Advertisement and close-range encounter call of *Arthroleptis schubotzi* NIEDEN, 1911, with notes on phonotaxis and sexual dimorphism in the third manual digit
(Anura: Arthroleptidae)

Anzeigeruf und Warnruf von *Arthroleptis schubotzi* NIEDEN, 1911 und Bemerkungen über die Phonotaxis und den Sexualdimorphismus des dritten Fingers
(Anura: Arthroleptidae)

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KURZFASSUNG

Es werden der Anzeigeruf und der Warnruf von *Arthroleptis schubotzi* NIEDEN, 1911 beschrieben. Die Aufnahmen erfolgten *in situ* auf dem Gelände der Makerere University Biological Field Station, Kibale Forest National Park, Uganda.

Der Anzeigeruf ist ein hochfrequenter metallisch klingender Ruf, der sich aus zwei oder drei Silben zusammensetzt. Die dominante Frequenz beträgt um 4700 Hz, die Rufdauer im Mittel 158 ms. Der kreischende Warnruf dieser Art war bisher unbekannt. Er setzt sich aus ein bis zwei gepulsten Silben und einer abschließenden hochfrequenten Silbe zusammen. Die dominante Frequenz der gepulsten Silben liegt bei 4400 Hz, die der darauffolgenden hochfrequenten Silbe bei 4600 Hz. Die mittlere Dauer des Warnrufes beträgt 541 ms, wobei die Dauer der ersten gepulste Silbe 334 ms beträgt.

ABSTRACT

The advertisement and encounter calls of *Arthroleptis schubotzi* NIEDEN, 1911 are described. Recordings were taken *in situ* at the Makerere University Biological Field Station, in Kibale Forest National Park, Uganda.

The advertisement call is a high-pitched metallic sound, with either two or three notes per call, a dominant frequency around 4700 Hz and a mean call duration of 158 ms. The encounter call, previously unknown for this species, is a screeching sound, consisting of a series of pulsed notes (pulse train) ending with a single high pitched note. Minor variations exist in the number of pulsed notes. The dominant frequency of the pulse train is 4400 Hz, the high-pitched sound centers around 4600 Hz. The mean duration of the encounter call is 541 ms. The pulsed note lasts 334 ms and is the longest note in the entire call repertoire of *A. schubotzi*.

KEY WORDS

Amphibia: Anura: Arthroleptidae: *Athroleptis schubotzi*, Schubotz's Squeaker, leaf litter frog, bioacoustics, advertisement call, encounter call, behaviour, ethology, Kibale Forest National Park, Uganda

INTRODUCTION

Schubotz's Squeaker, *Arthroleptis schubotzi* NIEDEN, 1911, is a terrestrial leaf-litter frog inhabiting moist undergrowth in savannah and forested areas of East Africa (CHANNING & HOWELL 2006). The taxonomy of arthroleptid frogs is complex and has experienced numerous phylogenetic reclassifications in recent years (FROST et al. 2006; BLACKBURN 2008). Species identification based on morphological traits alone can be misleading (LÖTTERS et al. 2004; ZIMKUS & BLACKBURN 2008) and careful analysis of species-specific vocalizations is a useful tool for resolving taxonomical uncertainties in anurans (KÖHLER et al. 2005). The vocalization of *A. schubotzi* has only crudely been described as a harsh series of double chirps (CHANNING & HOWELL 2006), resembling that of a loud cricket (DE WITTE 1941). Anecdotal descriptions are insufficient for clarifying taxonomic ambiguities. The aim of this study is to provide a formal description of the advertisement call of this species to complement existing morphological and phylogenetic descriptions (Channing & Howell 2006; Spawls et al. 2006; Blackburn 2008) and to document a second yet unknown call type, fitting the description of (and from here on referred to as) an encounter call (Wells 2007). Spectrograms as well as oscillograms are provided for both call types.

In addition, calls are discussed in an ecological and behavioral context with notes from field observations, highlighting the territoriality and phonotactic responses of males to playbacks with con-specific advertisement calls. Lastly, explanations for the sexually dimorphic elongation of the third manual digit in males are reviewed.

MATERIALS AND METHODS

Fieldwork was conducted from the 13th to 21st of August 2010, at the Makerere University Biological Field Station, in Kibale Forest National Park, Uganda (0°33'55"N 30°21'00"E).

Arthroleptis schubotzi have been observed at the end of the dry season and the first days during the beginning rainy season. The habitat of these frogs is preferentially on the ground at the edge of and partly in the rainforest. Males prefer hiding in undergrowth, under small branches, shrubs or dry leaves and in graminaceous vegetation. Due to these microhabitat conditions it is very difficult to spot them. *Arthroleptis schubotzi* call from below the leaf litter, and without the help of audio playback these notoriously well-hidden frogs are difficult to observe.

Arthroleptis schubotzi males (Fig. 1) reach a snout-vent-length of 22 mm (20.6 - 23.1 mm), with females being slightly larger, reaching 23 mm in length (Channing & Howell 2006).

Specimens were identified using morphological and distributional descriptions by Vonesh (2001), Channing & Howell (2006) and Spawls et al. (2006).

Daily Calling Activity

The calling activity of 25, well spaced individuals (mean distance of alternatively calling individuals > 5 m) was monitored three times per day, at 08:00 h, 14:30 h and 18:00 h between 13-08-2010 and 21-08-2010. These times were thought to best reflect the frogs' daily variation in activity based on a preliminary 24 hr observation period (13-08-2010). For each observation period, activity was recorded in a binomial fashion, either "calling" or "not calling", for each individual. Acoustically inactive males were stimulated with playbacks of conspecific calls, in order to elicit a response from as many of the 25 acoustically encountered males as possible. The vocalizations of eleven males recorded amounted to 55 individual calls used for the spectral analysis. The main focus of this study was the call production of males, for this reason females were disregarded.

Call Description

Advertisement calls of eleven individuals and encounter calls of two individuals were recorded *in situ* using a Marantz ® Professional (PMD660) digital recorder coupled to a Sennheiser® K6 directional transistor microphone, placed at a distance of 30-50 cm from calling males. Encounter calls were elicited using playback of prerecorded conspecific advertisement calls. The sound intensity was measured at one meter distance to the individuals using a Nady® Digital Sound Level Meter (C-DSM1-ED5S). Temperature and relative humidity were measured at the position of the calling male using a Maplin® Precision Gold (N09AQ) Environmental Meter, immediately after each recording. Call recordings were digitized with 16 bit resolution and analyzed using Raven Pro 1.4 software (Cornell University, Ithaka, USA).

Four representative specimens were collected, sedated by applying a small dose of benzocaine gel on top of their heads and photographed to act as photo-vouchers (Fig. 1). Specimens were subsequently released at their site of capture.

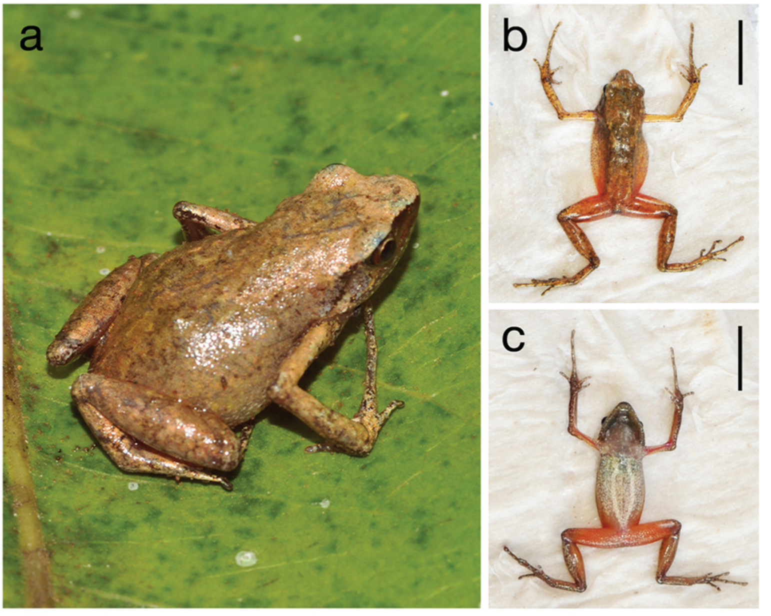

Fig. 1: Male of *Arthroleptis schubotzi* NIEDEN, 1911.
a - *in situ*; b - dorsal view; and c - ventral view under sedation. Scale bars: 10 mm.

Abb. 1: Männchen von *Arthroleptis schubotzi* NIEDEN, 1911.
a - *in situ*; b - Aufnahme von dorsal, c - von ventral unter Betäubung. Maßstab 10 mm.

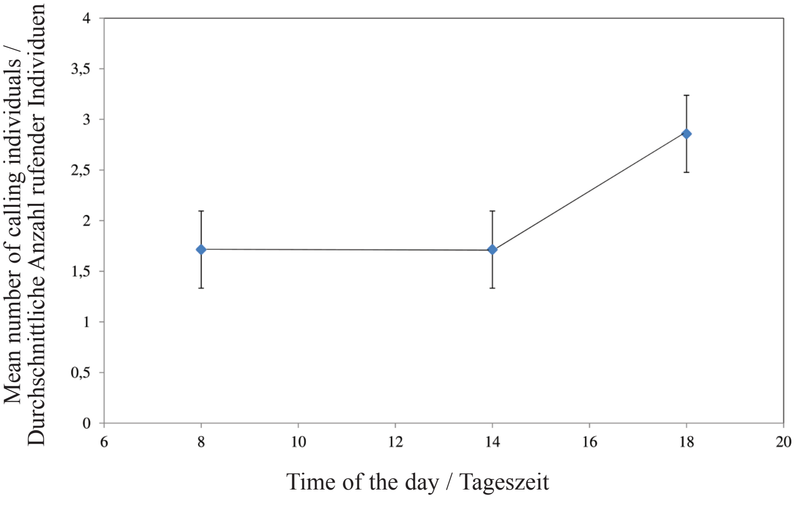

Fig. 2: Mean number of calling male *Arthroleptis schubotzi* NIEDEN, 1911, as observed at different times of the day, during an observation period of seven days at dry weather conditions (13-08-2010 to 21-08-2010).

Abb. 2: Durchschnittliche Anzahl rufender männlicher *Arthroleptis schubotzi* NIEDEN, 1911, zu verschiedenen Tageszeiten in einem Zeitraum von sieben Tagen während der Trockenperiode (13.8 bis 21.8.2010).

Table 1: Temporal and spectral analyses of calls of eleven *Arthroleptis schubotzi* Nieden, 1911, males. Call parameters are given as means (minimum-maximum), for each male. Samples of five calls each were analyzed. Separate averages were computed for short (a) or long (b) inter-call intervals.

Tab. 1: Zeitliche und spektrale Analyse der Rufe von *Arthroleptis schubotzi* Nieden, 1911. Von elf Männchen wurden jeweils fünf Rufe analysiert und die Mittelwerte (Minimum-Maximum) für charakteristische Rufparameter ermittelt. Für kurze (a) bzw. lange (b) Rufintervalle wurden getrennte Mittelwerte berechnet.

Male No. Männchen Nr.	1st note duration (ms) Dauer der 1. Silbe (ms)	2nd note duration (ms) Dauer der 2. Silbe (ms)	3rd note duration (ms) Dauer der 3. Silbe (ms)	inter-note interval 1-2 (ms) Intervall zwischen Silben 1 u. 2 (ms)	inter-note interval 2-3 (ms) Intervall zwischen Silben 2 u. 3 (ms)	call duration (ms) Rufdauer (ms)	inter-call interval (ms) Rufintervall (ms)	Frequency (Hz) Frequenz (Hz)
1	21 (18-28)	23 (18-30)	/	59 (52-65)	/	103 (94-111)	1428 (a)	4764
2	12 (11-13)	16 (15-17)	/	92 (90-94)	/	120 (118-121)	2128 (a)	4741
3	8 (8-10)	9 (7-11)	10 (9-11)	77 (75-79)	94 (85-108)	198 (93-212)	27899(b)	4810
4	9 (9-10)	11 (11-12)	/	88 (87-90)	/	108 (108-110)	2369 (a)	4892
5	10 (8-10)	14 (12-16)	/	71 (69-72)	/	95 (92-98)	2662 (a)	4548
6	12 (11-13)	16 (15-17)	/	92 (90-94)	/	120 (118-124)	2128 (a)	4796
7	14 (7-20)	18 (10-25)	18 (16-23)	78 (73-81)	84 (83-85)	212 (102-223)	3592 (a)	4650
8	10 (8-10)	11 (8-10)	/	71 (68-72)	/	92 (92-99)	3562 (a)	4564
9	12 (9-14)	14 (11-17)	15 (14-15)	72 (67-72)	86 (85-91)	199 (96-221)	2149 (a)	4462
10	18 (15-21)	20 (16-22)	24 (21-27)	98 (96-102)	113 (111-115)	273 (136-279)	13349(b)	4569
11	11 (9-15)	11 (9-15)	17 (12-21)	87 (86-90)	95 (87-103)	221 (114-276)	14681(b)	4478
Average / Mittel	12	15	17	80	94	158	(a) 2502 (b) 18643	4661

RESULTS

Arthroleptis schubotzi produce advertisement calls with distinct inter-call intervals, clearly separating individual calls. Males have dark brown to black throats on an otherwise pale ventrum with a single medial vocal sac, inflated only during sound production and deflating completely immediately after each note.

Daily Calling Activity

The calling activity of *A. schubotzi* was observed under both dry and wet weather conditions. Under dry conditions it was observed for nine days, mostly through stimulation with playback experiments. The mean calling activity of six males was higher in the evening hours than in the morning and at noon (SD = 2.06, 1.11 and 2.04, respectively) but the differences among different times of the day were not statistically significant (ANOVA; $F_{2, 18} = 0.87$, $p = 0.437$) (Fig. 2).

However, on the last two days of observation (20-08-2010 and 21-08-2010), it rained heavily and males were observed calling throughout the whole night. This discrepancy in the temporal distribution of calls between dry and rainy conditions could not be followed through. The calls of five males (out of eleven in total) were recorded during night hours. Even though calling activity in these five males was higher, there was no significant difference in note duration and inter-note intervals as compared to the calls produced in the dry period. In the calls emitted during the rainy conditions, three-note calls dominated over two-note vocalization and therefore there was a significant difference within the calling duration (ANOVA; $F_{1, 9} = 5{,}67$, $p = 0.41$).

One outstanding situation was the acoustic interaction between two males, which lasted conspicuously long and was recorded for 11 minutes and 8 seconds. During this period male A produced 30 calls, which were discharged rather alternatively to male B, which produced 42 calls leading to a call rate of seven calls per minute. The two males called alternatively at an inter-call interval of 6291 ms between 20 regularly alternated calls. There was no clear pattern as to the number of notes in the calls of the two males. With 16 three-note calls and 26 two-note calls male B produced more three-note calls then male A (8 three-note calls, 22 two-note calls).

Call Description

The advertisement call (Fig. 3) consisted of a series of high-pitched metallic sounds with a mean dominant frequency of 4661 Hz (4462-4892 Hz, *n* = 11) and mean call duration of 158 ms (92-273 ms) (Table 1). The intensity of the advertisment call at 1 m distance reached a total of 77 dB (75-79 dB).

Individual calls consisted of either two or three notes. No clear pattern in the number of notes could be determined, however, a pattern of two two-note calls followed by four three-note calls was common. Male 7 showed a remarkable consistency of four repeated series of five two-note calls followed by fourteen three-note calls. The notes in a call were separated by a mean inter-note interval of 80 ms (59-98 ms) between the first and the second note. With an average of 94 ms (84-113 ms), the inter-note interval between the second and third note clearly exceeded the first inter-note interval in length.

Inter-note intervals were significantly shorter than inter-call intervals, which were either long or short, and, thus, averaged separately (Table 1). In the males nos. 3, 10 and 11, the mean inter-call interval duration was 18643 ms (13349-27899 ms) versus 2502 ms (1428-3592 ms) in the other males. The extended duration in these three males resulted from a particular calling behavior (described in the section "Daily Calling Activity" above) in that two of the males interacted with each other.

The second recorded call-type was only sporadically elicited by acoustic playback signals, simulating an active rival male, fitting the description of an encounter call (Wells 1977). The pulsed vocalization was very distinct from the advertisement call (compare Fig. 3 & Fig. 4). The encounter calls consisted of either one or two elongated pulsed trains, followed by a single high-pitched metallic note similar to those of the advertisement call. The mean dominant frequency of the pulsed train was 4336 Hz (*n* = 2, range 4300 - 4800 Hz) with the mean note duration of 334 ms; the single high pitched metallic note had a frequency of 4644 Hz, and lasted 25 ms (Fig. 4).

The sound intensity of the pulsed sound, measured at one meter distance, reached a total of 57 dB (55-62 dB). The high-pitched notes had a sound intensity of 68 dB (65-72 dB). With their energy concentrating around 8600-9200, 12900-13800 and 17500-18400 Hz, the harmonic frequency bands of the pulsed and the pitched notes were similar. With the mean call duration of 541 ms, the complete encounter call was almost five times as long as the advertisement call. Encounter calls were produced spontaneously and infrequently, so their inter-call duration of 4600 ms is incomparable with the inter-call duration of the regularly repeated advertisement call.

DISCUSSION

Call Description

Spectral analyses of both call-types, the advertisement and the encounter call, indicate that they are two structurally different vocalizations. The advertisement call consists of regular notes within little temporal and spectral variation and shows little variation in call duration. Very distinct pulsed notes of varying duration, but always exceeding that the advertisement call characterize the encounter call. Its dominant frequency ranges from 4300 Hz to 4800 Hz. The latter call was exclusively produced during playback situations and never emitted spontaneously.

Compared to other *Arthroleptis* species, the call of *A. schubotzi* is quite unique. Mercurio (2009) described advertisement calls of three further species of *Arthroleptis*. There is a clear difference between these calls in that *A. schubotzi* produce two and three-note calls, the three other *Arthroleptis* only one-note calls. Within the calls, the inter-note intervals differ considerably between the *Arthroleptis* species described; *A. schubotzi* has a shorter inter-note interval (80-94 ms) than the other three species (*A. reichei*

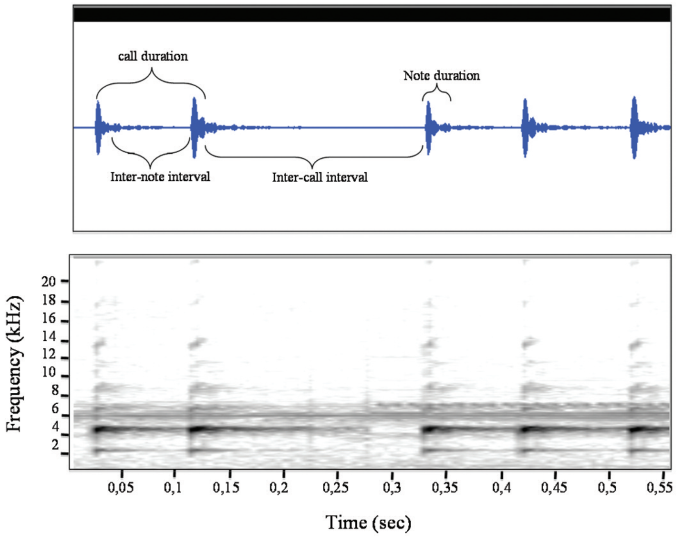

Fig. 3: Oscillogram (above) and sound spectrogram (below) of two advertisement calls of *Arthroleptis schubotzi* NIEDEN, 1911. A two-note call, followed by a three-note call, is shown.

Abb. 3: Oszillogramm (oben) und Spektrogramm (unten) zweier Anzeigerufe (advertisement call) von *Arthroleptis schubotzi* NIEDEN, 1911. Auf einen zweisilbigen folgt ein dreisilbiger Anzeigeruf.

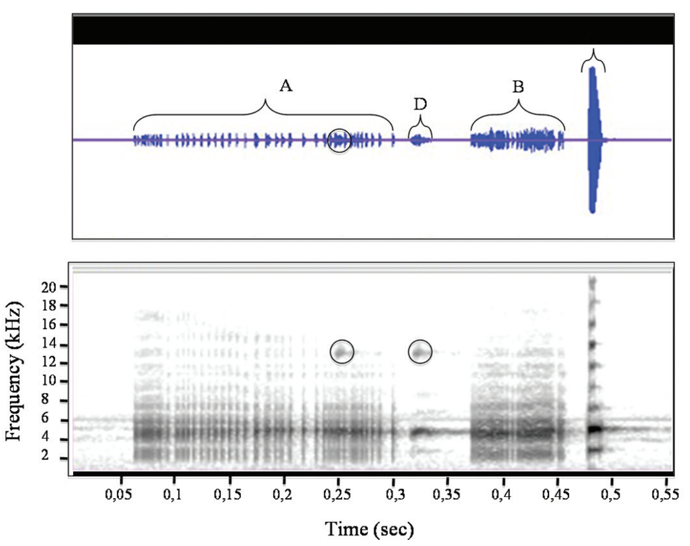

Fig. 4: Oscillogram (above) and sound spectrogram (below) of the encounter call of *Arthroleptis schubotzi* NIEDEN, 1911. Two pulsed trains (A, B) are followed by one high-pitched click (C). There is an overlap within and after the first pulsed train caused by a second calling male (D, ○).

Abb. 4: Oszillogramm (oben) und Spektrogramm (unten) eines Warnrufes (encounter call) von *Arthroleptis schubotzi* NIEDEN, 1911. Nach den zwei gepulsten Silben (A, B) folgt eine hochfrequente Silbe (C). In und nach der ersten gepulsten Silbe gibt es eine Überlappung mit dem Ruf eines zweiten Männchens (D, ○).

Nieden, 1911: 459 ms, *A. stenodactylus* Pfeffer, 1893: 254.9 ms, *A. xenodactyloides* Hewitt, 1933: 358.9 ms). The dominant frequencies lie between 3200 Hz and 4600 Hz, except for *A. xenodactyloides*, with a dominant frequency of about 6300 Hz.

The advertisement call of *A. schubotzi* is described as two or three high-pitched metallic notes; that of other species is described as a whistling note (*A. reichei*), a single, unpulsed, whistling note (*A. stenodactylus*), endless repetition of one single, clearly pulsed note (*A. xenodactyloides*) (Mercurio 2009), a loud slightly blurred whistle (*A. lönnbergi* [sic!] Nieden, 1915) [currently considered a synonym of *A. stenodactylus*] or a high pitched, plaintive squeak (*A. wahlbergii* Smith, 1849) as described in Pickersgill (2007). Since the morphology is sometimes cryptic, but the calls between *Arthroleptis* species are very different, the study of anuran vocalization is important for species identification and in the phylogenetic analysis of related species (Mercurio 2009).

Behavioral observations point to different purposes of the two call-types. In systems where females arrive at irregular intervals throughout an extended breeding season, territoriality in males could be an evolutionary strategy to overcome inefficient active searching for mates (Wells 1977; Rand 1988). *Arthroleptis schubotzi* show direct development and are thus well adapted to terrestrial life. They can be found far from water bodies. Without seasonal dependent reproductive sites, males may be more successful by remaining stationary and attracting females by means of establishing and defending territories (Wells 1977). Our study supports this hypothesis as the observed males showed strong site fidelity. Over the entire observation period, males were calling from the initially marked calling sites. When stimulated with playbacks of advertisement calls they responded antiphonally, suggesting that the advertisement call functions as a spacing mechanism (Wells 1977, 2007). When placing an active speaker within two meters of their location, males showed strong positive phonotaxis and produced the encounter call. Whether such an encounter would result in agonistic behavior, as is common in territorial species (Duellman 1966; Wells 2007), could not be determined in this study, and therefore we refer to this call as a behaviorally-neutral "encounter call" (Wells 1977).

Ecological and behavioral observations and comments on the large size of the third manual digit

Arthroleptis schubotzi is a purely terrestrial frog and found at sites far from permanent bodies of water. Males call from moist undergrowth (de Witte 1941) and their activity is positively correlated with rainfall. Most strikingly, *A. schubotzi* undergo direct development, skipping the free-swimming larval stage, a trait that evolved only once at the base of the *Arthroleptis* phylogeny (Blackburn 2008) and allowed this genus to be independent of aquatic breeding sites. Despite the independence from water, *A. schubotzi* is still prone to desiccation, a risk that is amplified by the frog's diurnal nature. Diurnal activity has evolved numerous times in anurans and is thought to be driven by the availability of day-active prey (Carey 1978). The calling activity of *A. schubotzi* reflects that of other diurnal anurans (e.g., Hatano et al. 2002) and is noticeably reduced during the hottest periods of the day. In this study, males in captivity were observed to bury themselves by alternating hind leg movements into moist soil, which may be a further adaptation to avoid desiccation. This was complemented by frequent displays of cleaning behavior in individuals covered with sand, by moving the arm upwards and brushing the elongated finger across the head and over the eyes, a possible secondary adaptation of this elongated digit.

Males of many frogs of the genus *Arthroleptis* and *Cardioglossa* have elongated third manual digits and in *A. schubotzi*, this sexual dimorphism is extreme with fingers reaching up to 40% of the snout-vent-length in males (Fig. 1) (Blackburn 2009). Although not all members of this taxonomic clade boast elongated digits, molecular data suggest that the evolution of this trait is deeply rooted in their phylogeny (Blackburn 2009). Despite being such a peculiar trait, little is known about the proximate function of the elongated digit and the two most supported ideas are mentioned here:

Being only evident in males, the elongation of the finger is likely driven by sexual selection. Anecdotal claims of the finger playing a role in male-male wrestling are reported in the literature (Amiet 1989), but have never been confirmed empirically. Blackburn (2009) showed that finger length dimorphism is correlated to forearm length dimorphism (thought to allow better grasping of females during amplexus) (Wells 2007) and henceforth proposes that the elongated finger may play a role during copulation.

No behavioral experiments were conducted to confirm or reject either hypotheses and the authors would like to note that they are not without flaws. First, the elongated digit is a delicate structure and its function as a weapon is therefore questionable. Secondly, the development of male nuptial structures for the clasping of females during amplexus is most often associated with aquatic environments (Duellman & Trueb 1994) and therefore seems redundant for a terrestrial species such as *A. schubotzi*. With these observations in mind, we propose an alternative hypothesis, in which the elongated digit has no practical function, but instead serves as an honest signal in sexual selection.

Zahavi's (1975) honest signalling hypothesis and, more precisely, Hamilton & Zuk's (1982) handicap principle predict that sexual selection drives the development of costly ornaments to advertise mate quality. Testosterone-dependent traits are key candidates for such signals because of the suppressive effect elevated testosterone levels have on the immune system (Folstad & Karter 1992). The positive correlation of enhanced secondary sexual characteristics and reduced immunocompetence as well as the preference for such signals by females have been widely established (Duffy & Ball 2002; Møller et al. 1999; Verhulst et al. 1999; Mougeot et al. 2004), and therefore our hypothesis is built on a solid basis. Furthermore, limb development in vertebrates is coordinated by the same subset of homeobox genes as gonad development (HoxA and HoxD; Kondo et al. 1997) and sexual dimorphism in digit length is evident in birds (Burley & Foster 2004), mammals (Manning 2002), reptiles (Rubolini et al. 2006) and amphibians (Chang 2008). More specifically, the direct influence of testosterone on digit development was experimentally tested as well (Mougeot et al. 2004; Romano et al. 2005), and therefore we propose that the elongated digit in male *A. schubotzi* is an honest signal of health much like the comb of roosters. The peculiarity of this trait certainly deserves more attention, and on the basis of our reasoning, would make an excellent character for investigating classical sexual selection theories. Why some male frogs of this genus have an elongated third manual digit remains therefore an open question.

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