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Original Article

Acoustic innovations in courtship sounds generated by hybridization in cichlid fish

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ABSTRACT

During courtship, prezygotic barriers are thought to maintain the diversity of species since differences in phenotypic traits and reproductive behaviours are likely to be involved in maintaining species boundaries. However, introgressive hybridization has been reported in many dif- ferent taxa and the resulting hybrids usually possess phenotypic features, including behaviours, that are intermediate between those of the parents. The outcome of hybrids may depend on the interactions between the intrinsic viability of the hybrids, the ecological environment of the species, and the fitness of hybrids in that ecological context. In cichlids, the mechanism of hybridization is increasingly documented as an important factor in their evolutionary radiation since it may provide novel gene combinations that promote speciation and adaptive radiation by generating new transgressive phenotypes. Cichlid species are separated mostly by pre-mating isolating mechanisms. Like colour patterns, acoustic communication is involved in sexual selection, but this pattern has been much less studied and the outcome of hybridization on acoustic features has never been examined. To gain novel insights into the evolution of their acoustic communication behaviour, we performed a hybrid cross between *Chindongo saulosi* and *Maylandia estherae*. Qualitative examination of courtship showed that the three groups possess the same sequence of behaviours. However, sounds produced during courtship showed specific signatures since all three groups differ at the level of sound duration and pulse period, with both features being intermediate in hybrids in comparison to the two parent species. Colour patterns in hybrids were also different from those of the parent species. These results show that hybridization can affect at least two kinds of prezygotic barriers, which may be important in the cichlid evolutionary process. However, playback experiments are required to test the strength of these features in sexual selection.

Keywords: acoustic communication; adaptive radiation; speciation; sound production; Cichlidae

INTRODUCTION

In biology, introgressive hybridization refers to the exchange of genes between evolutionary lineages leading to viable and fertile hybrids, as opposed to simple hybridization that provides exclusively inviable or infertile offspring (Seehausen 2004). The latter phenomenon has been considered a contentious issue (Burke and Arnold 2001). Some authors argue against any important role, because reduced fitness would typically render hybrids an evolutionary dead end. If performance trade-offs are associated with the respective adaptations of the two parent species, hybrids are expected to be intermediate in terms of performance and, consequently, to be less adapted than their parents to their respective ecological niches (Selz and Seehausen 2019). In contrast, it has been proposed that introgressive hybridization may provide novel gene combinations that promote speciation and adaptive radiation by generating new transgressive phenotypes (Genner and Turner 2012, Stelkens *et al.* 2015). New phenotypes can then fuel functional variation that can be of ecological relevance by allowing access to resources outside of the two parental species' niches. The outcome of hybrids may result from the multifactorial interaction between their intrinsic viability, ecological environment, and resulting fitness in that context (Abbott *et al.* 2013, Kagawa and Takimoto 2018, Selz and Seehausen 2019).

In vertebrates, introgressive hybridization has been re- ported in many different taxa such as birds (Grant and Grant 1992), mammals (Fitzpatrick 2004), amphibians (Gerhardt *etal.* 1980), cichlids (Seehausen 2004, Gerlai 2007), and other tropical fish taxa (Tea *et al.* 2020). Hybrids usually possess in- ternal and external phenotypic features that are intermediate between those of their parents (Weisel 1955, Smith 1973, Tea *et al.* 2020). Intermediate characteristics can also be found in behaviour. For example, in frog hybrids *Dryophytes chrysoscelis* Cope, 1880 × *Dryophytes femoralis* Daudin, 1800, the call pulse period (71 ms) is intermediate between that of *D. chrysoscelis* (22 ms) and *D. femoralis* (123 ms) (Doherty and Gerhardt 1984).

Within cichlids, hybridization has been observed in captivity and has also been reported to occur in nature (Rüber *et al.* 2001, Gerlai 2007, Keller *et al.* 2013). This fish taxa is also well known for its ability to produce calls in different behavioural contexts (Myrberg *et al.* 1965) such as territory and egg defence (Longrie *et al.* 2013), agonistic behaviours (Amorim and Almada 2005, Longrie *et al.* 2009), and courtship (Simões *et al.* 2006, Bertucci *et al.* 2010, Verzijden *et al.* 2010, Akian *et al.* 2020, Dussenne *et al.* 2022). There are at least 38 species of Cichlidae described as sound producers, of which 33 are mainly native to Africa, four to Central America, and one to South America (Longrie *et al.* 2013, Looby *et al.* 2022). In most of the cases, sounds are not produced alone but are associated with visual behaviours. During courtship, for example, dominant males produce pulsed broad- band sounds while displaying body quivers (Bertucci *et al.* 2010, Maruska *et al.* 2012, Longrie *et al.* 2013) or lateral displays (Smith and van Staaden 2009). As not all visual displays are associated with sound production, sounds are not merely a by-product of body movements; cichlids have some control over when and where sounds are produced (Maruska *et al.* 2012). Depending on the species, the mechanism of sound production may involve the pharyngeal jaws or the swim bladder (Lobel 2001, Amorim 2006, Longrie *et al.* 2009). For the latter mechanism, sounds are produced during a backward movement of the pectoral girdles and a forward movement of the anal fin, most probably resulting from a contraction of the body musculature (Longrie *et al.* 2009).

Courtship sounds are prezygotic barriers thought to maintain isolation between closely related cichlids (Kornfield and Smith 2000), since differences in phenotypic traits and reproductive behaviours are likely to be involved in preserving species boundaries (Kéver *et al.* 2018). Female mate choice, potentially based on male reproductive behaviour, has been suggested as the main barrier to hybridization in cichlids (Kocher 2004). However, studies on sexual selection have mainly focused on visual cues (Maan and Sefc 2013). In different fish species, including cichlids, acoustic communication has been shown to be important during reproduction, supporting that a specific match is required between the signaller and the receiver to maximize the detectability of the acoustic signals (Maruska *et al.* 2007, 2012). Cichlid hybrids should possess acoustic features that are intermediate between those of their parents. We aimed to test this hypothesis by investigating the acoustic communication during courtship in two mbuna species *Chindongo saulosi* Konings, 1990 and *Maylandia estherae* Konings, 1995—and in their hybrids *C. saulosi* × *M. estherae*. In case of divergence between the acoustic signals of the hybrids and their parents, the new calling features could serve as a new prezygotic barrier and favour the speciation process. Therefore, they should be integrated in the study of the evolvability of the taxa.

MATERIAL AND METHODS

Ethic statement

The experiments were carried out under the approval of the Animal Care Committee of the University of Liège (form 2280) in accredited experimental rooms (LA 1610429).

Biological material

The parent species came from an aquarium trade (Aquarium de Marbais, Villers-la-Ville Belgium) specialized in cichlids. Fifteen specimens of *C. saulosi*, 13 specimens of *M. estherae*, and 14 hybrids (resulting from the crossing of a female *C. saulosi* and a male *M. estherae*, hatched on 5 November 2020) were used. Fish were stocked in different tanks (350 L) according to the species, except for the parents of the hybrids that were stocked together in a 300-L tank. In each case, tanks had coarse substrate on the bottom and fish were provided with shelters. Fish were fed three times a week with commercial pellets and aquaria were maintained at 26 ± 2°C with a photoperiod of 12L : 12D (7 am−7 pm).

Courtship sounds of *C. saulosi* (standard length, SL: 65.5 ± 3 mm, mean ± standard deviation) and *M. estherae* (70.6 ± 3 mm) were recorded from March to July 2021. Hybrids (46 to 79 mm) were recorded from May to June 2022. Sound record- ings were made with an HTI-96-Min hydrophone (sensitivity: −163.9 dB re 1 V μPa^{-1}; flat frequency response range: 2 Hz to 30 kHz; High Tech Inc., Long Beach, MS, USA) connected to a TASCAM DR-05 portable audio recorder (sampling frequency: 44.1 kHz, 16-bit resolution; TEAC, Tokyo, Japan). In addition, a Handycam FDR-AX33 video camera (Sony, Tokyo, Japan) was used to film behaviours. Sound recordings were per- formed in three aquaria (150 × 40 × 60 cm, 150 × 40 × 50 cm, and 135 × 40 × 40 cm) with the same experimental conditions. For *C. saulosi* and *M. estherae*, a single male was placed in the tank with two females of their own species to elicit sounds. Once recorded (*N* = 25 sounds per individual), the male was placed back in the stock tank. For hybrids, it was not possible to deter- mine the sex prior to recordings. All the specimens were placed in the same tank for recordings. Once a specimen had produced sounds (*N* = 25 sounds per individual) during a reproductive behaviour context, it was removed from the community tank. All the sounds were recorded between 9 am and 6 pm.

Acoustic analysis

Sounds were digitized at 44.1 kHz (16-bit resolution) and were secondarily sub-sampled at 4 kHz with MatLab Routines (MathWorks, Natick, MA, USA) to avoid sounds that could result from the tank resonance (>2 kHz). Then, a high-pass filter at 50 Hz was applied. The analysis was carried out with Avisoft SASLAB Pro 4.33 software (Avisoft Bioacoustics, Glienicke, Germany). Only sounds with a high signal-to-noise ratio were used in the analysis. Temporal features were measured on oscillograms and frequency variables from power spectra (FFT size: 256 points and Hann window). The sound parameters measured were: sound duration (ms); number of pulses in a sound; pulse period (measured as the average peak-to-peak interval be- tween consecutive pulses in the entire sound, ms); and pulse duration (measured as the time from the beginning of a pulse to its end, ms).

Statistical methods

The description of the sounds was carried out on all the sounds analysed. After description, statistical analyses were carried out in R 4.0.2. (R Core Team, 2020). Acoustic features were assessed for normality (Shapiro–Wilk tests) and homoscedasticity of variances (Bartlett tests). Kruskal–Wallis tests with Dunn's tests as post hoc with a Benjamini–Hochberg correction were used to compare acoustic features between species because they did not meet parametric assumptions.

In different cichlids, the size appears to be important in some behavioural contexts such as agonistic interactions. Bigger fish would indeed be better suited than smaller ones to defend a territory (Amorim *et al.* 2019) or in courtship (Smith and van Staaden 2009), and preferred by females (Smith and van Staaden 2009). Moreover, acoustic features can also be related to fish size and, therefore, the calls can convey phenotypic differences between males: smaller individuals typically produce sounds of higher frequency and shorter duration than larger individuals (Myrberg *et al*. 1993, Connaughton *et al*. 2000, Parmentier and Fine 2016, Raick *et al*. 2020, 2021). Therefore, correlations between acoustic variables and body size (standard length) were calculated using Spearman correlation coefficients (rS), and associated *P*-values corrected by the Holm–Bonferroni method. As fish SL was positively correlated to acoustic features, these variables were divided by SL to limit the size effect.

RESULTS

Phenotype of the hybrids

Three kinds of hybrid phenotypes were obtained (Fig. 1). (i) Blue to purple specimens having six to seven dark bars on the body, a black border on the dorsal fin and a yellowish caudal fin. (ii) Dark-yellow specimens having six to seven dark bars on the body, a purple throat, a black border on the caudal fin, and a dull- yellow caudal fin. (iii) Yellow specimens with pink dots on the body. All three phenotypes had egg-spots on the anal fins. The first two phenotypes could become darker through social inter- actions. All recorded hybrids from the three phenotypes were males.

Behaviour

Courtship behaviours have been previously described in *C. saulosi* (McElroy and Kornfield 1990). Our video recordings allowed us to verify that the same behaviours are found in *M. estherae* and in the hybrids.

Male courtship display was initiated by the entrance of a female into the territory of the male. Courtships corresponded to the following sequence of events (McElroy and Kornfield 1990). Starting with the 'approach', the male swims rapidly toward a female entering his territory.

Then, during the ‘cut’, the male swims in the path of a female, perpendicular to her body, blocking her trajectory and forcing her to turn towards the centre of the territory. Then, the male performs a ‘lateral display’, orienting parallel to the stationary female and erecting his fins. During the lateral display, the male can display ‘quivers’ that correspond to fast low-amplitude lateral flexions of the body and caudal fin. Males can then perform ‘loops’ corresponding to fast, circular, and antiparallel movements that can be accompanied by a lateral display and quivers. During the ‘slow lead’, the male stops all behaviours and swims slowly to the territory with exaggerated tail-beats. If the female does not follow the male, it can go back to the female (‘return’) to exe- cute again the above-mentioned behaviours. In *C. saulosi*, *M. estherae* and hybrids, sounds were recorded during quivers, corresponding to fast lateral flexions at the level of the body and caudal fins.

Acoustic features

Fish SL was positively correlated with sound duration (rS = 0.29, $P < 0.001$) and pulse period (rS = 0.42, $P < 0.001$). Both acoustic features were divided by SL to limit the size effect. However, this did not change the results of the analyses, probably because all three recorded groups were in the same size range (70.6 ± 3 mm for *M. estherae*, 65.5 ± 3 mm for *C. saulosi* and 76.6 ± 2.2 mm for the hybrids).

Sounds of male *C. saulosi* ($N = 5$ fish and 125 sounds) had 10 ± 3 pulses, lasting 180 ± 90 ms with a pulse period of 20 ± 4 ms. Sounds of *M. estherae* ($N = 6$ fish and 150 sounds) had 10 ± 5 pulses, lasting 560 ± 340 ms with a pulse period of 65 ± 20 ms. In hybrids ($N = 4$ fish and 100 sounds), calls were composed of 9 ± 4 pulses and lasted 303 ± 167 ms with a pulse period of 37 ± 10 ms (Fig. 2). In each group, there was a regular increase of the pulse period towards the end of the call, the last period being more than two times longer than the first period (Fig. 3). Sound durations and the mean pulse period of hybrids appear to be intermediate between those of parental species (Fig. 3).

Sound duration and pulse period showed significant differences (Fig. 4) between hybrids, *C. saulosi* and *M. estherae* (Kruskal–Wallis: $\chi^2 = 153.92$ and 293.96, d.f. = 2, all $P < 0.0001$, Dunn: $Z = -4.87$, -12.33 and -6.51 for sound duration and $Z = -8.04$, -17.14, -7.72 for pulse period, all $P < 0.0001$). However, this was not the case for the number of pulses ($\chi^2 = 3.97$, d.f. = 2, P-value = 0.14).

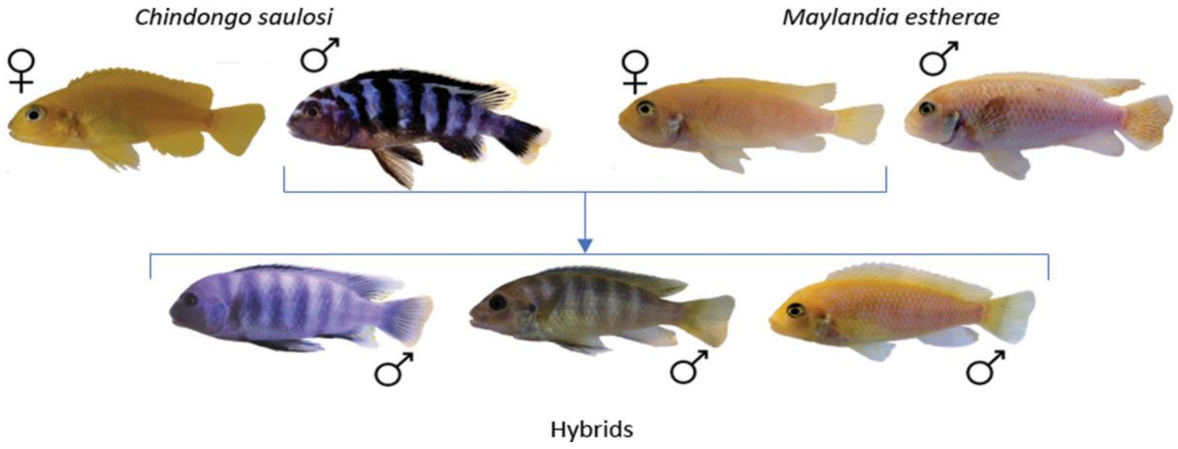

Figure 1. Colour pattern of *Chindongo saulosi*, *Maylandia estherae* and their hybrids.

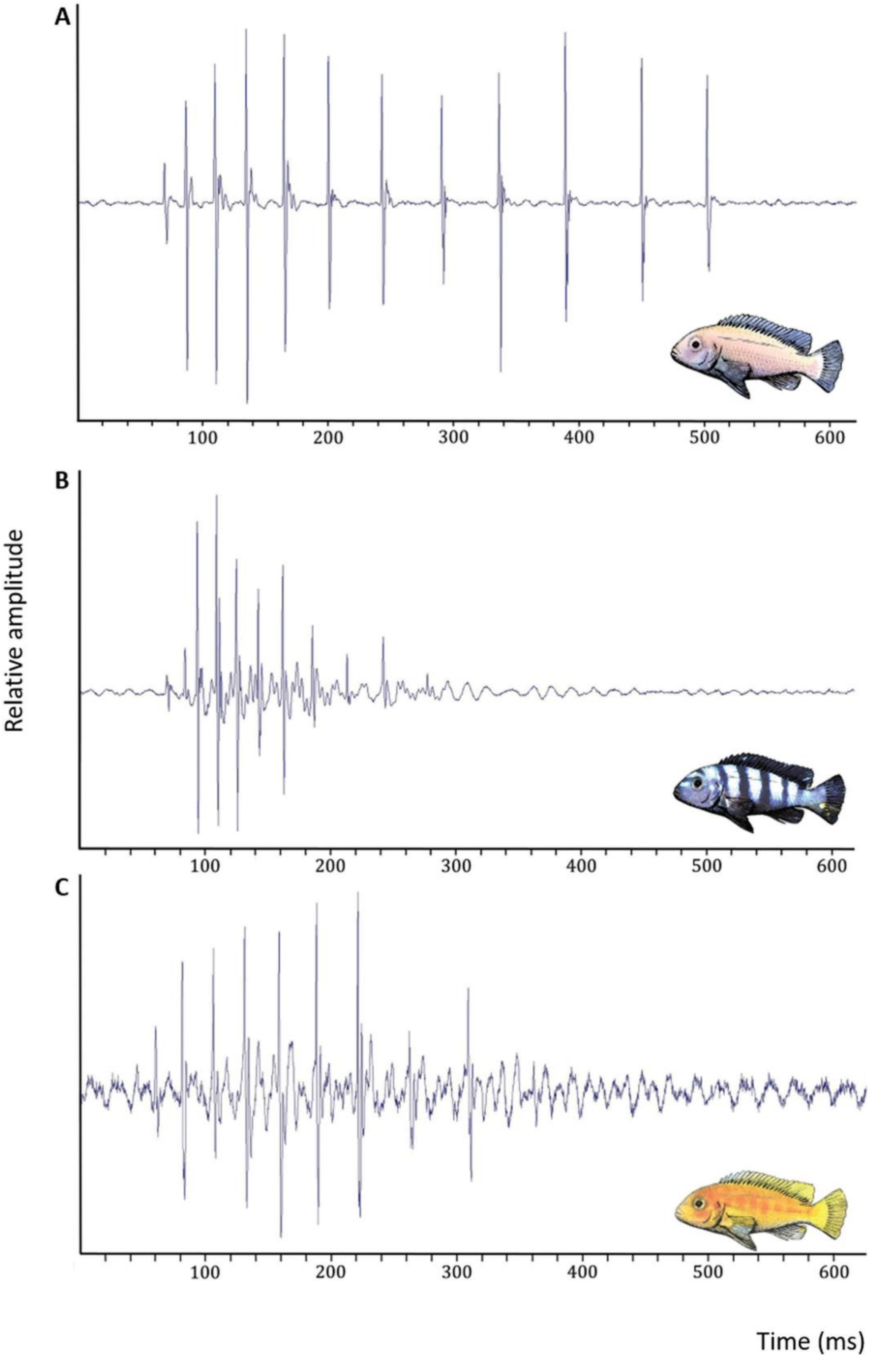

Figure 2. Oscillogram of a pulsed courtship sound in *Maylandia estherae* (A), *Chindongo saulosi* (B), and the hybrid (C).

DISCUSSION

Different explanations have been suggested to explain cichlid speciation and their high rate of diversification, including per se habitat divergence, differentiation of the feeding apparatus, or the action of sexual selection (Kocher 2004). In addition, there is now recognition that hybridization between different evolutionary lineages could cause rapid diversification of phenotypes (Kagawa and Takimoto 2018) because novel phenotypes that may facilitate adaptive invasion of organisms into new eco- logical niches are created (Barton 2001, Mallet 2007). Many animal species are reproductively isolated as sexual selection acts directly on mate-preference traits, promoting pre-mating reproductive isolation (Panhuis *et al.* 2001). Courtship and mating involves the production of sexual signals that convey crucial information about the sender's species, quality, motivation, readiness, and social status (Maruska *et al.* 2012).

Courtship behaviours are the same in both parent species studied here and correspond to previous examination of other mbuna species (*Cynotilapia afra*, *Melanochromis auratus*, *Maylandia barlowi*, or *Tropheops tropheops*). The mbuna display no evidence of behavioural innovation and show limited inter- specific differentiation in behavioural expression (McElroy and Kornfield 1990). The main difference between species is rather found at the level of the colour pattern. This shows that the courtship behaviour is stereotyped in the mbuna taxa (Venesky *et al.* 2005) and that visual display does not appear to be critical to species' recognition. This similarity in courtship behaviour could, in part, explain why hybridization took place between *C. saulosi* and *M. estherae* in experimental conditions.

Because both male and female colour patterns have been deeply considered in theories of speciation by sexual selection (Seehausen and van Alphen 1998, Seehausen *et al.* 1999, Couldridge and Alexander 2002), relatively little attention has focused on acoustic communication as a key innovation implied in adaptive radiation. In cichlids, while an acoustic signature may promote reproductive isolation (Amorim *et al.* 2008, 2015, Ladich 2015), prezygotic barriers are not always entirely impermeable (Kéver *et al.* 2018). As in many haplochromines (Amorim *et al.* 2004, Simões *et al.* 2006, Bertucci *et al.* 2012), *C. saulosi* and *M. estherae* produce short low-frequency pulsed sounds that appear to be species-specific since they are significantly different at least at the level of the duration and the pulse period. The same kind of species-specific sound has been also found in closely related species such as *Maylandia zebra, Maylandia callainos*, and *Maylandia* 'zebra gold' (Amorim *et al.* 2004, Simões *et al.* 2006, Bertucci *et al.* 2012). Vertical bars and horizontal stripes, the most common melanic patterns in East African cichlids, were found to be genetically independent mod- ules, indicating a multigenic basis for colour patterns and shed- ding light on how genetic modularity and the combination of loci have driven coloration diversification in East African Great Lake cichlids (Gerwin *et al.* 2021). Like colour patterns, new features resulting from intermediate characteristics in the sound signals of hybrids clearly support that this innate communication channel (Longrie *et al.* 2008) is subject to genetic constraints and should be fully considered in evolutionary studies. Acoustic features can thus provide new prezygotic barriers that could be involved in the promotion of speciation and adaptive radiation.

Our results support acoustic behaviour as a potential driver of speciation and species evolution. This opens new fields of investigation. Future studies should consider experiments dealing with further transgenerational evolution of acoustic signals. In addition, playback experiments are required to test the function of acoustic signals in sexual selection. Finally, genetics analyses could help to test the genetic coupling hypothesis, which postulates that both signal generation and recognition mechanisms share common circuitry specified by the same genes (Doherty and Gerhardt 1984).

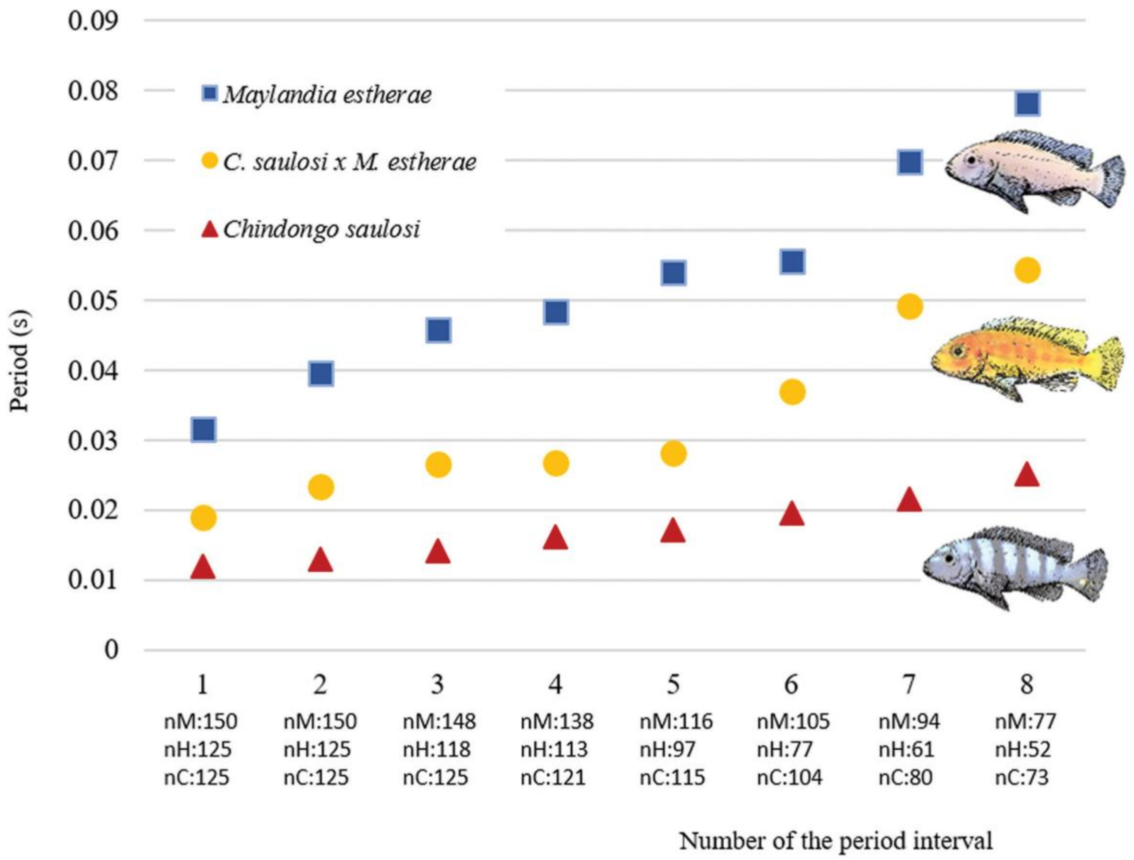

Figure 3. Comparison of the successive pulse period within courtship sounds between *Maylandia estherae* (A), *Chindongo saulosi* (B), and the hybrids (C). nM, nH, and nC corresponds to the number of periods that were analysed for *M. estherae*, the hybrid, and *C. saulosi*, respectively.

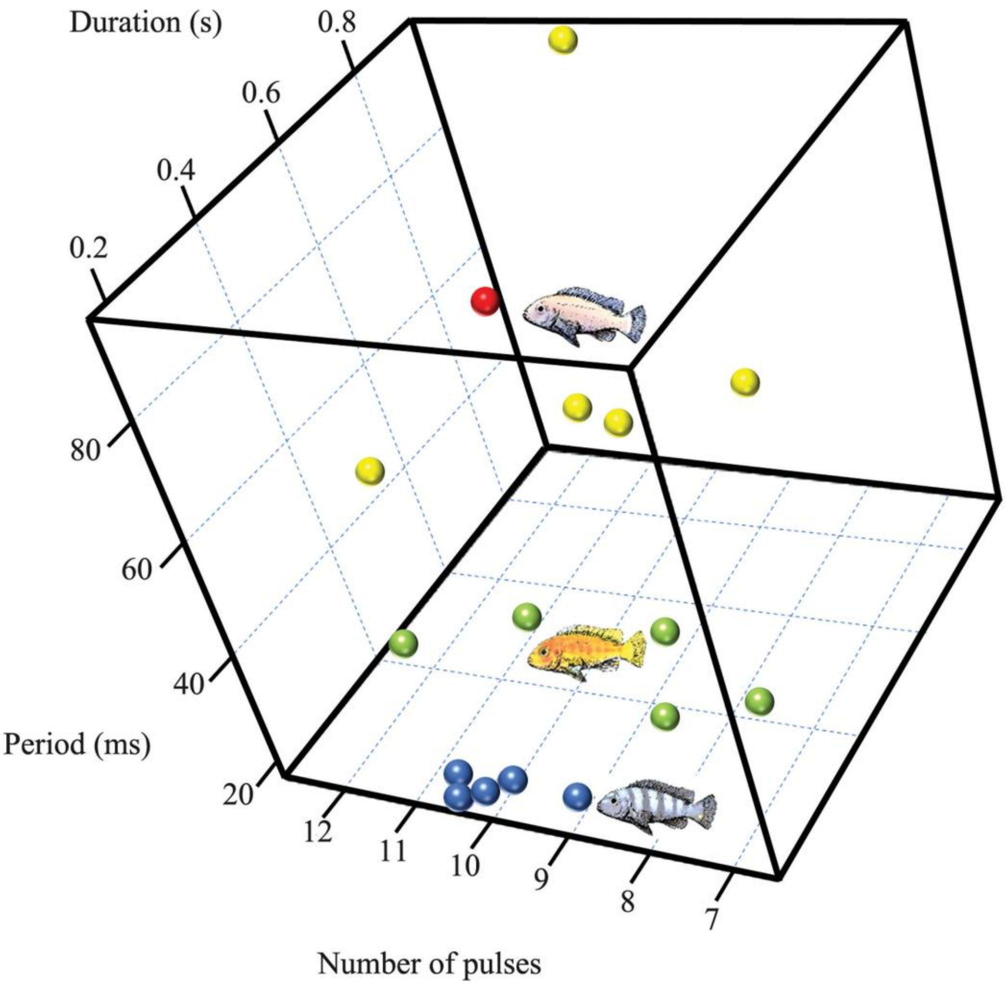

Figure 4. Comparison of temporal acoustic features between *Maylandia estherae* (yellow), *Chindongo saulosi* (blue), and the hybrid (green). The red dot corresponds to acoustic features recorded in the *Maylandia estherae* father of the hybrids.

CONCLUSION

Different studies have suggested that hybridization between species can facilitate adaptive radiation and the emergence of novel phenotypes. Hybrids typically possess intermediate phenotypic features, including behaviors, contributing to biological diversity. Our study demonstrates that hybridization can impact acoustic communication, with distinct acoustic signatures observed in hybrids compared to parent species. These findings reveal the influence of hybridization on behavioral prezygotic barriers in cichlids, which are integral to their evolutionary process. Integrating behavioral studies with genomic approaches can enhance our understanding of the cichlid model system and its role in the evolution of biological diversity. Such interdisciplinary investigations provide valuable insights into the mechanisms driving speciation and the generation of novel phenotypes, not only in cichlids but also in broader contexts.

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AUTHOR CONTRIBUTIONS

E.P. conceived and designed the study, E.P., N.L., G.S., and S.J.D.D. collected and analysed the acoustic data; X.R., E.P., N.L., and G.S. performed statistical analysis; A.V.D. performed fish breeding. E.P. wrote the first draft of the manuscript; X.R., M.B., and A.V.D. contributed substantially to revisions. All authors reviewed and approved the final draft of the paper.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author (E.P.) on request.

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