptiles in Field Research (SSAR, ASIH, and HL), and the legal requirements of Taiwan, R.O.C. Since *A. sagrei* is an exotic invasive species in Taiwan, which the authorities wishes to exterminate, and *J. swinhonis* is not listed as a protected species, and because the collection was not done within a National Park or other conservation area, no collection permit or other documentation was required.

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