Sound production in two species of damselfishes (Pomacentridae): *Plectroglyphidodon lacrymatus* and *Dascyllus aruanus*

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Agonistic sounds of two pomacentrid species, *Plectroglyphidodon lacrymatus* and *Dascyllus aruanus*, were recorded in captivity. *Plectroglyphidodon lacrymatus* produced trains of 2–5 pops, each composed of 18–25 cycles, with an average duration of 56 ms; most energy ranged from *c.* 100 to 1000 Hz. *Dascyllus aruanus* produced pops and chirps. Pops were generally composed of a single pulse, with 2–14 peaks and an average duration of 6·7 ms. Pops contained energy >4 kHz, and peak frequency ranged from 680 to 1300 Hz. Chirps consisted of trains of 12–42 short pulses of three to six cycles, with durations varying from 0·6 to 1·27 ms; peak frequency varied from 3400 to 4100 Hz. Sound production in *P. lacrymatus* suggested that pomacentrids are derived from an ancestral taxon capable of sound production and that this capacity is a synapomorphy for the family. Although in the Pomacentridae, pops are typically composed of a single pulse, which is longer and higher pitched than chirps composed of a series of shorter pulses, *D. aruanus* chirps were higher pitched than its pops. Thus, acoustic variation in the genus *Dascyllus* is probably not more restricted than in the Pomacentridae.   © 2006 The Authors

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Key words: bioacoustics; Pomacentridae; sound production.

INTRODUCTION

The Pomacentridae, commonly known as damselfishes, are a diverse group of marine fishes found throughout tropical oceans. The family includes 29 genera and 340 recognized species living mainly in coral reef environments (Allen, 1991; Nelson, 1994; Tang, 2001). Pomacentrids have been divided into four subfamilies: Amphiprioninae, Chrominae, Lepidozyginae (only one species) and Pomacentrinae (Allen, 1975, 1991). Among the three first sub-families, seven genera were reported as producing sound: *Amphiprion, Dascyllus, Stegastes, Chromis, Abudefduf, Premnas* and *Hemichromis* (Emery, 1973; Luh & Mok, 1986; Myrberg,

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1986; Chen & Mok, 1988; Amorim, 1996; Santiago & Castro, 1997; Mann & Lobel, 1998; Lobel & Kerr, 1999; Lagardère *et al.*, 2003). Within a species, pulsed calls exhibit generally small variations in temporal qualities such as pulse rate, pulse duration, number of pulses in a call and call duration (Ladich, 1997). Sounds therefore provide information on species identity (Myrberg & Spires, 1972). Unlike in other pomacentrids, the sound patterns of *Abudefduf sordidus* (Forsskål) are irregular and highly variable (Lobel & Kerr, 1999), suggesting specialized vocal abilities compared to others in the family. The adaptive radiation of a taxon results from morphological, physiological or behavioural modifications (Schluter, 2001) of an ancestral plan (Zelditch & Fink, 1996) or from the emergence of new characters. In this case, minor modifications of the sound producing system may promote or be indicative of speciation.

Field and laboratory studies have shown that sounds function in courtship (Spanier, 1979; Myrberg *et al.*, 1986; Lugli *et al.*, 1997), agonistic interactions (Ladich, 1997; Amorim *et al.*, 2003; Parmentier *et al.*, 2003) and competitive feeding (Amorim & Hawkins, 2000). Moreover, these behaviours are associated with different calls in the pomacentrids *Stegastes partitus* (Poey) (Myrberg, 1972, 1986; Myrberg & Spires, 1972; Myrberg *et al.*, 1993), *Dascyllus albisella* Gill (Mann & Lobel, 1995, 1998) and different species of clownfishes (Takemura, 1983; Chen & Mok, 1988). On the other hand, a single type of call was identified in different pomacentrids (Amorim, 1996; Santiago & Castro, 1997; Picciulin *et al.*, 2002) although these authors suggested the repertoire could include more calls than were described. Unfortunately, the lack of homogeneity employed by different authors in the sound descriptions and terminology (pop, chirp and grunt for the agonistic sounds) complicates comparisons (Amorim, 2006).

This study describes sounds produced by the pomacentrids *Plectroglyphidodon lacrymatus* (Quoy & Guimard) and *Dascyllus aruanus* (L.). The genus *Plectroglyphidodon* is placed in a basal position in pomacentrid phylogeny (Tang, 2001; Jang-Liaw *et al.*, 2002; Quenouille *et al.*, 2004), and its sounds may therefore provide a baseline for evolutionary comparison within the family. *Dascyllus aruanus* sounds will allow a comparison with other species in the genus and help determine if generic characteristics exist. Like *D. albisella* and *Dascyllus trimaculatus* (Rüppel), *D. aruanus* males are territorial and invite females to their nest to spawn and then protect the eggs.

MATERIALS AND METHODS

Six specimens of *P. lacrymatus* (6–8 cm total length, L_T) and 20 specimens of *D. aruanus* (5–7 cm L_T) were collected by scuba diving in the lagoon in front of Tulear (Mozambique channel, west coast of Madagascar, 23°22′ S; 46°39′ E). The sexes of specimens of both species were not identified. *Plectroglyphidodon lacrymatus* and *D. aruanus* were maintained in separate glass tanks (respectively $1 \times 0.5 \times 0.6$ m and $3.50 \times 0.7 \times 0.2$ m; 26° C, range ±1° C) without substratum except for two rocks placed 30 cm apart. These rocks were used by the fishes to delimit their territories.

RECORDINGS AND SIGNAL ACQUISITION

Sounds were recorded with an Orca hydrophone (sensitivity: −186 dB re\f 1V/μPa) connected *via* an Orca-made amplifier (ORCA Instrumentation, Brest, France) to

a mini-disc recorder (XM – 228BK; JVC, Liège, Belgium). This system has a flat frequency response range (range ± 3 dB) between 10·0 and 23·8 kHz. The hydrophone was placed midway between the two rocks.

Sounds were digitized at 44·1 kHz (16 bit resolution) and analysed with the Avisoft-SASLAB Pro 4·33 software (1024-point Hanning window fast Fourrier transform, FFT). Temporal features were measured from oscillograms, and frequency variables were obtained from power spectra (filter bandwidth 300 Hz, FFT size 256 points, time overlap 96·87% overlap and a flat top window). The resonant frequency of the tanks were calculated, respectively, as 3·9 and 2·56 kHz, using an equation in Akamatsu *et al.* (2002), and a low-pass filter of 3·9 and 2·56 kHz were applied for the pops of *D. aruanus* and *P. lacrymatus*, respectively. *Dascyllus aruanus* chirps contained higher frequency energy and were not filtered.

The following sound variables were measured: sound (or train) duration, *i.e.* the time elapsed from the start of the first pulse to the end of the last pulse; number of pulses in a sound; pulse duration, *i.e.* the time interval between the onset of one pulse and its end; pulse period, measured as the average peak to peak interval between consecutive pulse units in the entire sound; number of peaks in a pulse; dominant frequency; Q_{3dB}, *i.e.* the quotient of the dominant frequency divided by the bandwidth 3dB down from the peak frequency.

RESULTS

PLECTROGLYPHIDODON LACRYMATUS

Sounds were recorded with three fish in the aquarium. Pops were produced only when an observer approached the tank. The fish that was apparently responsible for making the sound faced the observer and spread its pectoral fins, showing an aggressive behaviour, probably in relation with the defence of the territory. Additional data, however, are needed to ascertain this behaviour. Sounds were produced in trains (218–697 ms) of two to five pulses (mean duration of each pulse = 56 ms), with a mean pulse period of 179 ms (Table I and Fig. 1). The number of pulses per call correlated with call duration ($r^2 = 0.95$, $P < 0.001$; Fig. 2). The first pulses in a train occurred as doublets [Fig. 1(c)], with a short low-amplitude prepulse, mean ± S.E. = $7.8 ± 0.7$ ms ($n = 7$), of three cycles followed by a pause of *c.* 20 ms (mean ± S.E. = $19.9 ± 2.5$ ms, $n = 7$). Doublets were occasionally observed in other pulses. Main pulses were composed of 18–25 cycles (mean ± S.E. = $21 ± 1.9$ cycles, $n = 42$; Table I and Fig. 1) and varied in duration from 48 to 60 ms (mean ± S.E. = $56 ± 4.4$ ms, $n = 42$). Number of peaks per pulse did not correlate with pulse duration ($r^2 = 0.09$, $P > 0.05$). Most energy ranged from *c.* 100 to 1000 Hz, and peak frequency averaged 328 Hz (Table I and Fig. 3). The amplitude of the peak energy in the pop [Fig. 3(c)] was similar (*c.* −40 dB) to the lower frequency peak in the pop power spectrum in *D. aruanus* [Fig. 3(b)].

DASCYLLUS ARUANUS

Sounds were recorded with 20 fish in the aquarium, making it impossible to identify the individual producing the call (hence, it was also impossible to associate possible sexual dimorphism in sound production). Two types of sounds, pops and chirps, were recorded. The pop was produced during agonistic interactions when a specimen approached another's shelter or during chases. Pops and chases, however, were not observed in each encounter. A pop was generally composed of a single pulse (91% of cases) although two-pulse pops with a

TABLE I. Descriptive statistics of agonistic pops produced by *Plectroglyphidodon lacrymatus*

	Minimum	Maximum	Mean ± S.E.	n
Pulse duration (ms)	47·5	60·1	56·0 ± 4·4	42
Number of peaks per pulse	18	25	21·0 ± 1·9	42
Q_{3dB}	0·4	40·6	2·8 ± 3·1	26
Peak frequency (Hz)	170	520	328 ± 132	42
Train duration (ms)	218	697	510 ± 171	10
Number of pulses per train	2	5	3·81 ± 1·16	10
Pulse period (ms)	145	263	179 ± 31	30

n, number of recordings; Q_{3dB}, quotient of the dominant frequency divided by the bandwidth 3dB down from the peak frequency.

period of 89–97 ms were produced [Fig. 4 (a)]. Pulses were composed of two to 14 peaks [mean ± S.E. = 6·4 ± 0·7 peaks, n = 22; Table II and Fig. 4(d)] and varied in duration from 2 to 10·3 ms (mean ± S.E. = 6·7 ± 0·8 ms, n = 22). Number of peaks in a pulse correlated with pulse duration (r^2 = 0·7, $P <$ 0·001; Fig. 5). The peak frequency ranged from 680 to 1300 Hz, with greater energy at the beginning of the sound [Fig. 3(c)]. Pulses started with a low-frequency, low-amplitude half cycle, increased immediately to a peak amplitude and frequency before starting to decrease in amplitude [Fig. 4(d)]. The pulse ended with one or two low-amplitude, low-frequency cycles.

Chirps were not associated with a specific behaviour and could function to announce the presence of the caller. They consisted of trains of 12–42 pulses varying from 26 to 121 ms (mean ± S.E. = 77 ± 37 ms, n = 27) in duration, with an average pulse period of 4·8 ms. In longer chirps, energy in pulses at the end of the train decreased in amplitude [Fig. 4(b)], suggesting fatigue or a slower motion. Chirp pulses contained three to six cycles and varied from 0·60 to 1·27 ms in duration. The number of peaks per pulse correlated with pulse duration (r^2 = 0·94, $P <$ 0·001; Fig. 5). Energy occurred in three bands and extended to >20 kHz. The peak frequency of the first band varied from 3400 to 4100 Hz and contained energy to *c.* 8 kHz (Table II and Figs 3 and 4). Compared to pops (Table II), chirps had a shorter pulse duration with fewer peaks per pulse (*t*-test, d.f. = 55, $P <$ 0·001) and a peak frequency that averaged about three times greater (*t*-test, d.f. = 45, $P <$ 0·001). The amplitude of the peak frequency was *c.* 12 dB greater in the pop although the amplitude of the first peak was similar in both calls (Fig. 3). The Q_{3dB} was twice as high in the pop than in the chirps (*t*-test, d.f. = 32, $P <$ 0·001; Table II).

DISCUSSION

In teleosts, the ability to emit sounds developed independently in distant phylogenetic taxa (Schneider, 1967; Carlson & Bass, 2000). Currently, members of >50 families include species with this capacity, but all members of these families are not necessarily able to produce sounds (Hawkins, 1993). The monophyly of pomacentrids is attested by three different phylogenetic studies,
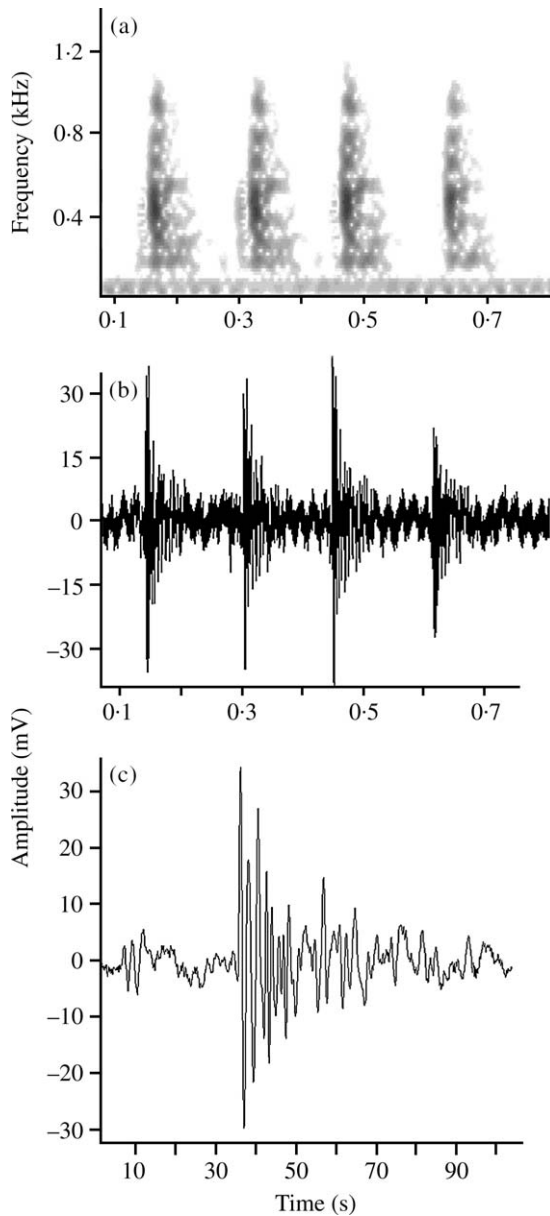
FIG. 1. (a) Sonagram and (b), (c) oscillograms of the same pop pulses in *Plectroglyphidodon lacrymatus*.

and the genus *Plectroglyphidodon* is placed in a basal position in the damselfish cladogram (Tang, 2001; Jang-Liaw *et al.*, 2002; Quenouille *et al.*, 2004). The presence of sounds in *P. lacrymatus* suggests that pomacentrids are derived from an ancestral taxon capable of sound production and that this capacity is a synapomorphy for the family. The absence of sound production in some species probably indicates a character lost secondarily. Pomacentrids are usually placed in the labroids with the Embiotocidae, Labridae and Cichlidae,
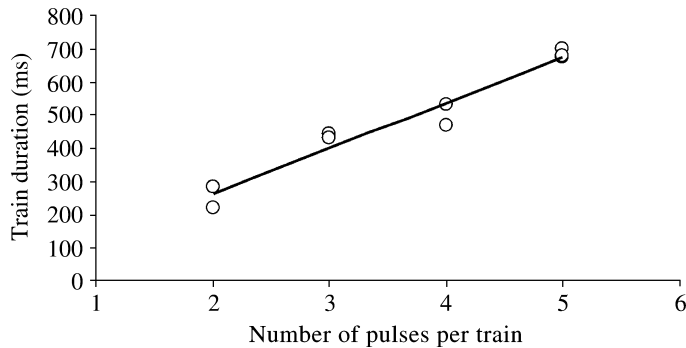
FIG. 2. Relationship of train duration to number of pulses in a call from *Plectroglyphidodon lacrymatus*. The curve was fitted by: $y = 136 \cdot 99x - 12 \cdot 044$ ($r^2 = 0 \cdot 96$, $n = 10$).

the last also being capable of sound production (Rice & Lobel, 2004; Amorim, 2006). The supra-familial relationships of the Pomacentridae, however, are not well defined since morphological studies (Kaufman & Liem, 1982; Stiassny & Jensen, 1987) are not compatible with genetic studies (Streelman & Karl, 1997). Since the sonic mechanism has not been explicitly demonstrated in pomacentrids and cichlids, it is unclear if they produce sound using a homologous mechanism. Note that the 'elastic spring apparatus' found in eight different extant catfish families is considered a homoplastic feature (de Pinna, 1998; Parmentier & Diogo, 2006), which seems to have evolved at least five times within the order Siluriformes. In this case, additional data dealing with the morphology and the sonic repertoire are needed to permit comparisons between cichlids and pomacentrids.

In pomacentrids, a more detailed study on the repertoire, including courtship signals, of *Plectroglyphidodon* and other members of its subfamily is needed to describe what could represent a basal sound pattern and to investigate how this sound has specialized among the pomacentrid species. Small differences exist in pulse number and pulse rate in four species of *Stegastes* (Spanier, 1979), and Myrberg & Spires (1972) demonstrated that interspecific differences in pulse interval are important in species recognition. Among five variables, Amorim *et al.* (2004) found differences only in the pulse duration and pulse number in sounds from three sympatric species of *Pseudotropheus* (Cichlidae).

In pomacentrids, 'pops' and 'chirps' have been recorded in agonistic interactions between conspecifics and across species. Unfortunately, these terms have been inconsistently applied (Amorim, 2006). Since both types of sounds have not been described for each species (Table III), the absence of either sound type could equally well indicate that the sound is not made or was simply not recorded. Sufficient data exist, however, to support generalizations about pops and chirps. Pops are composed mainly of a single pulse, which is longer and higher pitched than chirp pulses. Chirps are generally composed of a series of shorter pulses. A series of pops, however, can be emitted during long encounters in some species (Myrberg, 1972). In a series of pops, the pulse period is considerably longer than in the chirp, suggesting that each pop is emitted as a separate unit. The pulse period in the chirp averages 4·8 ms in *D. aruanus*, 8–16 ms
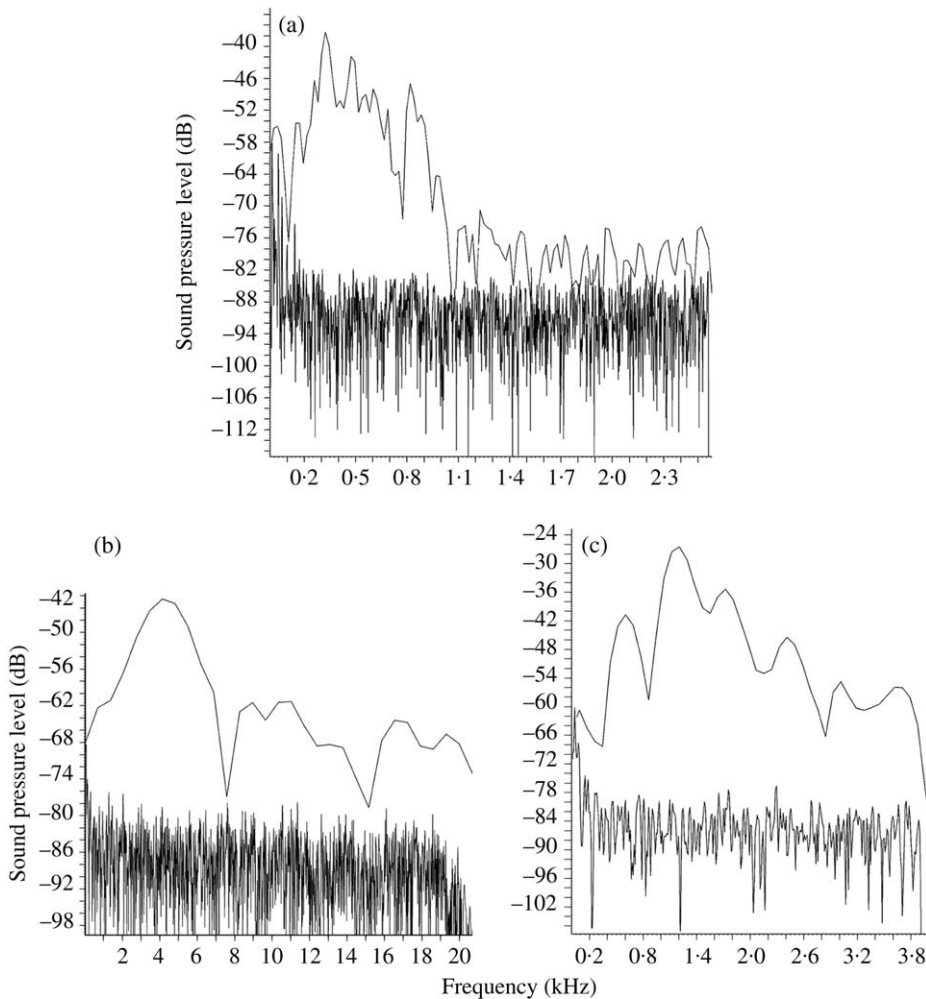
FIG. 3. Power spectra (upper trace) of one pulse. (a) A pop in *Plectroglyphidodon lacrymatus*, and (b) a chirp and (c) a pop in *Dascyllus aruanus*. The lower trace, the noise floor.

in *D. trimaculatus* (Luh & Mok, 1986) and 45·2 ms in *D. albisella* (Mann & Lobel, 1998). Since Mann & Lobel (1998) did not find differences in the pulse duration and in peak frequency in *D. albisella* sounds, the chirps they described could be a series of pops. Unlike *Stegastes* and *Amphiprion*, *D. aruanus* chirps have higher frequencies than their pops, which could be true in *D. trimaculatus* although the situation was not clarified in this species (Luh & Mok, 1986). More data are needed to determine if a common pattern exists in the genus *Dascyllus*.

Recently, Rice & Lobel (2004) noted that the sound emission of different pomacentrids could depend on a fixed mechanism because of the linear correlation between pulses per call and call duration. Similarly, the number of pulses per call in *P. lacrymatus* and in the number of peaks per pulse in *D. aruanus* correlated with duration (Figs 2 and 5). The mechanism of pomacentrid sound production is unclear and has been hypothesized to involve a swimbladder
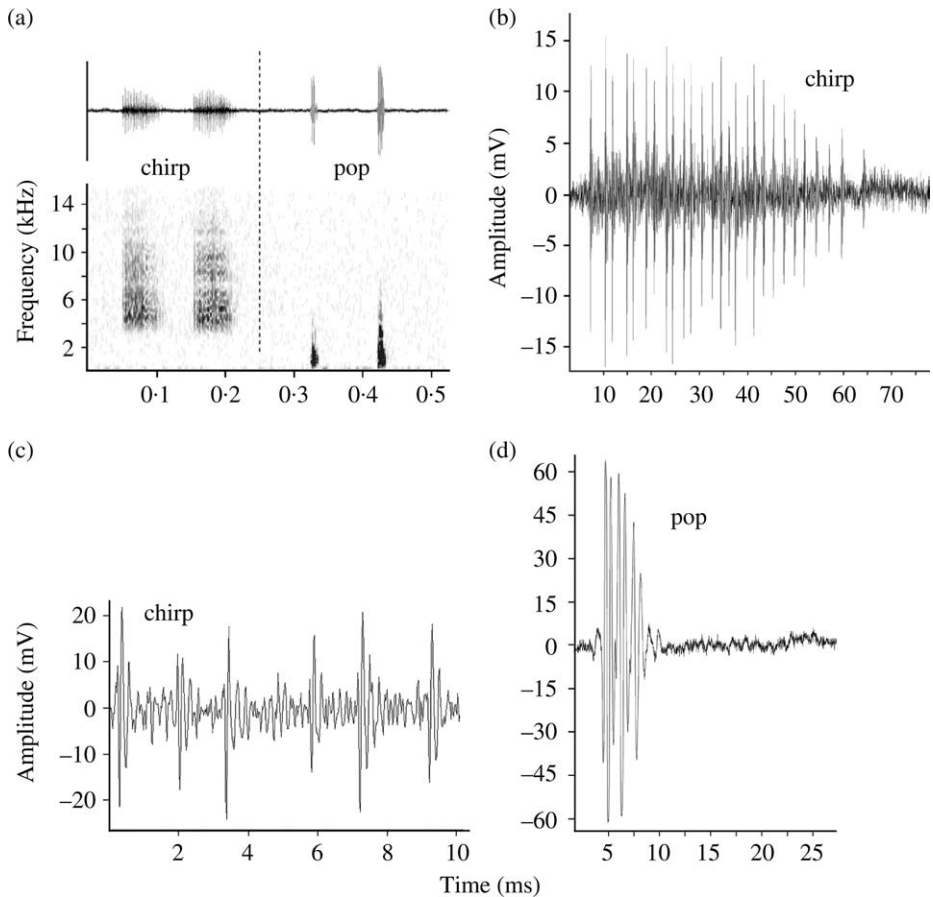
FIG. 4. *Dascyllus aruanus*: (a) sonagram of chirps and pops, and (b) oscillograms of a single chirp, (c) pulse structure of a chirp, and (d) a pop.

mechanism (Myrberg *et al.*, 1993; Santiago & Castro, 1997) or the action of the pharyngeal jaws amplified by the swimbladder (Takemura, 1983; Luh & Mok, 1986; Rice & Lobel, 2004). These two hypotheses reflect the usual division of the sonic emissions into two classes, stridulatory sounds and swimbladder vibration (Hawkins & Myrberg, 1983; Fine *et al.*, 2001). Stridulation sounds are emitted by rubbing parts of the body against each other (pharyngeal teeth and pectoral fins). In the second, the sound production would result from vibration of the swimbladder by the deformation of the swimbladder wall since there are no specialized sonic muscles attached to the bladder in this family. The difference in frequency and sharpness of tuning (*i.e.* Q_{3dB}) between pops and chirps in *D. aruanus* suggests that they are not caused by swimbladder res- onance, which would cause all sounds to have similar spectra dictated by the swimbladder's natural frequency. Further, Fine *et al.* (1997) demonstrated that removal of gas from the swimbladder of the channel catfish *Ictalurus punctatus* (Rafinesque) did not change the frequency spectrum or amplitude of its distress call. Although it is commonly assumed that the swimbladder can amplify

TABLE II. Descriptive statistics (see Table I) of the chirp and pop sounds produced by *Dascyllus aruanus*

	Pop				Chirp				
	Mean ± S.E.	Minimum	Maximum	n	Mean ± S.E.	Minimum	Maximum	n	P
Pulse duration (ms)	6·7 ± 0·8	2·0	10·2	22	0·70 ± 0·03	0·56	1·27	27	<0·001
Number of peaks per pulse	6·4 ± 0·7	2	14	22	3·5 ± 0·1	3	6	27	<0·001
Q_{3dB}	5·3 ± 0·4	4·0	8·5	22	2·4 ± 0·1	1·3	4·0	27	<0·001
Peak frequency (Hz)	1026 ± 49	680	1300	20	3859 ± 59	3400	4100	27	<0·001
Train duration (ms)					77 ± 37	26·6	121·2	16	
Number of pulses per train					26 ± 10	12	42	16	
Pulse period (ms)					4·8 ± 7·9	0·9	28·0	283	

P, results of unpaired tests.

sounds produced by nearby structures, as far as is known, this phenomenon has not been experimentally supported.

The report of different kinds of sounds in pomacentrids implies either two mechanisms of sound production or that the same mechanism depends on different motor patterns. If differences in pulse periods or pulse rate reflect variations in temporal pattern of the same mechanism, differences in the frequency and in the Q_{3dB} and in the pulse duration could be linked to the mechanism itself.

In anuran amphibians (Cocroft & Ryan, 1995) and Felidae (Peters & Tonkin-Leyhausen, 1999), calls comprise a set of characters, and these characters
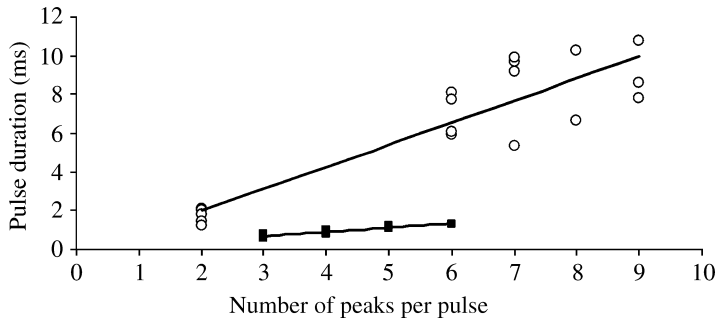

FIG. 5. Relationships of pulse duration to the number of peaks in a pulse in pops (○) and chirps (■) produced by *Dascyllus aruanus* (n, number of recordings). The curves were fitted by: pops $y = 1·14 x - 0·28$ ($r^2 = 0·91$, $n = 20$) and chirps $y = 0·22 x + 0·02$ ($r^2 = 0·94$, $n = 27$).

TABLE III. Description of sounds made by different pomacentrids in agonistic interactions

	Sound	Pulse duration (ms)	Number of pulses per call	Pulse period (ms)	Dominant frequency (Hz)	References
Chromis viridis	—	7·94	2	7	709	Amorim (1996)
Chromis chromis	—	9–16	1	—	710	Picciulin *et al.* (2002)
Abudefduf sordidus	—		2–10		200–600	Lobel & Kerr (1999)
Abudefduf luridus	Pop	15–20	1–2	64	<1000	Santiago & Castro (1997)
Stegastes partitus	Pop	10–40	1	100–400	700–1500	Myrberg (1972)
	Chirp	8–15	3–6	40–60	250–1000	Myrberg & Spires (1972)
Stegastes planifrons	Chirp	7–12	4	45–55	250–750	Myrberg & Spires (1972)
Stegastes leucostictus	Chirp	7–10	4	35–40	250–700	Myrberg & Spires (1972)
Amphiprion clarkii	Pop	80	1–2	790	<3000	Chen &
	Chirp	50	1–17	50–62	<1500	Mok (1988)
Amphiprion frenatus	Pop	50	1–2	102	<3000	Chen &
	Chirp	50	1–7	83	<1000	Mok (1988)
Amphiprion akallopisos	Pop	7–11		47–141	900	Lagardère *et al.* (2003)
	Chirp	3·1	8·7	11·2	665	Parmentier *et al.* (2005)
Dascyllus trimaculatus	Pop	13–55	1	—	4000–8000	Luh & Mok
	Chirp	13–55	3–6	8–16	4000–8000	(1986)
Dascyllus albisella	Pop	16·6	1–2	—	441	Mann &
	Chirp	15·5	5·4	45·2	?	Lobel (1998)
Dascyllus aruanus	Pop	6·4	1	89	1026	This study
	Chirp	0·8	12–42	4·8	3859	
Plectoglyphidodon lacrymatus	Pop	56	2–5	175	328	This study

evolve at different rates. Some characters are conserved through repeated speciation events and others change (Cocroft & Ryan, 1995). Various pomacentrids produce the same types of sounds, but each species quantitatively modifies its repertoire, allowing specific identification. This study suggests that a basic pattern is present for the sound production in pomacentrids and that individual taxa develop it differently.

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