



# Selection levels on vocal individuality: strategic use or byproduct

Megan T Wyman<sup>1,2</sup>, Britta Walkenhorst<sup>1,2</sup> and Marta B. Manser<sup>1,2</sup>

In animals, large variation for vocal individuality between and within call types exist, yet we know little on what level selection is taking place. Identifying the selection pressures causing this variation in individuality will provide insight into the evolutionary relationships between cognitive and behavioral processes and communication systems, particularly in group-living species where repeated interactions are common. Analyzing a species' full, large vocal repertoire on individual signatures, its biological function, and the respective selection pressures is challenging. Here, we emphasize that comparing the acoustic individual distinctiveness between life-history stages and different subjects within a call type will allow the identification of selection pressures and enhance the understanding of variation in individuality and its potential strategic use by senders.

## Addresses

<sup>1</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland

<sup>2</sup>Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, Zurich, Switzerland

Corresponding Author: M.B. Manser ([marta.manser@ieu.uzh.ch](mailto:marta.manser@ieu.uzh.ch)),

**Current Opinion in Behavioral Sciences** 2022, **46**:101140

This review comes from a themed issue on **Cognition in the Wild**

Edited by **Alexandra Rosati, Zarin Machanda and Katie Slocombe**

For complete overview of the section, please refer to the article collection, "**Cognition in the Wild**"

Available online 20th May 2022

<https://doi.org/10.1016/j.cobeha.2022.101140>

2352-1546/© 2022 Published by Elsevier Ltd.

## Introduction

The expression and recognition of individuality in vocalizations play a central role in social interactions, particularly in group-living species where the social dynamics are based on repeated interactions. In recent years, much research has been done on vocal individuality and its function (recent review [1]), but less is known on the strategic use of individual signatures and the fitness consequences in regard to advertising individuality. However, knowledge on the flexibility of signalers in the production of such signatures is crucial to understanding its strategic use or evolution as an anatomical byproduct. Here, we review the last 5 years of

research on vocal individuality including fundamental findings from previous years to emphasize the need for investigating the selection level on acoustic identity cues found across taxa.

To determine the level of strategic use, including the according selection for or against individuality in vocalizations, and to understand whether such cues are simply a byproduct, for example, of growth or maturation, requires not only the identification of the maximal range of individuality within the acoustics of a call type, but also factors related to traits of the involved animals on an individual as well as species scale. Additionally, the respective environment impacts call variation. Considering that selection can operate on the sender, receiver, and signal itself makes it necessary to disentangle these different parts into their specific components which then can be related to the context in which a call is produced. Thereby, the call context is defined by the social and ecological environment as well as the indexical traits (morphometric, motivational, and emotional state) of the sender and receiver. These context components vary along life stages differently, thereby enabling predictions on how individual signatures will change in relation to the impact of the social or ecological environment and the indexical traits.

Life history stages, clearly defined ontological and social periods in the life of an individual, are often associated with specific selective pressures that can impact variation in the production and recognition of individual signatures. This variation is predicted to correlate with the benefits and costs of caller discrimination for the caller and/or receivers [2] and indicates a large range of individual flexibility in a species' call repertoire and within its call types. Ultimately, considering individual variation at different life-history stages for different types of subjects allows us to identify the various responsible selective pressures on vocal individuality, and contribute to our understanding of the social dynamics within species.

## Individual signatures

Individual signatures have been documented in the acoustic parameters of many species across taxa (Supplemental Table 1) and are thought to be shaped by a species-specific mix of genetic, environmental (physical and social), and developmental factors [3–5]. They can be present in a range of acoustic signals,

from tonal to noisy calls, simple [6,7] to complex structured calls, notes, or songs [8–11], and from strongly stereotyped to highly variable calls [12]. Both innate [6,13] and learned calls [3,14] can contain individual signatures, also within the same species [15,16]. Cues for caller identity can be found within a few or across several spectral, temporal, and amplitude features [6,17–21], and in the timing, sequence, combinations, or repertoires of calls [9,16,22–24].

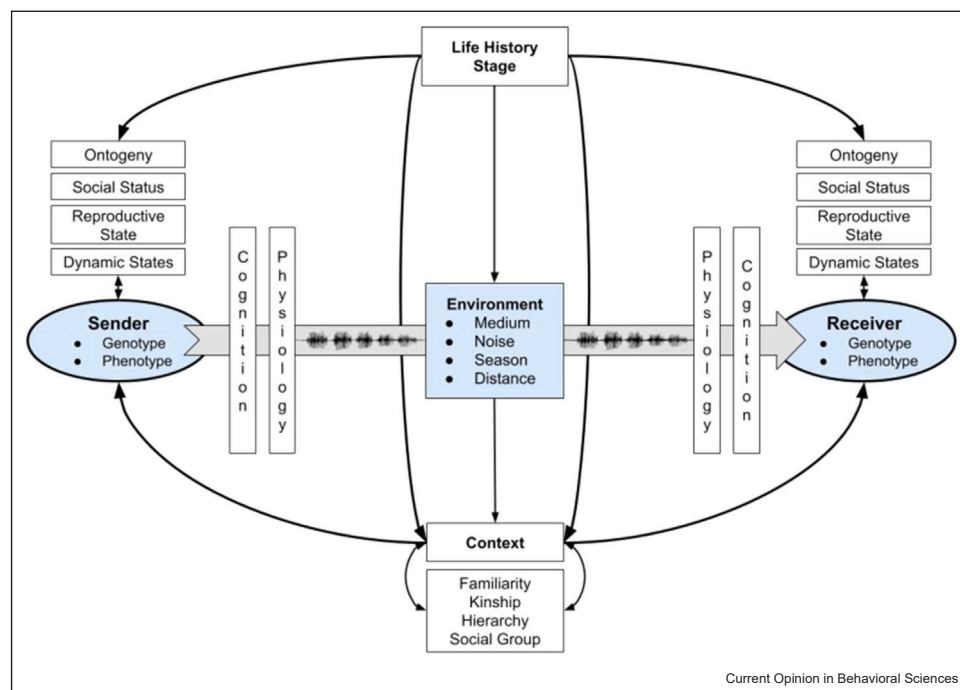
Individual signatures may vary across a species' full vocal repertoire. Levels of individual distinctiveness may be similar [25] or vary across call types [12,15,24,26–28]. Moreover, the acoustic features which most strongly encode identity can be similar or different [12,25,27] across call types, indicating that some species may need to memorize different acoustic features for recognition depending on the call type. Call function can also strongly impact individual signatures. The few studies examining individuality across call contexts within species have produced varied, and sometimes conflicting

results. In some species, the strongest signatures are found in affiliative calls used to facilitate social interactions [12,28–32] likely due to the importance of identity in maintaining social relationships, while in others they may be in high arousal or territorial calls where recognition strongly benefits the caller [26,30,33], although see [28], or in longer distance calls [34] where other sensory cues are absent.

### The recognition process

Individual recognition is a specific form of category-based recognition where identity cues or signals are produced by a sender, propagated through the environment, and perceived and recognized by a receiver(s), potentially resulting in a behavioral or physiological response (Figure 1) [2,35]. Individual recognition can be selected for if fitness benefits (e.g. conflict avoidance, ignoring unreliable signalers) outweigh the costs (e.g. energetic costs, time) for the sender and/or receiver [1,2,36–38]. Adaptations favoring this process can occur at any stage within the recognition process.

Figure 1



Interactions of factors affecting the production, propagation, and reception of acoustic identity information. Boxes show factors; black arrows indicate the direction of influence. The acoustic individual signature is represented by the bold gray arrow from sender to receiver. Identity information included in an acoustic signal is shaped by the sender's physiology and potential cognitive control before being filtered by the environment during transmission and propagation. The receiver physiologically perceives the signal and needs to cognitively process it. The motivation to encode or decode identity information is not only affected by the genotype as well as phenotype of an individual but is also influenced by the current ontogenetic and reproductive stage, social status, and dynamic state (e.g. arousal level) of the respective sender or receiver. Additionally, the context and familiarity between individuals based on their social and genetic relationship affect the usage of identity information. Overall, these factors can vary depending on an individual's life history stage (e.g. changes in physical and social environment across life stages as offspring move from more restricted birth locations such as nests or underground burrows to more open locations with potentially more distant intended receivers) and ultimately have an influence on the costs and benefits of encoding and decoding identity information in an acoustic signal.

### Production

Acoustic output is produced through a combination of processes involving neural activity, physiology and morphology, muscle activation, and physical mechanisms of sound production [39,40]. Voiced sound is typically produced when air from the lungs passes through a sound source (larynx in mammals, anuras, reptiles; syrinx in birds) to generate vocal fold oscillations [41,42] that form the glottal waveform (the ‘source’) containing a fundamental frequency (F0, related to vocal fold mass, tension, and length) and harmonics [43]. This ‘source’ signal passes through the remaining vocal tract (the ‘filter’) and is altered by resonance frequencies to form spectral peaks (formants, related to vocal tract size and shape) [43,44]. Natural variation, adaptations, and exaptations [45–48] to this system contribute significantly to the wide acoustic diversity in animals [45,49–53].

Identity signatures are often related to ‘static’ indexical traits of the caller that reflect characteristics of the vocal production anatomy [19,54]. For instance, spectral and temporal identity features are correlated with morphological characteristics in burrowing petrels (*Pterodroma axillaris*) [13]. In king penguins (*Aptenodytes patagonicus*), differing lengths of left-side and right-side vibratory tissues within the syrinx produce distinctive dual-source vocal output with unique signatures [55]. Formants in particular are thought to be reliable identity cues due to causal relationships between differing vocal tract morphology between callers, and resultant formant structures [19,54]. This relationship has been demonstrated across many species [28,56–58] though not universally [57,59].

Acoustic variation within call types can also provide a variety of information on ‘dynamic’ states of the caller (e.g. emotion or motivation [18], short-term endocrine states [45]), via modulations to source-related and filter-related anatomy that impact features such as F0, duration, and amplitude [43,60], formants [43,49,54,60–62], or timing. However, identity signatures can persist despite such acoustic alterations. Individual distinctiveness persists in zebra finch (*Taeniopygia guttata*) calls despite stress-induced flexibility in acoustic features [63]. Furthermore, identity signatures can also be encoded in consistent modulation patterns of acoustic features (e.g. modulation of F0 [9,64–69], amplitude [20], or formants [57]).

### Recognition by receivers

Recognition is typically tested via playback experiments, although care must be taken in the interpretation of the observed responses [1]. The presence of acoustic individual distinctiveness does not necessarily mean that receivers are able to discriminate between callers or even perceive a difference [70] and the most individually distinct calls may not elicit the strongest recognition

responses [15]. Mechanisms of recognition may involve template formation and matching [36] through processes such as innate or learned acquisition via habituation and/or associated learning and often depend upon context [36,37]. Recognition direction (unidirectional versus bidirectional) and levels (singular versus multiple individuals recognized) can vary [1,37] and the level of specificity (individuals in a set) and multiplicity (number of sets differentiated) can vary according to selection pressures but is predicted to remain as minimal as possible if increased recognition complexity leads to increased cognitive demands and costs [37]. Difficulties in recognition research is often based on the fact that we mainly rely on behavioral responses to playbacks to test individual recognition, while some test contexts might not require an immediate behavioral response or be of advantage [71], and the recognition of individuality may only induce unobserved physiological or neurobiological changes [72–77].

### Propagation

Acoustic signatures and perception abilities are predicted to be adapted to the local propagation environment depending on call context, function, and intended receivers with the salient distances that identity information travels (‘active space’) varying depending on these factors [78–86]. For example, the marine environment restricts visual communication and affects acoustic features in a way that promotes the use of frequency modulation patterns as individual signatures in dolphins [87]. In mammals, signatures travel shorter distances for calls utilized in close-distance contexts and noisy/closed habitats (e.g. mother–offspring interactions [88,89] or close-distance sexual calls [90]), and further in open-habitat species in long-distance contexts (e.g. territorial [69] and long-distance contact calls [91]). In the complex pant hoots of male chimpanzees (*Pan troglodytes schweinfurthii*), identity signatures are strongest in the early low-amplitude phases and high-amplitude climax phase but not the later let-down phase, potentially indicating the importance of advertising identity to receivers at both close and far distances [11]. Identity cues in distance calls are salient over longer distances in male zebra finches than females, due to increased F0 modulation in males, indicating different sex-based selection pressures for identity signaling [66]. Furthermore, the acoustic features that best encode identity may differ across distances [66].

### Evolutionary drivers of individual recognition

The benefits of establishing and maintaining relationships with specific individuals in social species can act as a selective force for individual recognition [2,36–38]. Selection is thought to be especially strong in species with large social group sizes [92–94] although see [95], highly temporally and/or spatially dynamic [3,5,92,96] or colonial social systems [5,97,98]. For example, individual

recognition of learned contact calls in many parrot species [3,99] and signature whistles in dolphins [92] are likely selected due to recognition benefits within their fission–fusion societies. In non-nesting colonial penguins, the benefits of identifying mates and offspring in noisy, dense groups likely drove vocal anatomy adaptations [55] resulting in unique dual voice signatures [10,100]. By comparison, the identity signatures observed within fixed-site nesting penguins are relatively simple [7,101,102]. Additionally, individual recognition may be stronger in species with high levels of cooperative behaviors [37,103,104] or social complexity [24], although see [95].

### Flexibility in vocal production and response: impacts on individual recognition

#### *Flexibility in vocal production and recognition*

While the range of producible acoustic features varies between individuals due to differences in the sender's current physiology, morphology, and internal states [18,19,52,54], the current environment or social context can add acoustic variation via vocal modulation [45,105,106]. Modifications to acoustic output in response to changes in ambient noise or microhabitat propagation properties [107–117], and changes induced by social conditions or contexts [45,106,118–122] including the presence or characteristics of the intended receivers [120,123] can have significant impacts on individual recognition. The current social environment ('audience effect') can also impact the receiver's response: male zebra finches respond more strongly to their mate's distance calls versus a familiar female if they are in the presence of a mated pair but show no response difference when in the presence of an unmated pair or males [124], although see [15]. Furthermore, some species can exert varying degrees of volitional control or flexibility (beyond simple arousal-based triggers) over their vocal output [125–130] which can strongly influence vocal identity [131]. Such control can form the basis of vocal learning processes [132], including vocal accommodation [133], which can also impact identity coding [134], for example, parrots contact calls [3], dolphin signature whistles [92], and birdsong [135,136]. Despite these gradual or rapid changes to acoustic features, identity information within a call can still be maintained by retaining certain fine-scale structural features [134,137–139]. Diverging from previously encountered auditory models can even enhance individual distinctiveness if recognition is beneficial [132]. Ravignani and Garcia [140] suggest that vocal production learning resulting in frequency shifts to deviate from existing call ranges could lead to enhanced individual recognition. All of these factors involved in vocal modification are strongly impacted by changes in life-history stage and social status (Figure 1) [132].

#### *Life stage impacts on individual recognition*

Vocal distinctiveness and recognition abilities may vary across ontological stages [3,116,135,136,141–144], due to differences in recognition costs and benefits depending on age and/or call contexts [30,145,146] or morphological diversification of vocal anatomy with age. Subadult males show lower vocal distinctiveness than adults in Cape fur seals (*Arctocephalus pusillus*) [30] and northern elephant seals (*Mirounga angustirostris*) [147], likely reflecting lower selective pressures for individual recognition in younger age classes. In contrast, mother–offspring attraction calls in Cape fur seals [30] and other colonial pinnipeds [97] have high levels of distinctiveness in both adults and pups due to selection pressure in noisy, dense colonies. Zebra finch fledglings of both sexes respond similarly to parental calls, but male responses diminished faster with age than female responses, potentially linked to the continued importance of parental recognition during mate choice in females [148]. Changes in signature production and recognition can also be influenced by social and auditory experience through vocal learning-related modifications [149–153]. Male zebra finches initially produce innate individualized distance calls with high heritability and relatively low interindividual variation (as do females), but these are overwritten over time through social experience-based vocal learning resulting in lower heritability and higher interindividual variation, while 'indexical' cues to body morphology remain [16,154]. Through tutors, males also learn to produce complex songs that have even higher individuality [16]. The production and recognition to specific call types can vary by sex and reproductive state [118,155]: during breeding, female zebra finches (but not males) show differences in their auditory perception and responses to contact calls emitted from familiar but not unfamiliar senders, suggesting a potential functional benefit recognizing and responding to familiar individuals during critical life stages such as breeding [118]. Male winter wrens (*Troglodytes hiemalis*) show stronger responses to neighbors than strangers but only during territorial settlement [156]. Life-stage related trade-offs may also occur between signaling identity and other aspects such as quality [157,158], although see [159] or social closeness following vocal accommodation [134].

#### *Stability of vocal recognition*

While individual recognition requires some degree of signature stability over time, the timing and duration of such stability may be strongly influenced by the costs and benefits of individual recognition within the call context in particular life stages (e.g. mate recognition, territorial defense, social affiliation). For instance, species that derive fitness benefits from long-term social bonds are likely to exhibit higher vocal identity stability over time, as seen in two socially important call types of African penguins (*Spheniscus demersus*), a long-term



monogamous seabird with strong territorial site-fidelity [160], also see [161–164]. However, stability can change even within life stages: in Magellanic penguins (*Spheniscus magellanicus*), females responded less to their mate's call when mated for more years and male responses to mutual display calls increased over the breeding season [165]. Signatures that have high individuality, but only over short time periods may reflect changes in the costs and benefits of recognition across life history or social status stages, changes to local physical or social environments, or experience-based modifications to vocal output, see [166–172].

## Conclusion

Studies within the last five years examine acoustic signatures of individuality across a range of subjects, aspects of interest, call types, social contexts, and analysis methods (Supplemental Table 1). In their review of the receiver side of the recognition process, Carlson et al. [1] highlight research gaps, such as taxonomic biases towards birds and mammals, and make suggestions for future research, for example, temporal stability and levels of recognition. Here we wish to emphasize, while most research on individual recognition has been done at the mechanistic level, that is, *how* individual information is encoded and recognized, we need to evaluate the plasticity of individuality at the functional level, that is, *why* individual information is encoded and recognized. Investigating the selection level on vocal individuality will provide a vital part of the evolutionary relationships between specific cognitive and behavioral processes and communication systems.

In order to gain a clearer understanding of the drivers and mechanisms of individual recognition, it is important to consider a species' entire vocal repertoire. While assessing vocal recognition in multiple species across their vocal repertoires in comparison with ecological and social influences on call function and content would be optimal [27], it can be challenging. Especially in species with large vocal repertoires, given it requires extensive knowledge and testing, as receiver discrimination abilities need to be considered, which may not be highly correlated with measured distinctiveness [173]. To aid such comparisons, future studies should utilize individuality measures which are more comparable both within and across species [174,175], based on the understanding on which of the different context components selection happens. Furthermore, playback presentations paired with physiological (e.g. heart rate [176–178], hormone levels [179,180], body temperature [181,182]) or neural [72,183] response measures in addition to behavioral responses could help address challenges in assessing receiver recognition of specific individuals. For instance, little blue penguin chicks (*Eudyptula minor*) respond with higher heart rates to

playbacks of familiar individuals than strangers despite showing no outward behavioral response differences [176]. However, we acknowledge the potential difficulty in incorporating such methodologies across species.

Focused approaches can elucidate where selection acts on individuality versus being a byproduct that can be utilized by the receivers. To understand the selection processes on the flexible use on the production and recognition side, the comparison of individual signatures in different call types related to different life stages enables us to discriminate innate and ontogenetic effects versus voluntary control. Such investigations could be performed using species that have both innate and volitional or learned calls [184], as seen in some species of bats [185,186], for example, Greater sac-winged bats, *Saccopteryx bilineata* [139,187], and songbirds [136], for example, zebra finches [16,154]. Intraindividual flexibility of acoustic features in animals is seldom examined [45,188]. Therefore, studying how identity is expressed within the same call type across multiple behavioral contexts can decode the selection pressures and mechanisms driving individual recognition. While this approach is not universally possible in all species, it could be applied in certain cases, such as some Rallidae [6,189] or mongoose [190] species where structurally similar calls are produced across multiple contexts. Lastly, testing for changes of individual signatures along different life stages within the same call type will bring conclusions on the flexibility of acoustic individuality including connected proximate mechanisms (e.g. anatomical, physiological change) and to what extent it is under volitional control allowing for strategic use in social interactions.

## Funding

MW was self-funded and BW and MM were funded by the University of Zurich, Switzerland.

## Conflict of interest statement

Nothing declared.

## Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.cobeha.2022.101140.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest.

1. Carlson NV, Kelly EM, Couzin I: **Individual vocal recognition across taxa: a review of the literature and a look into the future.** *Philos Trans R Soc B Biol Sci* 2020, **375**:20190479.

Review of the receiver side of the individual recognition process with a focus on the methodology being used and current weaknesses.

2. Tibbetts EA, Dale J: **Individual recognition: it is good to be different.** *Trends Ecol Evol* 2007, **22**:529-537.
  3. Bradbury JW, Balsby TJS: **The functions of vocal learning in parrots.** *Behav Ecol Sociobiol* 2016, **70**:293-312.
  4. King SL, Harley HE, Janik VM: **The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*.** *Anim Behav* 2014, **96**:79-86.
  5. Aubin T, Charrier I, Courvoisier H, Rybak F: **Penguins and Otariids as models for the study of individual vocal recognition in the noisy environment of a colony.** *New Res Acoust* 2008, **285**:285-298.
  6. Fu C, Kathait A, Lu G, Li X, Li F, Xing X: **A small vocal repertoire during the breeding season expresses complex behavioral motivations and individual signature in the common coot.** *BMC Zool* 2021, **6**:24.
- Explores vocal information content in a species with a small vocal repertoire: four innate single syllable call types are used in association with nine behaviors. Temporal variation in the most, common call type used in multiple contexts provided information on identity and behavioral motivation.
7. Jouventin P, Aubin T: **Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins.** *Anim Behav* 2002, **64**:747-757.
  8. Chen G, Xia C, Zhang Y: **Individual identification of birds with complex songs: the case of green-backed flycatchers *Ficedula elisae*.** *Behav Processes* 2020, **173**:104063.
  9. Toth CA, Parsons S: **The high-output singing displays of a lekking bat encode information on body size and individual identity.** *Behav Ecol Sociobiol* 2018, **72**:102.
  10. Aubin T, Jouventin P, Hildebrand C: **Penguins use the two-voice system to recognize each other.** *Proc R Soc London Ser B Biol Sci* 2000, **267**:1081-1087.
  11. Fedurek P, Zuberbühler K, Dahl CD: **Sequential information in a great ape utterance.** *Sci Rep* 2016, **6**:38226.
  12. Bouchet H, Blois-Heulin C, Pellier A-S, Zuberbühler K, Lemasson A: **Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*).** *J Comp Psychol* 2012, **126**:45-56.
  13. Gémard C, Aubin T, Bonadonna F: **Males' calls carry information about individual identity and morphological characteristics of the caller in burrowing petrels.** *J Avian Biol* 2019, **50**:jav.02270.
  14. Janik VM: **Cetacean vocal learning and communication.** *Curr Opin Neurobiol* 2014, **28**:60-65.
  15. D'Amelio PB, Klumb M, Adreani MN, Gahr ML, ter Maat A: **Individual recognition of opposite sex vocalizations in the zebra finch.** *Sci Rep* 2017, **7**:5579.
  16. Forstmeier W, Burger C, Temnow K, Derégnaucourt S: **The genetic basis of zebra finch vocalizations.** *Evolution* 2009, **63**:2114-2130.
  17. Verzola-Olivio P, Ferreira BL, Frei F, Monticelli PF: **Guinea pig's courtship call: cues for identity and male dominance status?** *Anim Behav* 2021, **174**:237-247.
  18. Briefer EF: **Coding for 'dynamic' information: vocal expression of emotional arousal and valence in non-human animals.** In *Coding Strategies in Vertebrate Acoustic Communication*. Edited by Aubin T, Mathevon N. Springer Nature; 2020:137-162.
  19. Charlton BD, Pisanski K, Raine J, Reby D: **Coding of static information in terrestrial mammal vocal signals.** In *Coding Strategies in Vertebrate Acoustic Communication*. Edited by Aubin T, Mathevon N. Springer Nature; 2020:115-136.
  20. Sèbe F, Poindron P, Ligout S, Sèbe O, Aubin T: **Amplitude modulation is a major marker of individual signature in lamb bleats.** *Bioacoustics* 2018, **27**:359-375.
  21. Fukushima M, Doyle AM, Mullarkey MP, Mishkin M, Averbeck BB: **Distributed acoustic cues for caller identity in macaque vocalization.** *R Soc Open Sci* 2015, **2**:150432.
  22. Clink DJ, Tasirin JS, Klinck H: **Vocal individuality and rhythm in male and female duet contributions of a nonhuman primate.** *Curr Zool* 2020, **66**:173-186.

Investigated female and male duet contributions in tarsiers on a pair and individual scale in order to examine nonhuman primate vocal flexibility in

vocalizations heard over long distances. Results show a higher degree of identity information encoded in the female phrases compared with male duet parts, which is in line with previous findings from gibbons. Females were also more variable in rhythm than males and showed a higher interindividual variation in the number of rhythm bands. The study also provides evidence for the modification of note rate relative to the duetting partner.

23. Rauber R, Kranstauber B, Manser MB: **Call order within vocal sequences of meerkats contains temporary contextual and individual information.** *BMC Biol* 2020, **18**:119.
- Explored what types of information were contained within the ordering of graded, acoustically distinct but functionally related call types. Results demonstrated that the temporal variation of call type composition in vocal sequences provided stable identity information with females showing higher interindividual differences compared with males and sub-adults.
24. Gero S, Whitehead H, Rendell L: **Individual, unit and vocal clan level identity cues in sperm whale codas.** *R Soc Open Sci* 2016, **3**:150372.
  25. Salmi R, Hammerschmidt K, Doran-Sheehy DM: **Individual distinctiveness in call types of wild western female gorillas.** *PLoS One* 2014, **9**:e101940.
  26. Keenan S, Mathevon N, Stevens JMG, Nicolè F, Zuberbühler K, Guéry J-P, Levréro F: **The reliability of individual vocal signature varies across the bonobo's graded repertoire.** *Anim Behav* 2020, **169**:9-21.
- Examines identity signatures across a graded call repertoire in bonobos. They found that the identity cues were present in all call types examined but notably the reliability of the signature decreased from calls used in high-arousal contexts to calls used in contexts of low arousal.
27. Elie JE, Theunissen FE: **Zebra finches identify individuals using vocal signatures unique to each call type.** *Nat Commun* 2018, **9**:4026.
  28. Rendall D, Owren MJ, Rodman PS: **The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations.** *J Acoust Soc Am* 1998, **103**:602-614.
  29. Linn SN, Schmidt S, Scheumann M: **Individual distinctiveness across call types of the southern white rhinoceros (*Ceratotherium simum simum*).** *J Mammal* 2021, **102**:440-456.
- Tested three rhinoceros' call types of different structures and used in different contexts on evolutionary pressures assumed by long-distance, acoustic structure and social function hypothesis. While the hypotheses are not mutually exclusive, individual distinctiveness was best explained by social function of the call with the highest individuality found in call type mediating intragroup interactions.
30. Martin M, Gridley T, Elwen SH, Charrier I: **Extreme ecological constraints lead to high degree of individual stereotypy in the vocal repertoire of the Cape fur seal (*Arctocephalus pusillus pusillus*).** *Behav Ecol Sociobiol* 2021, **75**:104.
- Comparison of individual signatures across call types in Cape fur seals. Distinctiveness is highest in mother – offspring affiliative calls and adult male territorial calls. An interspecies comparison among pinnipeds with similar and lower colony size and social structure also revealed higher individuality in these call types showing an interaction with ecological constraints.
31. Lemasson A, Hausberger M: **Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*).** *J Acoust Soc Am* 2011, **129**:3341-3352.
  32. Charrier I, Jouventin P, Mathevon N, Aubin T: **Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*.** *Polar Biol* 2001, **24**:378-382.
  33. Rubow J, Cherry MI, Sharpe LL: **Dwarf mongooses use sex and identity cues in isolation calls to discriminate between callers.** *Anim Behav* 2017, **127**:23-31.
  34. Mitani JC, Gros-Louis J, Macedonia JM: **Selection for acoustic individuality within the vocal repertoire of wild chimpanzees.** *Int J Primatol* 1996, **17**:569-583.
  35. Yorzinski JL: **The cognitive basis of individual recognition.** *Curr Opin Behav Sci* 2017, **16**:53-57.
  36. Tumulty JP, Sheehan MJ: **What drives diversity in social recognition mechanisms?** *Front Ecol Evol* 2020, **7**:517.
- An exploration of how interactions between senders and receivers, especially receiver agreement on sender categorization, influences the mechanisms and evolution of recognition systems.
37. Wiley RH: **Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour.** *Biol Rev* 2013, **88**:179-195.

38. Johnstone RA: **Recognition and the evolution of distinctive signatures: when does it pay to reveal identity?** *Proc R Soc London Ser B Biol Sci* 1997, **264**:1547-1553.
39. Kelley DB, Ballagh IH, Barkan CL, Bendesky A, Elliott TM, Evans BJ, Hall IC, Kwon YM, Kwong-Brown U, Leininger EC, et al.: **Generation, coordination, and evolution of neural circuits for vocal communication.** *J Neurosci* 2020, **40**:22-36.
40. Elemans CP, Rasmussen JH, Herbst CT, Düring DN, Zollinger SA, Brumm H, Srivastava K, Svane N, Ding M, Larsen ON, et al.: **Universal mechanisms of sound production and control in birds and mammals.** *Nat Commun* 2015, **6**:8978.
41. Titze IR: **The Myoelastic Aerodynamic Theory of Phonation.** National Center for Voice and Speech; 2006.
42. van den Berg J: **Myoelastic-aerodynamic theory of voice production.** *J Speech Hear Res* 1958, **1**:227-244.
43. Titze IR: **Principles of Voice Production.** Prentice Hall; 1994.
44. Fant G: **Acoustic Theory of Speech Production.** Mouton; 1960.
45. Fernández-Vargas M, Riede T, Pasch B: **Mechanisms and constraints underlying acoustic variation in rodents.** *Anim Behav* 2021, **184**:135-147, <https://doi.org/10.1016/j.anbehav.2021.07.011>.  
Review of vocal production and sources of acoustic variation due to ontogenetic, social, endocrine factors in rodents.
46. Riede T, Pasch B: **Pygmy mouse songs reveal anatomical innovations underlying acoustic signal elaboration in rodents.** *J Exp Biol* 2020, **223**:jeb223925, <https://doi.org/10.1242/jeb.223925>
47. Taylor JRA, DeVries MS, Elias DO: **Growling from the gut: co-option of the gastric mill for acoustic communication in ghost crabs.** *Proc R Soc B Biol Sci* 2019, **286**:20191161.
48. Kingsley EP, Eliason CM, Riede T, Li Z, Hiscock TW, Farnsworth M, Thomson SL, Goller F, Tabin CJ, Clarke JA: **Identity and novelty in the avian syrinx.** *Proc Natl Acad Sci* 2018, **115**:10209-10217.
49. Pisanski K, Anikin A, Reby D: **Vocal size exaggeration may have contributed to the origins of vocalic complexity.** *Philos Trans R Soc B Biol Sci* 2022, **377**:20200401.
50. Garcia SM, Kopuchian C, Mindlin GB, Fuxjager MJ, Tubaro PL, Goller F: **Evolution of vocal diversity through morphological adaptation without vocal learning or complex neural control.** *Curr Biol* 2017, **27**:2677-2683 e3.
51. Charlton BD, Reby D: **The evolution of acoustic size exaggeration in terrestrial mammals.** *Nat Commun* 2016, **7**:1-8.
52. Riede T, Goller F: **Morphological basis for the evolution of acoustic diversity in oscine songbirds.** *Proc R Soc B Biol Sci* 2014, **281**:20132306.
53. Fitch WT, Hauser MD: **Unpacking "honesty": vertebrate vocal production and the evolution of acoustic signals.** In *Acoustic Communication*. Edited by Simmons AM, Fay RR, Popper AN. Springer; 2003:65-137.
54. Taylor AM, Charlton BD, Reby D: **Vocal production by terrestrial mammals: source, filter, and function.** In *Vertebrate Sound Production and Acoustic Communication*. Edited by Suthers RA, Fitch WT, Fay RR, Popper AN. Springer International Publishing; 2016:229-259.
55. Kriesell HJ, Le Bohec C, Cerwenka AF, Hertel M, Robin J-P, Ruthensteiner B, Gahr M, Aubin T, Düring DN: **Vocal tract anatomy of king penguins: morphological traits of two-voiced sound production.** *Front Zool* 2020, **17**:5.  
Anatomical adaptations for identity signaling in king penguins: vibratory tissues of different lengths in the syrinx produce unique dual-source vocal output used in individual recognition at noisy colonies.
56. Frühholz S, Schweinberger SR: **Nonverbal auditory communication – evidence for integrated neural systems for voice signal production and perception.** *Prog Neurobiol* 2021, **199**:101948.
57. Favaro L, Gamba M, Gili C, Pessani D: **Acoustic correlates of body size and individual identity in banded penguins.** *PLoS One* 2017, **12**:e0170001.
58. Gamba M, Favaro L, Araldi A, Matteucci V, Giacoma C, Friard O: **Modeling individual vocal differences in group-living lemurs using vocal tract morphology.** *Curr Zool* 2017, **63**:467-475.
59. Budka M, Osiejuk TS: **Formant frequencies are acoustic cues to caller discrimination and are a weak indicator of the body size of corncrake males.** *Ethology* (11) 2013, **119**:960-969, <https://doi.org/10.1111/eth.12141>
60. Hollien H: **Vocal fold dynamics for frequency change.** *J Voice* 2014, **28**:395-405.
61. Boë L-J, Sawallis TR, Fagot J, Badin P, Barbier G, Captier G, Ménard L, Heim J-L, Schwartz J-L: **Which way to the dawn of speech?: reanalyzing half a century of debates and data in light of speech science.** *Sci Adv* 2019, **5**:eaaw3916.
62. Ohms VR, Snelderwaard PC, ten Cate C, Beckers GJL: **Vocal tract articulation in zebra finches.** *PLoS One* 2010, **5**:e11923.
63. Soula HA, Carnino D, Fernandez MSA, Perez EC, Villain AS, Vignal C: **Stress-induced flexibility and individuality in female and male zebra finch distance calls.** *Behav Process* 2019, **163**:113-120.
64. Wijers M, Trethowan P, Du Preez B, Chamailé-Jammes S, Loveridge AJ, Macdonald DW, Markham A: **Vocal discrimination of African lions and its potential for collar-free tracking.** *Bioacoustics* 2021, **30**:575-593.
65. Fearey J, Elwen SH, James BS, Gridley T: **Identification of potential signature whistles from free-ranging common dolphins (Delphinus delphis) in South Africa.** *Anim Cogn* 2019, **22**:777-789.
66. Mouterde SC, Theunissen FE, Elie JE, Vignal C, Mathevon N: **Acoustic communication and sound degradation: how do the individual signatures of male and female zebra finch calls transmit over distance?** *PLoS One* 2014, **9**:e102842.
67. Briefer E, Mcelligott AG: **Mutual mother – offspring vocal recognition in an ungulate hider species (Capra hircus).** *Anim Cogn* 2011, **14**:585-598, <https://doi.org/10.1007/s10071-011-0396-3>
68. Charlton BD, Keating JL, Kersey D, Rengui L, Huang Y, Swaisgood RR: **Vocal cues to male androgen levels in giant pandas.** *Biol Lett* 2011, **7**:71-74.
69. Mitchell BR, Makagon MM, Jaeger MM, Barrett RH: **Information content of coyote barks and howls.** *Bioacoustics* 2006, **15**:289-314.
70. Schibler F, Manser MB: **The irrelevance of individual discrimination in meerkat alarm calls.** *Anim Behav* 2007, **74**:1259-1268.
71. Reber SA, Townsend SW, Manser MB: **Social monitoring via close calls in meerkats.** *Proc R Soc B Biol Sci* 2013, **280**:20131013.
72. Rose MC, Styr B, Schmid TA, Elie JE, Yartsev MM: **Cortical representation of group social communication in bats.** *Science* (6566) 2021, **374**: eaba9584.  
Neural representation of group social communication in bats. Evidence for 'identity selective' neurons in listening bats during group social communication.
73. Boros M, Gábor A, Szabó D, Bozsik A, Gácsi M, Szalay F, Faragó T, Andics A: **Repetition enhancement to voice identities in the dog brain.** *Sci Rep* 2020, **10**:3989.  
Neuroimaging analysis determined that auditory identity processing is performed in similar brain regions in dogs as in humans and nonhuman primates.
74. Mathias SR, von Kriegstein K: **Voice processing and voice-identity recognition.** In *Timbre: Acoustics, Perception, and Cognition*. Edited by Siedenburg K, Saitis C, McAdams S, Popper AN, Fay RR. Springer International Publishing; 2019:175-209.
75. Maguinness C, Roswandowitz C, von Kriegstein K: **Understanding the mechanisms of familiar voice-identity recognition in the human brain.** *Neuropsychologia* 2018, **116**:179-193.
76. Perrodin C, Kayser C, Abel TJ, Logothetis NK, Petkov CI: **Who is that? Brain networks and mechanisms for identifying individuals.** *Trends Cogn Sci* 2015, **19**:783-796.
77. Petkov CI, Logothetis NK, Obleser J: **Where are the human speech and voice regions, and do other animals have anything like them?** *Neurosci* 2009, **15**:419-429.
78. Hardt B, Benedict L: **Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis.** *Bioacoustics* 2021, **30**:716-742.
79. Mikula P, Valcu M, Brumm H, Bulla M, Forstmeier W, Petrusková T, Kempenaers B, Albrecht T: **A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection.** *Ecol Lett* 2021, **24**:477-486.



80. Charlton BD, Owen MA, Swaisgood RR: **Coevolution of vocal signal characteristics and hearing sensitivity in forest mammals.** *Nat Commun* 2019, **10**:2778.
81. Cummings ME, Endler JA: **25 Years of sensory drive: the evidence and its watery bias.** *Curr Zool* 2018, **64**:471-484.
82. Brumm H, Naguib M: **Chapter 1 environmental acoustics and the evolution of bird song.** *Adv Study Behav* 2009, **40**:1-33.
83. Ey E, Fischer J: **The “acoustic adaptation hypothesis”—a review of the evidence from birds, anurans and mammals.** *Bioacoustics* 2009, **19**:21-48.
84. Endler JA: **Signals, signal conditions, and the direction of evolution.** *Am Nat* 1992, **139**:S125-S153.
85. Wiley RH, Richards DG: **Adaptations for acoustic communication in birds: sound propagation and signal detection.** In: *Acoustic Communication in Birds*. Edited by Kroodsma DE, Miller EH. vol 1, Academic Press; 1982:131-181.
86. Morton ES: **Ecological sources of selection on avian sounds.** *Am Nat* 1975, **109**:17-34.
87. Janik VM, Sayigh LS, Wells RS: **Signature whistle shape conveys identity information to bottlenose dolphins.** *Proc Natl Acad Sci* 2006, **103**:8293-8297.
88. Pitcher BJ, Harcourt RG, Charrier I: **Individual identity encoding and environmental constraints in vocal recognition of pups by Australian sea lion mothers.** *Anim Behav* 2012, **83**:681-690.
89. Charrier I, Pitcher BJ, Harcourt RG: **Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints.** *Anim Behav* 2009, **78**:1127-1134.
90. Charlton BD, Owen MA, Keating JL, Martin-Wintle MS, Zhang H, Swaisgood RR: **Sound transmission in a bamboo forest and its implications for information transfer in giant panda (*Ailuropoda melanoleuca*) bleats.** *Sci Rep* 2018, **8**:12754.
91. McComb K, Reby D, Baker L, Moss C, Sayialel S: **Long-distance communication of acoustic cues to social identity in African elephants.** *Anim Behav* 2003, **65**:317-329.
92. Janik VM, Sayigh LS: **Communication in bottlenose dolphins: 50 years of signature whistle research.** *J Comp Physiol A* 2013, **199**:479-489.
93. Pollard KA, Blumstein DT: **Social group size predicts the evolution of individuality.** *Curr Biol* 2011, **21**:413-417.
94. Mathevon N, Charrier I, Jouventin P: **Potential for individual recognition in acoustic signals: a comparative study of two gulls with different nesting patterns.** *C R Biol* 2003, **326**:329-337.
95. Bergman TJ: **Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis.** *Proc R Soc B Biol Sci* 2010, **277**:3045-3053.
96. Buhman-Deever SC, Hobson EA, Hobson AD: **Individual recognition and selective response to contact calls in foraging brown-throated conures, *Aratinga pertinax*.** *Anim Behav* 2008, **76**:1715-1725.
97. Charrier I: **Mother-offspring vocal recognition and social system in pinnipeds.** In *Coding Strategies in Vertebrate Acoustic Communication*. Edited by Aubin T, Mathevon N. Springer Nature; 2020:231-246.
98. Medvin MB, Stoddard PK, Beecher MD: **Signals for parent-offspring recognition: a comparative analysis of the begging calls of cliff swallows and barn swallows.** *Anim Behav* 1993, **45**:841-850.
99. Smith-Vidaurre G, Araya-Salas M, Wright TF: **Individual signatures outweigh social group identity in contact calls of a communally nesting parrot.** *Behav Ecol* 2020, **31**:448-458.
- Showing relaxed selection for complexity in learned calls used for individual recognition in a reduced population size of parrots due to invasion.
100. Lengagne T, Aubin T, Jouventin P, Lauga J: **Perceptual salience of individually distinctive features in the calls of adult king penguins.** *J Acoust Soc Am* 2000, **107**:508-516.
101. Favaro L, Gamba M, Alfieri C, Pessani D, McElligott AG: **Vocal individuality cues in the African penguin (*Spheniscus demersus*): a source-filter theory approach.** *Sci Rep* 2015, **5**:17255.
102. Searby A, Jouventin P, Aubin T: **Acoustic recognition in macaroni penguins: an original signature system.** *Anim Behav* 2004, **67**:615-625.
103. Tumulty JP, Miller SE, Van Belleghem SM, Weller HI, Jernigan CM, Vincent S, Staudenraus RJ, Legan AW, Polnaszek TJ, Uy FMK, et al.: **Evidence for a selective link between cooperation and individual recognition.** *bioRxiv* 2021, <https://doi.org/10.1101/2021.09.07.459327>
104. Sheehan MJ, Miller C, Reeve HK: **Identity signaling and patterns of cooperative behavior.** *Integr Comp Biol* 2017, **57**:580-588.
105. Matzinger T, Fitch WT: **Voice modulatory cues to structure across languages and species.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200393.
106. Seyfarth R, Cheney D: **Pragmatic flexibility in primate vocal production.** *Curr Opin Behav Sci* 2018, **21**:56-61.
107. Torres Borda L, Jadoul Y, Rasilo H, Salazar Casals A, Ravignani A: **Vocal plasticity in harbour seal pups.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200456.
108. Duquette CA, Loss SR, Hovick TJ: **A meta-analysis of the influence of anthropogenic noise on terrestrial wildlife communication strategies.** *J Appl Ecol* 2021, **58**:1112-1121.
109. Brumm H, Zollinger SA: **Vocal plasticity in a reptile.** *Proc R Soc B Biol Sci* 2017, **284**:20170451.
110. Vieira M, Beauchaud M, Amorim MCP, Fonseca PJ: **Boat noise affects meagre (*Argyrosomus regius*) hearing and vocal behaviour.** *Mar Pollut Bull* 2021, **172**:112824.
111. Courter JR, Perruci RJ, McGinnis KJ, Rainieri JK: **Black-capped chickadees (*Parus atricapillus*) alter alarm call duration and peak frequency in response to traffic noise.** *PLoS One* 2020, **15**:e0241035.
112. Derryberry EP, Phillips JN, Derryberry GE, Blum MJ, Luther D: **Singing in a silent spring: birds respond to a half-century soundscape reversion during the COVID-19 shutdown.** *Science* 2020, **370**:575-579 (80-).
113. Semple S, Zuberbühler K, Arnold K, Price T: **Pyow but not hack calls of the male putty-nosed monkey (*Cercopithecus nictitans*) convey information about caller identity.** *Behaviour* 2009, **146**:871-888.
114. Gallego-Abenza M, Mathevon N, Wheatcroft D: **Experience modulates an insect's response to anthropogenic noise.** *Behav Ecol* 2020, **31**:90-96.
115. Song J, Sun R, Fang K, Zhang B, Tang Y, Fang G: **Flexibility as a strategy for avoiding call overlap in male Anhui treefrogs.** *Asian Herpetol Res* 2020, **11**:230-240.
116. Zhao L, Roy S, Wang X: **Rapid modulations of the vocal structure in marmoset monkeys.** *Hear Res* 2019, **384**:107811.
117. Ziegler L, Arim M, Bozinovic F: **Combined effects of physiological condition and environmental attributes in determining call plasticity.** *Behav Processes* 2018, **153**:25-30.
118. Adreani NM, D'Amelio PB, Gahr M, ter Maat A: **Life-stage dependent plasticity in the auditory system of a songbird is signal and emitter-specific.** *Front Neurosci* 2020, **14**:588672.
- Testing for familiarity rather than individuality but showing the importance of changes depending on current life stage: during breeding, female zebra finches (but not males) show differences in their auditory perception and responses to calls emitted from familiar but not unfamiliar senders, suggesting a potential functional benefit in critical life stages.
119. Warren MR, Clein RS, Spurrier MS, Roth ED, Neunuebel JP: **Ultrasound-range, high-frequency communication by female mice shapes social interactions.** *Sci Rep* 2020, **10**:2637.
120. Coen P, Xie M, Clemens J, Murthy M: **Sensorimotor transformations underlying variability in song intensity during *Drosophila* courtship.** *Neuron* 2016, **89**:629-644.
121. Scarl JC, Bradbury JW: **Rapid vocal convergence in an Australian cockatoo, the galah *Eolophus roseicapillus*.** *Anim Behav* 2009, **77**:1019-1026.
122. Janik VM: **Whistle Matching in wild bottlenose dolphins (*Tursiops truncatus*).** *Science* 2000, **289**:1355-1357 (80-).
123. Crockford C, Wittig RM, Zuberbühler K: **Vocalizing in chimpanzees is influenced by social-cognitive processes.** *Sci Adv* 2017, **3**:e1701742.
124. Vignal C, Mathevon N, Mottin S: **Audience drives male songbird response to partner's voice.** *Nature* 2004, **430**:448-451.
125. Brecht KF, Hage SR, Gavrilov N, Nieder A: **Volitional control of vocalizations in corvid songbirds.** *PLoS Biol* 2019, **17**:e3000375.



126. Ghazanfar AA, Liao DA, Takahashi DY: **Volition and learning in primate vocal behaviour.** *Anim Behav* 2019, **151**:239-247.
127. Lameira AR, Shumaker RW: **Orangutans show active voicing through a membranophone.** *Sci Rep* (1) 2019, **9**:1-6.
128. Lattenkamp EZ, Vernes SC, Wiegbebe L: **Volitional control of social vocalisations and vocal usage learning in bats.** *J Exp Biol* 2018, **221**:jeb180729, <https://doi.org/10.1242/jeb.180729>
129. Bianchi S, Reyes LD, Hopkins WD, Tagliatela JP, Sherwood CC: **Neocortical grey matter distribution underlying voluntary, flexible vocalizations in chimpanzees.** *Sci Rep* 2016, **6**:34733.
130. Pisanski K, Cartei V, McGettigan C, Raine J, Reby D: **Voice modulation: a window into the origins of human vocal control?** *Trends Cogn Sci* 2016, **20**:304-318.
131. Scott SK: **The neural control of volitional vocal production—from speech to identity, from social meaning to song.** *Philos Trans R Soc B Biol Sci* 2022, **377**:20200395.
- A review of neural control of human vocal production as a flexible network, including a perspective on how this influences identity traits expressed in voice.
132. Vernes SC, Kriengwatana BP, Beeck VC, Fischer J, Tyack PL, ten Cate C, Janik VM: **The multi-dimensional nature of vocal learning.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200236.
133. Ruch H, Zürcher Y, Burkart JM: **The function and mechanism of vocal accommodation in humans and other primates.** *Biol Rev* 2018, **93**:996-1013.
134. Zürcher Y, Willems EP, Burkart JM: **Trade-offs between vocal accommodation and individual recognisability in common marmoset vocalizations.** *Sci Rep* 2021, **11**:15683.
- Examine the extent and consequences of vocal accommodation on identity signatures, across three call types. They find evidence for a trade-off between signaling social closeness, and identity based on call context and function.
135. Rundstrom P, Creanza N: **Song learning and plasticity in songbirds.** *Curr Opin Neurobiol* 2021, **67**:228-239.
136. Searcy WA, Soha J, Peters S, Nowicki S: **Variation in vocal production learning across songbirds.** *Philos Trans R Soc B Biol Sci* (1836) 2021, **376**:20200257.
137. Thomsen HM, Balsby TJS, Dabelsteen T: **The imitation dilemma: can parrots maintain their vocal individuality when imitating conspecifics?** *Behaviour* 2019, **156**:787-814.
138. King SL, Friedman WR, Allen SJ, Gerber L, Jensen FH, Wittwer S, Connor RC, Krützen M: **Bottlenose dolphins retain individual vocal labels in multi-level alliances.** *Curr Biol* 2018, **28**:1993-1999 e3.
139. Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O: **Learned vocal group signatures in the polygynous bat *Saccopteryx bilineata*.** *Anim Behav* 2012, **84**:761-769.
140. Ravignani A, Garcia M: **A cross-species framework to identify vocal learning abilities in mammals.** *Philos Trans R Soc B Biol Sci* 2022, **377**:20200394.
141. Carouso-Peck S, Goldstein MH, Fitch WT: **The many functions of vocal learning.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200235.
142. Johnson KE, Clark CJ: **Ontogeny of vocal learning in a hummingbird.** *Anim Behav* 2020, **167**:139-150.
143. Genzel D, Desai J, Paras E, Yartsev MM: **Long-term and persistent vocal plasticity in adult bats.** *Nat Commun* (1) 2019, **10**:1-12.
144. Tachibana RO, Takahasi M, Hessler NA, Okanoya K: **Maturation-dependent control of vocal temporal plasticity in a songbird.** *Dev Neurobiol* 2017, **77**:995-1006.
145. Lau AR, Clink DJ, Bales KL: **Individuality in the vocalizations of infant and adult coppery titi monkeys (*Plecturocebus cupreus*).** *Am J Primatol* 2020, **82**:e23134.
- Compared identity information contained in infant close-range calls versus adult long-distance duet contributions in a species lacking sex specificity in the vocal repertoire. Results show high levels of individuality in adult titi monkeys' duets but noticeably lower interindividual variation in infant calls thereby possibly indicating a link to the different functions of the call types and individuality as an adaptive trait.
146. Goncharova MV, Klenova AV, Bragina EV: **Development of cues to individuality and sex in calls of three crane species: when is it good to be recognizable?** *J Ethol* 2015, **33**:165-175.
147. Casey C: **Acoustic coding of information in a complex social network: identity signaling in northern elephant seals.** In *Coding Strategies in Vertebrate Acoustic Communication*. Edited by Aubin T, Mathevon N. Springer Nature; 2020:247-269.
148. Mulard H, Vignal C, Pelletier L, Blanc A, Mathevon N: **From preferential response to parental calls to sex-specific response to conspecific calls in juvenile zebra finches.** *Anim Behav* 2010, **80**:189-195.
149. Barker AJ, Vevjurko G, Bennett NC, Hart DW, Mograby L, Lewin GR: **Cultural transmission of vocal dialect in the naked mole-rat.** *Science* 2021, **371**:503-507 (80-).
150. Janik VM, Knörnschild M: **Vocal production learning in mammals revisited.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200244.
151. Gultekin YB, Hage SR: **Limiting parental interaction during vocal development affects acoustic call structure in marmoset monkeys.** *Sci Adv* 2018, **4**:ear4012.
152. Prat Y, Azoulay L, Dor R, Yovel Y: **Crowd vocal learning induces vocal dialects in bats: playback of conspecifics shapes fundamental frequency usage by pups.** *PLoS Biol* 2017, **15**:e2002556.
153. Chen Y, Matheson LE, Sakata JT: **Mechanisms underlying the social enhancement of vocal learning in songbirds.** *Proc Natl Acad Sci* 2016, **113**:6641-6646.
154. Zann R: **Ontogeny of the zebra finch distance call: i. Effects of cross-fostering to Bengalese finches.** *Z Tierpsychol* 1985, **68**:1-23.
155. Araya-Salas M, Hernández-Pinsón HA, Rojas N, Chaverri G: **Ontogeny of an interactive call-and-response system in Spix's disc-winged bats.** *Anim Behav* 2020, **166**:233-245.
- Showing general ontological changes in two call types in bats, with significant sex-dependent changes in response calls. While individuality was high across age and call types, response calls exhibit a decrease in intermediate ontogenetic stage before increasing again towards adulthood.
156. Courvoisier H, Camacho-Schlenker S, Aubin T: **When neighbours are not 'dear enemies': a study in the winter wren, *Troglodytes troglodytes*.** *Anim Behav* 2014, **90**:229-235.
157. Sheehan MJ, Bergman TJ: **Is there an evolutionary trade-off between quality signaling and social recognition?** *Behav Ecol* 2016, **27**:2-13.
158. Briefer E, Vannoni E, McElligott AG: **Quality prevails over identity in the sexually selected vocalisations of an ageing mammal.** *BMC Biol* 2010, **8**:35.
159. Shultz S, Gersick AS: **The evolution of signaling complexity: a comment on Sheehan and Bergman.** *Behav Ecol* 2016, **27**:16-17.
160. Calcari C, Pilenga C, Baciadonna L, Gamba M, Favaro L: **Long-term stability of vocal individuality cues in a territorial and monogamous seabird.** *Anim Cogn* 2021, **24**:1165-1169.
- Long-term stability over four breeding seasons in identity signature of two call types of territorial and monogamous seabird that may facilitate mate as well as neighbor recognition and improve fitness.
161. Wierucka K, Henley MD, Mumby HS: **Acoustic cues to individuality in wild male adult African savannah elephants (*Loxodonta africana*).** *PeerJ* 2021, **9**:e10736.
- Previously understudied elephant male's social rumbles used across contexts stayed stable.
162. Takagi M: **Vocalizations of the Ryukyu Scops Owl *Otus elegans*: individually recognizable and stable.** *Bioacoustics* 2020, **29**:28-44.
163. Choi W, Lee J-H, Sung H-C: **A case study of male tawny owl (*Strix aluco*) vocalizations in South Korea: call feature, individuality, and the potential use for census.** *Animal Cells Syst* 2019, **23**:90-96.
164. Klenova AV, Zubakin VA, Zubakina EV: **Inter- and intra-season stability of vocal individual signatures in a social seabird, the crested auklet.** *Acta Ethol* 2012, **15**:141-152.
165. Clark JA, Boersma PD, Olmsted DM: **Name that tune: call discrimination and individual recognition in Magellanic penguins.** *Anim Behav* 2006, **72**:1141-1148.
166. Melotti L, Siestrup S, Peng M, Vitali V, Dowling D, von Kortzfleisch VT, Bračić M, Sachser N, Kaiser S, Richter SH: **Individuality, as well as genetic background, affects syntactical features of courtship songs in male mice.** *Anim Behav* 2021, **180**:179-196.

Investigated courtship song in four strains of laboratory mice, showing differences in composition as well as complexity of the songs' syntax based on genetic background. A second study examined the temporal consistency of song features in two strains resulting in evidence for the repeatability of interindividual differences in syntax but also revealed high individual variation and therefore plasticity in syntax similarity over time.

167. Raymond S, Spotswood S, Clarke H, Zielonka N, Lowe A, Durrant KL: **Vocal instability over time in individual male European nightjars, *Caprimulgus europaeus*: recommendations for acoustic monitoring and surveys.** *Bioacoustics* 2020, **29**:280-295.
168. Deng Z, Lloyd H, Xia C, Li D, Zhang Y: **Within-season decline in call consistency of individual male Common Cuckoos (*Cuculus canorus*).** *J Ornithol* 2019, **160**:317-327.
169. Průchová A, Jaška P, Linhart P: **Cues to individual identity in songs of songbirds: testing general song characteristics in Chiffchaffs *Phylloscopus collybita*.** *J Ornithol* 2017, **158**:911-924.
170. Schneiderová I, Volodina EV, Matrosova VA, Volodin IA: **One plus one: binary alarm calls retain individual signature for longer periods than single-note alarms in the European ground squirrel (*Spermophilus citellus*).** *Behav Processes* 2017, **138**:73-81.
171. Delgado M, del M, Caferri E, Méndez M, Godoy JA, Campioni L, Penteriani V: **Population characteristics may reduce the levels of individual call identity.** *PLoS One* 2013, **8**:e77557.
172. Ellis JMS: **Decay of apparent individual distinctiveness in the begging calls of adult female white-throated magpie-jays.** *Condor* 2008, **110**:648-657.
173. Kojima S, Izumi A, Ceugniet M: **Identification of vocalizers by pant hoots, pant grunts and screams in a chimpanzee.** *Primates* 2003, **44**:225-230.
174. Linhart P, Osiejuk TS, Budka M, Šálek M, Špinka M, Policht R, Sýrová M, Blumstein DT: **Measuring individual identity information in animal signals: overview and performance of available identity metrics.** *Methods Ecol Evol* 2019, **10**:1558-1570.
175. Beecher MD: **Signalling systems for individual recognition: an information theory approach.** *Anim Behav* 1989, **38**:248-261.
176. Nakagawa S, Waas J, Miyazaki M: **Heart rate changes reveal that little blue penguin chicks (*Eudyptula minor*) can use vocal signatures to discriminate familiar from unfamiliar chicks.** *Behav Ecol Sociobiol* 2001, **50**:180-188.
177. Briefer EF, Mandel R, Maigrot A-L, Briefer Freymond S, Bachmann I, Hillmann E: **Perception of emotional valence in horse whinnies.** *Front Zool* 2017, **14**:8.
178. Wascher CAF: **Heart rate as a measure of emotional arousal in evolutionary biology.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200479.
179. Rukstalis M, French JA: **Vocal buffering of the stress response: exposure to conspecific vocalizations moderates urinary cortisol excretion in isolated marmosets.** *Horm Behav* 2005, **47**:1-7.
180. Perez EC, Elie JE, Boucaud ICA, Crouchet T, Soulage CO, Soula HA, Theunissen FE, Vignal C: **Physiological resonance between mates through calls as possible evidence of empathic processes in songbirds.** *Horm Behav* 2015, **75**:130-141.
181. Edgar JL, Paul ES, Harris L, Penturn S, Nicol CJ: **No evidence for emotional empathy in chickens observing familiar adult conspecifics.** *PLoS One* 2012, **7**:e31542.
182. Dezechache G, Zuberbühler K, Davila-Ross M, Dahl CD: **Skin temperature changes in wild chimpanzees upon hearing vocalizations of conspecifics.** *R Soc Open Sci* 2017, **4**:160816.
183. Mouterde SC, Elie JE, Mathevon N, Theunissen FE: **Single neurons in the avian auditory cortex encode individual identity and propagation distance in naturally degraded communication calls.** *J Neurosci* 2017, **37**:3491-3510.
184. Nieder A, Mooney R: **The neurobiology of innate, volitional and learned vocalizations in mammals and birds.** *Philos Trans R Soc B Biol Sci* 2020, **375**:20190054.
185. Knörnschild M: **Vocal production learning in bats.** *Curr Opin Neurobiol* 2014, **28**:80-85.
186. Vernes SC, Wilkinson GS: **Behaviour, biology and evolution of vocal learning in bats.** *Philos Trans R Soc B Biol Sci* 2020, **375**:20190061.
187. Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O: **Complex vocal imitation during ontogeny in a bat.** *Biol Lett* 2010, **6**:156-159.
188. Leongómez JD, Pisanski K, Reby D, Sauter D, Lavan N, Perlman M, Varella Valentova J: **Voice modulation: from origin and mechanism to social impact.** *Philos Trans R Soc B Biol Sci* 2021, **376**:20200386.
189. Røk P: **High functional complexity despite an extremely small repertoire of calls in the Spotted Crake (*Porzana porzana*).** *Auk* 2015, **132**:613-623.
190. Manser MB, Jansen DAWAM, Graw B, Hollén LI, Bousquet CAH, Furrer RD, le Roux A: **Vocal complexity in meerkats and other mongoose species.** In *Advances in the Study of Behavior*. Academic press. 2014:281-310.