

Does caudal autotomy affect the abdominal fat and liver masses of free-living reproductively mature Brown Anoles, *Anolis sagrei* DUMÉRIL & BIBRON, 1837, from southwestern Taiwan?

(Squamata: Sauria: Dactyloidae)

Beeinflußt ein autotomierter Schwanz die Bauchfett- und Lebermasse bei freilebenden, fortpflanzungsreifen *Anolis sagrei* DUMÉRIL & BIBRON, 1837 von Südwesttaiwan?
(Squamata: Sauria: Dactyloidae)

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KURZFASSUNG

Im Rahmen einer Studie zum Fortpflanzungszyklus von *Anolis sagrei* DUMÉRIL & BIBRON, 1837, wurden Tiere beiderlei Geschlechts in der Zeit von März 2002 bis März 2003 in einem Landwirtschaftsgebiet in Santzepu, Bezirk Sheishan, Kreis Chiayi, Südwest-Taiwan gesammelt. Mittels unabhängiger *t*-Tests und wenn die Voraussetzungen für *t*-Tests wesentlich verletzt waren mit Mann-Whitney U-Tests wurden die monatlichen Veränderungen in den mittleren Massenzahlen des abdominalen Fettkörpers und der Leber bei *A. sagrei* Exemplaren mit autotomierten und solchen mit unversehrten Schwänzen verglichen. Dabei ließen sich keine statistisch signifikanten Unterschiede in den Monatsmittelwerten der Massenzahlen des abdominalen Fettkörpers und der Leber zwischen *A. sagrei* Exemplaren mit autotomierten und solchen mit unversehrten Schwänzen feststellen. Die Autoren vermuten, daß die Ergebnisse der Studie durch eine Zunahme der aufgenommenen Nahrungsmenge bei *A. sagrei* Exemplaren mit autotomiertem Schwanz bedingt sind.

ABSTRACT

Anolis sagrei DUMÉRIL & BIBRON, 1837, of both genders, were collected from an agricultural area in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan, during the period March 2002 to March 2003, as part of a reproductive cycle study. Unpaired *t*-tests, or where the assumptions of the *t*-test were substantially violated, the Mann-Whitney U-test were used to compare the monthly variations in the mean abdominal fat body mass index and mean liver mass index of the *A. sagrei* specimens that had not experienced tail autotomy and those that had. No statistically significant variations in the monthly mean abdominal fat body mass indexes or monthly mean liver mass indexes of lizards that had not experienced caudal autotomy and those that had were noted. The authors hypothesize that the results of this study is due to an increase in foraging activity in *A. sagrei* specimens that experienced tail autotomy.

KEY WORDS

Reptilia: Squamata: Sauria: Dactyloidae, Iguanidae s. l.: *Anolis sagrei*, caudal autotomy, defense mechanism, energy allocation, tail regeneration, ecology, physiology, behavior, Taiwan

INTRODUCTION

Autotomy, i.e., the sacrifice of parts of the body of an animal, as a means of allowing escape during an encounter with a predator, is a defensive mechanism in some vertebrates and invertebrates (GOODENOUGH et al. 2001). Some animals actually utilize luring by, and autotomy of, less significant anatomical parts to draw predatory strikes away from the more vital parts. The most

well known form of such an adaptation and behavior is tail (caudal) coloration and autotomy in tailed amphibians and saurians, in which the tail, or at least its more distal part, is conspicuously marked and lures predator strikes toward the tail and away from the more vulnerable head and body region (ARNOLD 1984; VAN BUSKIRK et al. 2004; BATEMAN & FLEMING 2009).

Tail autotomy is a common defensive mechanism in lizards as a response to attempted predation (VITT et al. 1977; ARNOLD 1984; BATEMAN & FLEMING 2009). However, since the tails of lizards may be utilized 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 & WHITING 2003; BATEMAN & FLEMING 2009).

The present study was prompted by the following observations: On the 19th of July, 2002, a male Brown Anole, *Anolis sagrei* DUMÉRIL & BIBRON, 1837, which is an invasive species in Taiwan (NORVAL et al. 2002), was collected from the edge of a rice paddy next to a tarred road in Santzepu, Sheishan District, Chiayi County, Taiwan (23°25'46"N, 120°28'54"E; datum: WGS84). As it was removed from the fine-meshed fishing scoop net, which was used for capturing it, it was noted that it had two tails (Fig. 1). The lizard had a snout-vent length (SVL) of 53 mm, and body mass (BM) of 4.1 g. The tail to the left had a length of 65 mm, and the tail length (TL) to the right was 56 mm. Dissection and a subsequent histological examination revealed that a section of its tail had been lost, and the lizard then had started to regenerate a new tail. The lizard subsequently suffered a second injury to the left side of its tail in a

region of the remaining original tail. This injury entered the muscles and possibly involved some damage to the nerve tissue in the tail, but it was not sufficient to cause the loss of the tail. It did however trigger the development of another regenerated tail. Even though the lizard had no abdominal fat bodies, which was the case in ca. 50 % of the males sampled that month (including specimens that had not experienced tail autotomy and some that had), the histological examination of the right testis revealed that it contained an abundance of sperm, spermatids, and metamorphosing spermatids (maximum stage of spermatogenesis), indicating that the animal was not only able to regenerate a tail twice, but it could also still meet the energetic demands for reproduction. This is surprising because the metabolic costs of regenerating a lost portion of the tail will bring an additional energetic burden to a lizard (MCCONNACHIE & WHITING 2003; NAYA et al. 2007).

A lizard that suffered caudal autotomy can meet the energetic demands for regenerating a lost portion of its tail by increased foraging activities and/or by directing energy away from growth, maintenance and reproduction (ARNOLD 1988). In this study, the authors attempted to address the question of whether there are differences in the abdominal fat body and liver masses of *A. sagrei* specimens that had suffered tail autotomy and conspecifics that had not, which could be an indication of the expenditure of stored energy for regenerating a lost tail.

MATERIALS AND METHODS

Study area.— This study was conducted in an agricultural area (23°25'N, 120°28'E) in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan. Small stands of secondary forests, fallow fields, cultivated fields, and the gardens of a county government and several smaller private nurseries are the main habitat types in this area. Several crop types, such as betel nut (*Areca catechu*), papaya (*Carica papaya*), lime (*Citrus aurantifolia*), banana (*Musa sapientum*), and rice (*Oryza sativa*) are cultivated in this area and with the exception of

rice, usually on a relatively small scale. A small creek flows from the foothills, northeast from the study site, in a southwestern direction through the study site.

Field data.— For this study, *A. sagrei* males and females, which were sampled during the period March 2002 to March 2003 as part of a reproductive cycle study, were utilized (for the number of specimens studied see RESULTS). The collected lizards were treated as follows: Each lizard was killed with ether; the snout-vent length (SVL) and tail length (TL) were measured with a

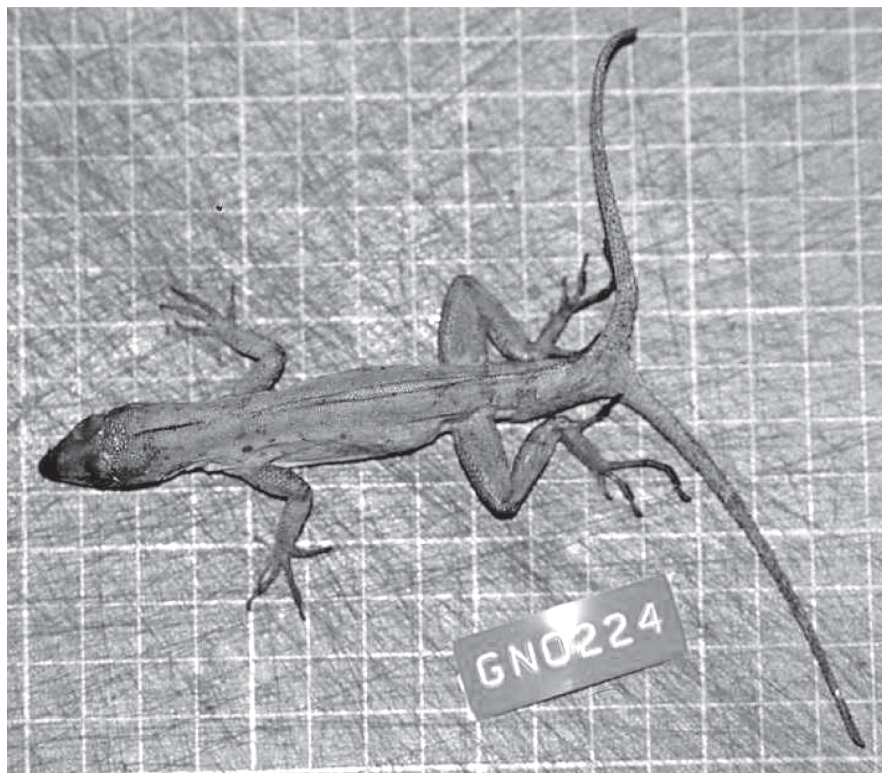


Fig. 1: Dorsal view of the Brown Anole (*Anolis sagrei*) male with bifurcated tail, collected on the 19th of July 2002, prior to dissection (photographed by Gerrut Norval).

Abb. 1: Rückenansicht eines gabelschwänzigen männlichen Bahama-Anolis, *Anolis sagrei* DUMÉRIL & BIBRON, 1837, gesammelt am 19. Juli 2002, vor der Sektion (Photo: Gerrut Norval).

transparent plastic ruler to the nearest mm. The tail was scored as complete or broken, and if the animal had experienced tail autotomy, the regenerated portion was measured with a transparent plastic ruler to the nearest mm. The lizard was then weighed to the nearest 0.1 g with a YC e68 digital scale, and dissected by making a mid-ventral incision, after which the abdominal fat body (corpora adiposa) of both sides, the liver and the stomach were removed. The abdominal fat body of both sides and the liver were weighed (wet weight) to the nearest 0.01 g with an FX-1200, A & D Weighing electronic scale. All the specimens, except for the right testis, stomachs and stomach contents, were fixed in 10 % formalin and preserved in 75 % ethanol. The stomach and stomach

contents were preserved in 75 % ethanol only, and the testis was treated as required for histology.

To determine the reproductive state of the males, the right testis was dehydrated with a tissue processor (ETP-300CV, Sakura, Tokyo, Japan), embedded in paraffin, sectioned at 5µm, 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 contain spermatogonia and Sertoli cells only; (3) recrudescence –

seminiferous tubules exhibit markedly increased cellularity, with primary spermatocytes predominating; or (4) spermiogenic – sperm, spermatids, and metamorphosing spermatids abundant (NORVAL et al. 2012).

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 (NORVAL et al. 2012).

To eliminate factors such as inconsistent tail lengths due to tail autotomy, and the mass of stomach and gut contents, the abdominal fat body and liver masses of the *A. sagrei* specimens used in this study were

expressed as a proportionate index (organ mass / SVL $\times$ 100); i.e., mean abdominal fat-body mass index (AFBMI) and mean liver mass index (LMI).

Statistical study. – The normality of the distribution of the data was checked with one-sample Kolmogorov-Smirnov tests. Unpaired *t*-tests with Welch correction, or where the assumptions of the *t*-test were substantially violated (i.e., non-normal distribution), Mann-Whitney *U*-tests, were used to compare the monthly variations in the mean abdominal fat body mass indexes (AFBMI) and mean liver mass indexes (LMI) of lizards that had not experienced caudal autotomy and those that had. All the statistical analyses were performed with the statistics software package Prism 6 (Graphpad Software, San Diego, CA). When applying statistical decision theory, $\alpha \leq 0.05$ was used to assign significance.

RESULTS

Two hundred and twenty-three male and 215 female *Anolis sagrei* specimens were collected. The males ranged in SVL, TL and BM, from 36 to 64 mm, 13 to 125 mm, and 1.3 to 6.6 g respectively, while the SVL, TL and BM of the females ranged from 28 to 47 mm, 8 to 90 mm, and 0.6 to 3.0 g respectively. Stages of spermiogenesis were observed in males as small as 30 mm SVL (NORVAL et al. 2012), so this was considered the size at which the males can become sexually mature. Females attained a sexually mature size at a SVL of 34 mm (NORVAL et al. 2012). Of the 215 female *A. sagrei* collected, ten females were not yet sexually mature (juveniles). Two males and a female specimen were found to suffer from clinical conditions (NORVAL et al. 2005; NORVAL et al. 2006) and during biopsy four male specimens were damaged. All the specimens that were juveniles, damaged or suffering from clinical conditions, were excluded from the study. The mean SVL, TL and BM of the male specimens used in this study were 51.0 mm (SD $\pm$ 6.07), 92.03 mm (SD $\pm$ 19.97), and 3.86 g (SD $\pm$ 1.32) respectively, while that of the female specimens were 40.82 mm (SD $\pm$ 3.23), 69.28

mm (SD $\pm$ 14.49), and 1.88 g (SD $\pm$ 0.48), respectively.

For this study, only reproductively mature animals were used. Male ($N = 21$) and female ($N = 11$) lizards that had suffered caudal autotomy, but that lacked indications of caudal regeneration, were also excluded, since the possibility 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 and August 2002. The male samples from these months were thus also excluded from the analyses. The number of lizards from every month, used in this study, are given in Tables 1 and 2, and a summary of the means of SVL, TL, TL/SVL, AFBMI, LMI and the regenerated portion of the tail (expressed as a percentage of the total tail length) of the specimens that experienced tail autotomy and regeneration, are presented in Table 3.

No statistically significant variations in the monthly mean AFBMI and monthly mean LMI of lizards that had not experienced caudal autotomy, and those that had, were noted (Table 4).

Table 1: The numbers (N) of the sampled male specimens of *Anolis sagrei* DUMÉRIL & BIBRON, 1837, used in the caudal autotomy study, and the monthly range, mean $\pm$ standard deviation and median (in parenthesis) of their mean abdominal fat body mass indexes (AFBMI) and mean liver mass indexes (LMI).

Tab. 1: Anzahl (N) der in der Schwanz-Autotomiestudie untersuchten Männchen von *Anolis sagrei* DUMÉRIL & BIBRON, 1837 sowie Spannweite, Mittelwert $\pm$ Standardabweichung und Median (in Klammern) der Monatsmittelwerte der Massenzahlen des abdominalen Fettkörpers (AFBMI) und der Leber (LMI).

Month / Monat	Males with an original tail Männchen mit unversehrtem Schwanz			Males with a regenerated tail Männchen mit Schwanzregenerat		
	N	AFBMI	LMI	N	AFBMI	LMI
Apr 2002	10	0.03 $\pm$ 0.04 (0.02)	0.25 $\pm$ 0.07 (0.24)	3	0.08 $\pm$ 0.07 (0.10)	0.32 $\pm$ 0.45 (0.30)
May 2002	9	0.06 $\pm$ 0.05 (0.06)	0.29 $\pm$ 0.08 (0.30)	4	0.03 $\pm$ 0.04 (0.03)	0.29 $\pm$ 0.07 (0.29)
Jun 2002	11	0.16 $\pm$ 0.11 (0.14)	0.33 $\pm$ 0.06 (0.33)	2	0.18 $\pm$ 0.03 (0.18)	0.39 $\pm$ 0.02 (0.39)
Jul 2002	9	0.05 $\pm$ 0.06 (0.03)	0.24 $\pm$ 0.08 (0.23)	6	0.03 $\pm$ 0.05 (0.00)	0.28 $\pm$ 0.09 (0.25)
Sep 2002	12	0.15 $\pm$ 0.09 (0.16)	0.20 $\pm$ 0.04 (0.20)	3	0.30 $\pm$ 0.25 (0.22)	0.20 $\pm$ 0.06 (0.20)
Oct 2002	13	0.21 $\pm$ 0.15 (0.19)	0.26 $\pm$ 0.06 (0.26)	7	0.15 $\pm$ 0.12 (0.21)	0.25 $\pm$ 0.08 (0.23)
Nov 2002	8	0.41 $\pm$ 0.16 (0.34)	0.32 $\pm$ 0.07 (0.30)	3	0.34 $\pm$ 0.24 (0.35)	0.30 $\pm$ 0.05 (0.29)
Dec 2002	12	0.32 $\pm$ 0.12 (0.29)	0.32 $\pm$ 0.09 (0.31)	2	0.29 $\pm$ 0.03 (0.29)	0.17 $\pm$ 0.02 (0.17)
Jan 2003	16	0.22 $\pm$ 0.10 (0.21)	0.27 $\pm$ 0.06 (0.26)	2	0.26 $\pm$ 0.22 (0.26)	0.26 $\pm$ 0.15 (0.26)
Feb 2003	8	0.30 $\pm$ 0.15 (0.31)	0.38 $\pm$ 0.08 (0.37)	7	0.23 $\pm$ 0.13 (0.18)	0.31 $\pm$ 0.10 (0.25)
Mar 2003	8	0.09 $\pm$ 0.08 (0.08)	0.28 $\pm$ 0.06 (0.26)	7	0.13 $\pm$ 0.10 (0.13)	0.26 $\pm$ 0.06 (0.28)

Table 2: The numbers (N) of the sampled female specimens of *Anolis sagrei* DUMÉRIL & BIBRON, 1837, used in the caudal autotomy study, and the monthly range, mean $\pm$ standard deviation and median (in parenthesis) of their mean abdominal fat body mass indexes (AFBMI) and mean liver mass indexes (LMI).

Tab. 2: Anzahl (N) der in der Schwanz-Autotomiestudie untersuchten Weibchen von *Anolis sagrei* DUMÉRIL & BIBRON, 1837 sowie Spannweite, Mittelwert $\pm$ Standardabweichung und Median (in Klammern) der Monatsmittelwerte der Massenzahlen des abdominalen Fettkörpers (AFBMI) und der Leber (LMI).

Month / Monat	Females with an original tail Weibchen mit unversehrtem Schwanz			Females with a regenerated tail Weibchen mit Schwanzregenerat		
	N	AFBMI	LMI	N	AFBMI	LMI
Mar 2002	11	0.20 $\pm$ 0.08 (0.21)	0.25 $\pm$ 0.07 (0.24)	4	0.18 $\pm$ 0.08 (0.17)	0.27 $\pm$ 0.08 (0.28)
Apr 2002	15	0.05 $\pm$ 0.05 (0.05)	0.26 $\pm$ 0.05 (0.28)	5	0.03 $\pm$ 0.03 (0.05)	0.24 $\pm$ 0.02 (0.24)
May 2002	12	0.06 $\pm$ 0.06 (0.05)	0.32 $\pm$ 0.08 (0.31)	7	0.09 $\pm$ 0.09 (0.07)	0.35 $\pm$ 0.10 (0.32)
Jun 2002	11	0.10 $\pm$ 0.08 (0.07)	0.38 $\pm$ 0.13 (0.36)	7	0.15 $\pm$ 0.09 (0.16)	0.36 $\pm$ 0.06 (0.34)
Jul 2002	5	0.03 $\pm$ 0.06 (0.00)	0.26 $\pm$ 0.07 (0.27)	12	0.03 $\pm$ 0.04 (0.00)	0.33 $\pm$ 0.08 (0.35)
Aug 2002	11	0.05 $\pm$ 0.08 (0.00)	0.22 $\pm$ 0.07 (0.21)	4	0.00 (0.00)	0.26 $\pm$ 0.03 (0.24)
Sep 2002	9	0.05 $\pm$ 0.09 (0.03)	0.22 $\pm$ 0.06 (0.22)	4	0.06 $\pm$ 0.07 (0.05)	0.23 $\pm$ 0.06 (0.23)
Oct 2002	11	0.08 $\pm$ 0.09 (0.05)	0.23 $\pm$ 0.09 (0.20)	5	0.12 $\pm$ 0.17 (0.00)	0.23 $\pm$ 0.07 (0.21)
Nov 2002	11	0.25 $\pm$ 0.11 (0.29)	0.23 $\pm$ 0.07 (0.22)	4	0.26 $\pm$ 0.21 (0.28)	0.23 $\pm$ 0.06 (0.23)
Dec 2002	2	0.27 $\pm$ 0.03 (0.27)	0.20 $\pm$ 0.05 (0.20)	8	0.24 $\pm$ 0.15 (0.23)	0.27 $\pm$ 0.11 (0.26)
Jan 2003	5	0.21 $\pm$ 0.06 (0.21)	0.23 $\pm$ 0.06 (0.21)	5	0.27 $\pm$ 0.08 (0.28)	0.21 $\pm$ 0.05 (0.21)
Feb 2003	6	0.16 $\pm$ 0.07 (0.13)	0.22 $\pm$ 0.04 (0.21)	4	0.33 $\pm$ 0.13 (0.29)	0.32 $\pm$ 0.06 (0.34)
Mar 2003	6	0.20 $\pm$ 0.14 (0.20)	0.34 $\pm$ 0.08 (0.32)	9	0.13 $\pm$ 0.10 (0.13)	0.27 $\pm$ 0.09 (0.28)

DISCUSSION

Anolis sagrei is a diurnal trunk-ground species that favors a variety of sunny habitat types and areas disturbed by anthropogenic activities (SCHWARTZ & HENDERSON 1991). This lizard is primarily a predator of arthropods and small mollusks (SCHOENER

1968; RODRIGUEZ SCHETTINO 1999; NORVAL et al. 2010), although some large males occasionally also consume smaller lizards (CAMPBELL & GERBER 1996; NORVAL 2007; KRYSKO & WASILEWSKI 2012). These sit-and-wait (ambush) predators usually perch

Table 3: Summary of the ranges, with the mean and standard deviation in parenthesis, of the snout-vent length (SVL), tail length (TL), and the ratio TL/SVL of the specimens of *Anolis sagrei* DUMÉRIL & BIBRON, 1837, used in this study. For lizards that had regenerated tails, the ranges, with the mean and standard deviation in parenthesis, of the regenerated portion are expressed as a percentage of the tail's total tail length (Regenerated %).

Tab. 3: Übersicht über Spannweiten, Mittelwerte und Standardabweichungen (letzte beiden in Klammern) in der Kopf-Rumpflänge (SVL), Schwanzlänge (TL) und dem Verhältnis TL/SVL bei den untersuchten Exemplaren von *Anolis sagrei* DUMÉRIL & BIBRON, 1837. Für die Echsen mit Schwanzregenerat sind Spannweiten, Mittelwerte und Standardabweichungen (letzte beiden in Klammern) des regenerierten Schwanzanteils (Regenerated %) als Prozentsatz seiner gesamten Länge angegeben.

	Males / Männchen		Females / Weibchen	
	with original tails (N = 116)	with regenerated tails (N = 46)	with original tails (N = 115)	with regenerated tails (N = 78)
	Schwanz unversehrt	Schwanz regeneriert	Schwanz unversehrt	Schwanz regeneriert
SVL (mm)	39 – 63 (51.1 ± 5.6)	38 – 64 (51.5 ± 7.0)	34 – 47 (40.4 ± 3.2)	34 – 47 (41.5 ± 3.3)
TL (mm)	70 – 125 (100.3 ± 12.1)	26 – 120 (75.7 ± 22.7)	60 – 90 (76.1 ± 7.0)	11 – 82 (62.8 ± 13.8)
TL/SVL	1.8 – 2.2 (2.0 ± 0.1)	0.5 – 2.1 (1.5 ± 0.4)	1.8 – 2.2 (1.9 ± 0.1)	0.3 – 2.0 (1.5 ± 0.3)
Regenerated (%)	—	1.4 – 76.5 (39.2 ± 23.8)	—	1.3 – 82.0 (32.1 ± 22.9)

Table 4: The mean ± standard deviation and median (in parenthesis) of the monthly mean abdominal fat body mass indexes (AFBMI) and monthly mean liver mass indexes (LMI) of the specimens of *Anolis sagrei* DUMÉRIL & BIBRON, 1837, that had not experienced caudal autotomy and those that had, and the results of their comparisons.

Tab. 4: Mittelwert ± Standardabweichung und Median (in Klammern) der Monatsmittelwerte der Massenzahlen des abdominalen Fettkörpers (AFBMI) und der Leber (LMI) bei *Anolis sagrei* DUMÉRIL & BIBRON, 1837 mit unversehrten und regenerierten Schwänzen sowie die Signifikanz des Unterschiedes.

		Lizards with original tails Echsen mit unversehrt Schwanz	Lizards with regenerated tails Echsen mit Schwanz- regenerat	Result / Ergebnis
Males / Männchen	AFBMI	0.18 ± 0.12 (0.16)	0.18 ± 0.11 (0.18)	$t = 0.0313, df = 19, p = 0.9754$
	LMI	0.29 ± 0.05 (0.28)	0.28 ± 0.06 (0.29)	$t = 0.4094, df = 19, p = 0.6868$
Females / Weibchen	AFBMI	0.13 ± 0.09 (0.10)	0.15 ± 0.11 (0.13)	$t = 0.3759, df = 23, p = 0.7104$
	LMI	0.26 ± 0.05 (0.23)	0.28 ± 0.05 (0.27)	$U = 60, p = 0.2226$

head-downward and frequently make forays to catch prey, after which they return to their perch (SCHWARTZ & HENDERSON 1991). Studies involving *Anolis carolinensis* VOIGT, 1832, have found that tail autotomy impedes the jumping (GILLIS et al. 2009) and sprinting (McELROY & BERGMANN 2013) abilities of these lizards. *Anolis sagrei* and *A. carolinensis* are fairly similar in lifestyle, so an *A. sagrei* individual that suffered tail autotomy would most likely not only have a reduced ability to escape from predators, but it would also have some difficulty in capturing prey more successfully. SCHWARTZ & HENDERSON (1991) made reference to an *A. sagrei* male (SVL not stated) that regenerated almost one inch of an autotomized tail in 26 days, and in another study in Taiwan it

was found that *A. sagrei* males can regenerate an autotomized tail at a rate of on average 8.9 mm (SD ± 11.3) per month, and females at a rate of on average 6.9 mm (SD ± 7.6) per month (NORVAL et al. 2014). Since it was found that tail autotomy is of minor consequence to an *A. sagrei* male once it has established a territory, and that tail autotomy does not result in the loss of its territory (KAISER & MUSHINSKY 1994), it can be assumed that the rapid regeneration of an autotomized tail is most likely related to primarily restoring locomotor stabilization.

However, the regeneration of an autotomized tail would require energy and material, diverted from other bodily functions, or from increased food intake (BALLINGER &

TINKLE 1979; ALTHOFF & THOMPSON 1994). In the study by NORVAL et al. (2014) it was found that *A. sagrei* males and females that had suffered 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). It was however found that *A. sagrei* males that had not suffered tail autotomy had a significantly faster tail growth rate than conspecific females (NORVAL et al. 2014). Since females tend to be more terrestrial than the males (SCHOENER 1968; SCHWARTZ & HENDERSON 1991; RODRIGUEZ SCHETTINO 1999), and may thus jump less frequently, the differences in tail regeneration rates are likely to reflect differences in the life styles of the sexes.

It is unlikely that the energy for tail regeneration is only from energy diverted away from growth. In *A. sagrei* females, reproduction is energy demanding and reproductively active females tend to exhibit reduced growth and survival (COX et al. 2010), since energy is only diverted away from reproduction and towards other bodily functions once the demands for reproduction have been met (VITT et al. 1977). In many *Anolis* species males spend less time

foraging and more time displaying during the breeding season (LOSOS 2009). The authors are unaware of daily activity pattern studies involving *A. sagrei*, but in studies pertaining to reproduction in this species it is evident that during the breeding season males experience a reduction in stored abdominal fat body mass (LICHT & GORMAN 1970; SEXTON & BROWN 1977; LEE et al. 1989; TOKARZ et al. 1998; SANZ OCHOTORENA & URIBE ARANZÁBAL 1999), suggesting that sperm production and reproductive behavior are energetically costly for males. It is thus surprising that the present study did not find significant differences in the abdominal fat and liver masses of the *A. sagrei* specimens that had not experienced tail autotomy and those that had. Since it has been found that in some lizards reduced body growth rate during tail regeneration can be minimized by increased food ingestion (BALLINGER & TINKLE 1979), it is very likely that the outcome of this study is the result of an increased foraging activity in *A. sagrei* specimens that experienced tail autotomy. An empirical study into the activity patterns and foraging frequency of *A. sagrei* specimens that experienced tail autotomy and conspecifics that had not can substantiate this hypothesis.

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REFERENCES

- ALTHOFF, D. M. & THOMPSON, J. M. (1994): The effects of tail autotomy on survivorship and body growth of *Uta stansburiana* under conditions of high mortality.- *Oecologia*, Berlin etc.; 100: 250-255.
- ARNOLD, E. N. (1984): Evolutionary aspects of tail shedding in lizards and their relatives.- *Journal of Natural History*, London; 18: 127-169.
- ARNOLD, E. N. (1988): Caudal autotomy as a defense; pp. 236-273. In: GANS, C. & HUEY, R. B. (Eds.): *Biology of the Reptilia*. Vol. 16; New York (Alan R. Liss, Inc.).
- BALLINGER, R. E. & TINKLE, D. W. (1979): On the cost of tail regeneration to body growth in lizards.- *Journal of Herpetology*, Houston, etc.; 13 (3): 374-375.
- BATEMAN, P. W. & 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*, London; 277: 1-14.
- CAMPBELL, T. S. & GERBER, G. P. (1996): *Anolis sagrei* (Brown anole). *Sauropagy*.- *Herpetological Review*, New York; 27 (4): 200.
- COX, R. M. & PARKER, E. U. & CHENEY, D. M. & LIEBL, A. L. & MARTIN, L. B. & CALSBEEK, R. (2010): Experimental evidence for physiological costs underlying the trade-off between reproduction and survival.- *Functional Ecology*, Oxford; 24: 1262-1269.
- GILLIS, G. B. & BONVINI, L. A. & IRSCHICK, D. J. (2009): Losing stability: tail loss and jumping in the

- arboreal lizard *Anolis carolinensis*.- Journal of Experimental Biology, Cambridge; 212: 604-609.
- GOLDBERG, S. R. & KRAUS, F. & BURSEY, C. R. (2002): Reproduction in an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawaii.- Pacific Science, Honolulu; 56 (2): 163-168.
- GOODENOUGH, J. & MCGUIRE, B. & WALLACE, R. A. (2001): Perspectives on animal behavior. New York (John Wiley and Sons, Inc.), pp. 542.
- KAISER, B. W. & MUSHINSKY, H. R. (1994): Tail loss and dominance in captive adult male *Anolis sagrei*.- Journal of Herpetology, Houston, etc.; 28 (3): 342-346.
- KRYSKO, K. L. & WASILEWSKI, J. A. (2012): *Anolis sagrei* (Brown anole). Saurorhagy.- Herpetological Review, New York; 43 (3): 477-478.
- LEE, J. C. & CLAYTON, D. & EISENSTEIN, S. & PEREZ, I. (1989): The reproductive cycle of *Anolis sagrei* in southern Florida.- Copeia, Washington; 1989 (4): 930-937.
- LICHT, P. & GORMAN, G. C. (1970): Reproductive and fat cycles in Caribbean *Anolis* lizards.- University of California Publications in Zoology, Berkeley; 95: 1-52.
- LOSOS, J. B. (2009): Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Berkeley, California (University of California Press), pp. 507.
- MCCONNACHIE, S. & WHITING, M. (2003): Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*.- African Zoology, Pretoria; 38 (1): 57-65.
- MCLEROY, E. J. & BERGMANN, P. J. (2013): Tail autotomy, tail size, and locomotor performance in lizards.- Physiological and Biochemical Zoology, Chicago; 86 (6): 669-679.
- NAYA, D. E. & VELOSO, C. & MUÑOZ, J. L. P. & BOZINOVIC, F. (2007): Some vaguely explored (but not trivial) costs of tail autotomy in lizards.- Comparative Biochemistry and Physiology, New York; (A) 146: 189-193.
- NORVAL, G. (2007): A report on male *Anolis sagrei* saurorhagy in Chiayi County, Taiwan.- Herpetological Bulletin, London; 102: 34-37.
- NORVAL, G. & GOLDBERG, S. R. & MAO, J. J. (2012): The reproductive cycle of the brown anole (*Anolis sagrei*), an invasive lizard species in Taiwan.- Russian Journal of Herpetology, Moskva; 19 (1): 75-81.
- NORVAL, G. & HSIAO, W. F. & HUANG, S. C. & CHEN, C. K. (2010): The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan.- Russian Journal of Herpetology, Moskva; 17 (2): 131-138.
- NORVAL, G. & HUANG, S. C. & MAO, J. J. (2014): Notes on the growth rates of *Anolis sagrei* DUMÉRIE & BIBRON, 1837, from a small betelnut palm (*Areca catecha*, L.) plantation in southwestern Taiwan.- [International Reptile Conservation Foundation] IRCF Reptiles & Amphibians; 21 (1): 9-15. [Journal available at < <http://www.ircf.org/journal/> >].
- NORVAL, G. & MAO, J. J. & CHU, H. P. & CHEN, L. C. (2002): A new record of an introduced species, the brown anole (*Anolis sagrei*) (DUMÉRIE & BIBRON, 1837), in Taiwan.- Zoological Studies, Taipei; 41 (3): 332-336.
- NORVAL, G. & TUNG, C. L. & COOPER, J. E. (2005): A report of hepatic granuloma in free-living brown anoles (*Anolis sagrei*) in Taiwan: two cases.- Herpetological Bulletin, London; 93: 9-13.
- NORVAL, G. & TUNG, C. L. & COOPER, J. E. (2006): *Anolis sagrei* (Brown anole). Testicular pathology.- Herpetological Review, New York; 37 (2): 219-220.
- RODRIGUEZ SCHETTINO, L. R. (1999): The iguanid lizards of Cuba. Gainesville, Florida (University Press of Florida), pp. 428.
- SANZ OCHOTORENA, A. & 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, La Habana; 13: 26-32.
- SCHOENER T. W. (1968): The *Anolis* lizards of Bimini: resource partitioning in a complex fauna.- Ecology, New York; 49 (4): 704-726.
- SCHWARTZ, A. & HENDERSON, R. W. (1991): Amphibians and reptiles of the West Indies: descriptions, distributions and natural history. Gainesville, Florida (University of Florida Press), pp. XVI, 720.
- SEXTON, O. J. & BROWN, K. M. (1977): The reproductive cycle of an iguanid lizard *Anolis sagrei*, from Belize.- Journal of Natural History, London; 11: 241-250.
- TOKARZ, R. R. & MCMANN, S. & SEITZ, L. & JOHN-ADLER, H. (1998): Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*).- Physiological Zoology, Chicago; 71 (2): 139-146.
- VAN BUSKIRK, J. & ASCHWANDEN, J. & BUCKELMÜLLER, I. & REOLON, S. & RÜTTIMAN, S. (2004): Bold tail coloration protects tadpoles from dragonfly strikes.- Copeia, Washington; 2004 (3): 599-602.
- VITT, L. J. & CONGDON, J. D. & DICKSON, N. A. (1977): Adaptive strategies and energetics of tail autotomy in lizards.- Ecology, New York; 58: 326-337.

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