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Why signal softly? The structure, function and evolutionary significance of low-amplitude signals

Dustin G. Reichard [a], Rindy C. Anderson [b,*]

[a] Department of Evolution and Ecology, University of California, Davis, CA, U.S.A.
[b] Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL, U.S.A.

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Acoustic signalling is a taxonomically widespread form of animal communication consisting of long-range, high-amplitude signals and short-range, low-amplitude signals. Research on acoustic communication has emphasized high-amplitude signals and often overlooked low-amplitude signals, even though they are produced in behavioural contexts that directly influence fitness. Low-amplitude signals are referred to by a variety of names such as soft songs, courtship songs, whispers, close calls, contact calls, grunts and moans, but all of these signals share a reduced amplitude and an active space that is limited to close-proximity receivers. In this review, we establish a general definition for low-amplitude signals and investigate the similarities and differences between low- and high-amplitude signals with respect to their acoustic structure and function. Then, we critically evaluate some proximate and ultimate evolutionary mechanisms that may explain why these signals are produced at low amplitude using examples from a variety of taxa. We conclude by suggesting priorities for future research on low-amplitude signals and highlighting how studying these signals will lead to a more complete understanding of how and why animals communicate acoustically.

Research on acoustic communication has provided important insights into the fields of sexual selection, sensory perception and the evolution of behaviour (Andersson, 1994; Bradbury & Vehrencamp, 2011; McGregor, 2005; Searcy & Nowicki, 2005). Until recently, most research on this topic has focused on high-amplitude signals that project over long distances and can simultaneously influence multiple types of receivers (Wiley & Richards, 1978, 1982). Because high-amplitude signals propagate widely, they can serve a variety of functions including attracting mates, competing with rivals, avoiding predators and mediating social interactions within groups (Bradbury & Vehrencamp, 2011).

However, acoustic signals are produced over a wide range of amplitudes (e.g. Anderson, Searcy, Peters, & Nowicki, 2008), and the repertoires of some species include signals that are produced exclusively at low amplitudes (e.g. Reichard & Welklin, 2015; Titus, 1998). The occurrence of low-amplitude signalling has been documented for decades (e.g. Alexander, 1961; Nice, 1943), but this form of communication remains understudied and poorly understood. Low-amplitude signals are produced in the same social contexts as high-amplitude signals such as directed courtship (Rebar, Bailey, & Zuk, 2009; Reichard, Rice, Schultz, & Schrock, 2013), intense aggressive interactions (Ballentine, Searcy, & Nowicki, 2008; Hof & Hazlett, 2010; Searcy, Anderson, & Nowicki, 2006), alarm signalling (Greene & Meagher, 1998; Smith, 1978), group movements and foraging (Radford & Ridley, 2008; Townsend, Hollen, & Manser, 2010), and parent–offspring communication (Horn & Leonard, 2002). Low-amplitude signals appear to serve many functions that influence fitness, which raises the question of why selection has repeatedly favoured the evolution of these signals in so many disparate social contexts. Furthermore, low-amplitude signals are taxonomically widespread, with evidence for these signals being present in amphibians, birds, fish, insects and mammals (Table 1). Collectively, low-amplitude signals present an interesting case study in behavioural evolution that has the potential to provide novel insights into topics such as honest signalling, audience effects, signal transmission and perception, physiological constraints on signal production, and signal development.

* Correspondence: R. C. Anderson, Florida Atlantic University, 3200 College Avenue, Davie, FL 33314, U.S.A.
E-mail address: andersonr@fau.edu (R. C. Anderson).

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Table 1
Selected examples of low-amplitude signalling across five taxonomic classes

Class	Scientific name	Behavioural context					Source
		Male–Male	Male–Female	Group	Parent–Offspring	Predation	
Actinopterygii	*Hippocampus reidi*		X				Oliveira, Ladich, Abed-Navandi, Souto, and Rosa (2014)
	Porichthys notatus		X				Brantley and Bass (1994)
	Parablennius parvicornis		X				De Jong, Bouton, and Slabbekoorn (2007)
	Trichopsis vittata		X				Ladich (2007)
	Pempheris adspersa			X			Radford, Ghazali, Jeffs, and Montgomery (2015)
	Pomacentrus partitus		X				Kenyon (1994)
	Macropodus opercularis	X					Bischof (1996)
	Astatotilapia burtoni		X				Maruska, Ung, and Fernald (2012)
	Metriaclima zebra	X					Bertucci, Beauchaud, Attia, and Mathevon (2010)
	Pseudotropheus zebra	X	X				Simões, Duarte, Fonseca, Turner, and Amorim (2008); Simões, Fonseca, Turner, and Amorim (2008)
	Pseudotropheus emmiltos		X				Simões, Fonseca, et al. (2008)
	Pseudotropheus fainzilberi		X				Simões, Fonseca, et al. (2008)
Amphibia	*Leptopelis viridis*	X					Grafe, Steffen, and Stoll (2000)
	Rana italica[a]						Razzetti, Sacchi, and Platz (2006)
	Colostethus beebei		X				Bourne et al. (2001)
	Dendrobates speciosus		X				Jungfer (1985)
	Nectophrynoides asperginis	X	X				Arch, Richards-Zawaki, and Feng (2011)
Aves[b]	*Melospiza melodia*	X					Anderson et al. (2007)
	Melospiza georgiana	X					Ballentine et al. (2008)
	Junco hyemalis	X	X				Reichard et al. (2013), Titus (1998)
	Sylvia communis		X				Balsby (2000)
	Sylvia atricapilla	X	X				Collins et al. (2009)
	Turdus merula	X	X				Dabelsteen (2005)
	Turdus cardis		X		X		Ishizuka (2009)
	Catharus fuscescens	X					Belinsky, Nemes, and Schmidt (2015)
	Anthus petrosus			X			Elfström (1992)
	Setophaga caerulescens	X					Hof and Hazlett (2010)
	Geothlypis trichasi		X				Ritchison (1995)
	Cettia fortipes	X					Xia et al. (2013)
	Gerygone igata				X		Anderson, Brunton, and Hauber (2010)
	Troglodytes aedon		X				Johnson and Kermott (1991)
	Turdoides bicolor			X			Radford and Ridley (2008)
	Aegithalos caudatus			X			Sharp and Hatchwell (2005)
	Crex crex	X	X				Ręk and Osiejuk (2011)
Insecta[c]	*Acheta* spp.		X				Alexander (1961)
	Miogryllus spp.		X				Alexander (1961)
	Gryllodes spp.		X				Alexander (1961)
	Nemobius spp.		X				Alexander (1961)
	Gryllus spp.		X				Alexander (1961)
	Anurogryllus spp.		X				Alexander (1961)
	Scapsipedus spp.		X				Alexander (1961)
	Teleogryllus oceanius		X				Zuk et al. (2008)
	Spodoptera litura		X				Nakano et al. (2009)
	Herminia tarsicrinalis		X				Nakano et al. (2009)
	Spilosoma punctarium		X				Nakano et al. (2009)
	Eilema japonica		X				Nakano et al. (2009)
	Ascotis selenaria		X				Nakano et al. (2009)
	Chilo suppressalis		X				Nakano et al. (2009)
	Glyphodes pyloalis		X				Nakano et al. (2009)
	Palpita nigropunctalis		X				Nakano et al. (2009)
	Spoladea recurvalis		X				Nakano et al. (2009)
	Ostrinia furnacalis		X				Nakano et al. (2006)
	Tibicina haematodes		X				Sueur and Aubin (2004)
	Tibicina tomentosa		X				Sueur and Aubin (2004)
	Tibicina corsica		X				Sueur and Aubin (2004)
	Tibicina quadrisignata		X				Sueur and Aubin (2004)
	Tibicina nigronervosa		X				Sueur and Aubin (2004)
	Tibicina garricola		X				Sueur and Aubin (2004)
	Dendroctonus ponderosae	X	X				Fleming et al. (2013)
Mammalia[d]	*Saccopteryx bilineata*		X				Behr and von Helverson (2004)
	Suricata suricatta			X			Townsend et al. (2010)
	Bos taurus				X		Padilla de la Torre et al. (2015)
	Orcinus orca			X			Saulitis et al. (2005)
	Tamiasciurus hudsonicus					X	Greene and Meagher (1998)
	Urocitellus richardsonii					X	Wilson and Hare (2004)
	Eutamias sonomae					X	Smith (1978)
	Lasiopodomys mandarinus		X				Rutovskaya (2011)
	Theropithecus gelada		X	X	X		Gustison et al. (2012)
	Papio ursinus			X	X		Gustison et al. (2012)
	Macaca fascicularis			X			Palombit (1992)
	Chlorocebus pygerythrus					X	Seyfarth et al. (1980)
	Callicebus nigrifrons					X	Cäsar, Byrne, Hoppitt, Young, and Zuberbühler (2012)