


Population divergence in the acoustic properties of crickets during the COVID-19 pandemic

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In 2020, the COVID-19 crisis resulted in many countries around the world going into nationwide lockdowns that lasted between weeks and months (Rutz et al. 2020). Anecdotal observations and social media revealed that some wildlife—both species that have been accustomed to human presence and those less so—returned to the previously human-dominated landscape during the lockdowns. This suggests that animals may have become more willing to explore novel environments or those previously considered dangerous (Manenti et al. 2020). Singing behaviors and communication in sound-producing animals can also be modified by changes in anthropogenic activities (e.g., Orci et al. 2016, Erregger and Schmidt 2018), including during lockdowns. The lockdowns caused by the COVID-19 pandemic enabled several researchers to conduct natural experiments to learn how human activities affect animal behaviors (Rutz et al. 2020). So far, birds have been found to respond to changes in human behaviors during the COVID-19 crisis. Jiang et al. (2020) revealed that birds showed reduced fear responses to people wearing face masks. Derryberry et al. (2020) also demonstrated that birds' acoustics have changed during the lockdown in San Francisco. However, we are not aware of any study centering on invertebrates.

The males of eneopterine crickets explore and call while searching for females, unlike typical gryllid crickets (ter Hofstede et al. 2015), making them an ideal

model organism to study their exploratory behaviors and acoustic displays simultaneously. We initially aimed to investigate population differences of these behaviors in a common brachypterous species, i.e., *Lebinthus laue* Robillard and Tan 2013 from Singapore (Fig. 1). We collected crickets from three isolated forest patches around Singapore (Fig. 1), and recorded their call properties under controlled conditions for 2 h each in an insect cage isolated from the other crickets. From the recordings, we randomly selected at least 25 calling bouts per individual and measured the acoustic properties (e.g., dominant frequency, call duration; Appendix S1). We also performed five repeated behavioral assays during which each cricket was video-recorded for 40 min per trial while exposed to a novel environment (Appendix S1). The study was interrupted by the Singaporean nationwide lockdown called “Circuit Breaker” (CB) that lasted 7.5 weeks (between 7 April and 1 June 2020), which afforded us the opportunity to investigate how the calling properties and exploratory behaviors of *Lebinthus laue* differ between populations, but also before and after the CB period. In total, 39 male crickets (18 before and 21 after CB) were used for the observations, collected from Pulau Ubin (12 crickets), Labrador Nature Reserve (12), and Hindhede Nature Park (15) (Table 1).

Using model simplification and controlling for confounders (i.e., using individual crickets as random intercepts, ambient temperature and time of calling as random slopes; Appendix S1), call duration was significantly different between populations before and after CB, and the difference between populations was evidently not influenced by CB ($R^2_m = 0.13$, $R^2_c = 0.85$; Table 1, Fig. 2). Syllable period, dominant frequency, and exploratory behaviors (i.e., emergence time into the novel environment and total exploration duration) were not different between populations and between the two time periods ($R^2_m = 0.00$; Appendix S2: Table S1). However, we found that crickets from the Hindhede population have shorter trill duration than other populations ($R^2_m = 0.45$, $R^2_c = 0.81$). This difference between the Hindhede population and the others was reinforced after CB: the trill duration in the Hindhede population after CB (0.52 ± 0.01 s) was significantly shorter than before CB (0.55 ± 0.01 s; Table 1, Fig. 2).

The significant differences in both call and trill durations between the three populations may indicate microevolution of these traits driven by differing levels of human pressures in the three sites. The Hindhede and Ubin populations faced greater human pressure prior to the COVID-19 crisis, because Hindhede Nature Park and Pulau Ubin are popular sites for hikers, mountain bikers, and exercisers. Shorter call and trill durations

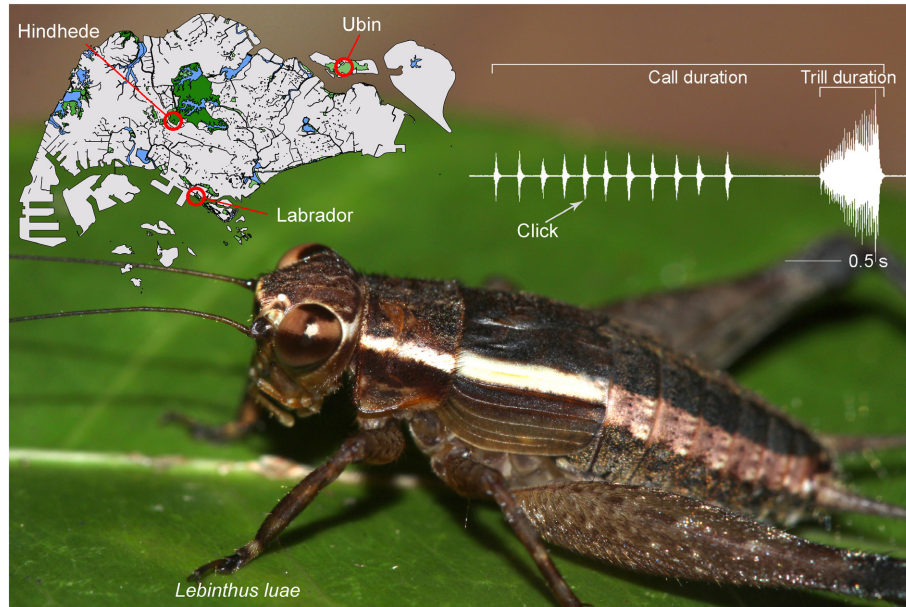


FIG. 1. A *Lebinthus luae* male adult exploring among leaf foliage near the forest floor. The inset map indicates the three forest patches where the crickets were collected. The inset oscillogram shows a typical call of this species, consisting of numerous clicks and ending with a trill part. Syllable period was obtained by dividing the trill duration by the number of pulses.

TABLE 1. Trill and call durations (s) of *Lebinthus luae* before and after CB. Standard errors are shown, and the number of crickets recorded (*N*) are stated within the parentheses.

	Trill duration		Call duration
	Before CB (4–15 April)	After CB (21 June–15 July)	
Hindhede (<i>N</i> = 15)	0.55 ± 0.01 (9)	0.52 ± 0.01 (6)	2.6 ± 0.3
Labrador (<i>N</i> = 12)	0.60 ± 0.01 (3)	0.62 ± 0.01 (9)	5.6 ± 0.8
Pulau Ubin (<i>N</i> = 12)	0.56 ± 0.01 (6)	0.60 ± 0.01 (6)	3.4 ± 0.4

may be an antipredation response to such human disturbance. That only crickets from the Hindhede population significantly shortened trill duration by 5.5% after CB may be a plastic antipredation response to short-term increase in human activities and disturbance in Hindhede Nature Park because of the COVID-19 crisis. Being surrounded by dense housing estates in the heart of Singapore and traditionally a popular hotspot for hikers, Hindhede Nature Park may have received even higher visitorship from nearby residents (owing to teleworking and school closure) compared to Labrador Nature Reserve at the outskirts of the deserted Central Business District area and the distant offshore island of Pulau Ubin during CB (Tan 2020, Wong 2020). But because the CB was a relatively short and partial lockdown, plasticity of the calling pattern may not be that apparent in other populations. Frequency remained stable between populations and sampling periods because spectral call property is related to the sound-generation anatomy,

and is hence less plastic than temporal properties (Bertram et al. 2012).

Our findings of population divergence in call duration indicate that the populations have probably undergone microevolution. This change could be a response to human presence. That trill duration remains plastic to additional pressures during the CB period—despite also showing population divergence—is an indicator of considerable behavioral plasticity, a prerequisite for further microevolution. Because producing a trill is probably more energy consuming, and more conspicuous to predators than the initial clicks (number of clicks correlates with the call duration), reduction in trill duration can be an additional short-term adaptation to COVID-19-induced human pressures, which may be fixed in the population if the pressure caused by human presence persists after the COVID-19 crisis. Considering that *L. luae* is widely distributed across Southeast Asia (Baroga-Barbecho et al. 2020), detectable population differences

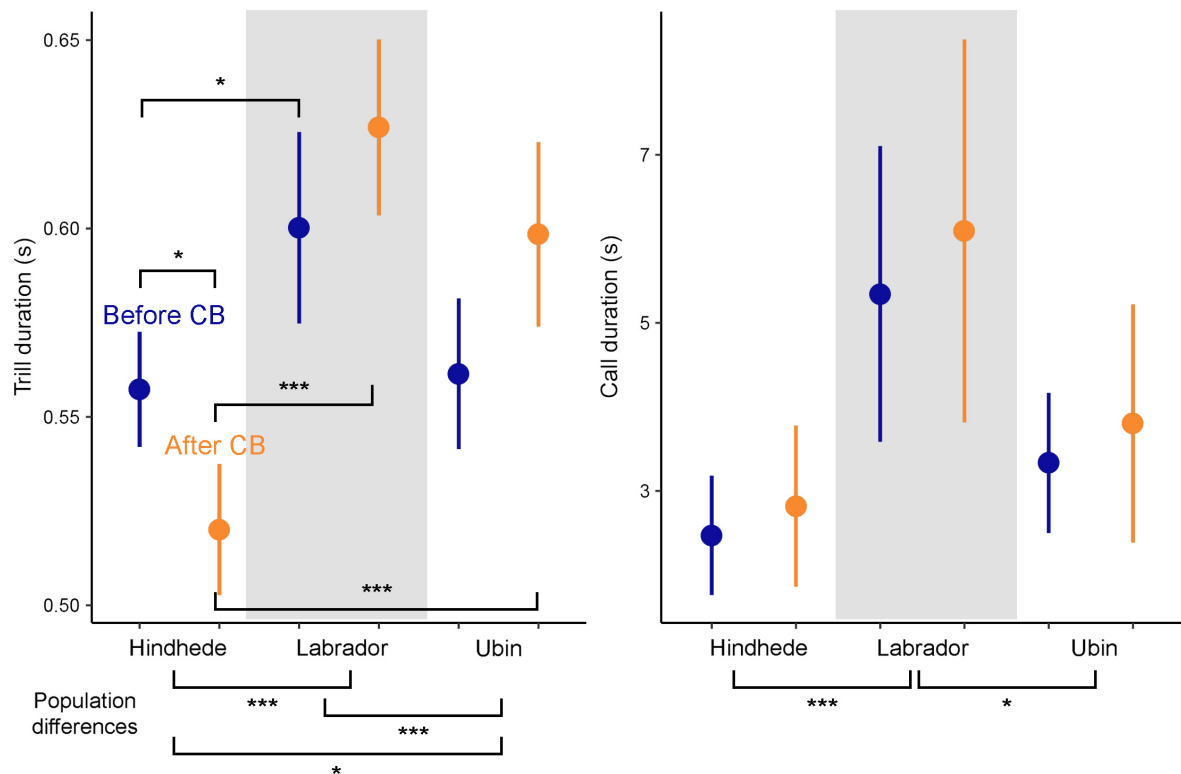


Fig. 2. Mean plots showing how the trill duration decreased in the Hindhede population after CB but not other populations and call duration differing between populations. The plots are based on univariate mixed-effects models with the individual cricket as the random intercept and time of the recording and ambient temperature as random slopes. The circle represents the estimated marginal mean; vertical line represents the 95% confidence interval range. Nonoverlapping vertical lines between two single effects can be considered significant. Asterisks represent significant effects: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in the call properties within a small part of its distribution raises further questions on how plasticity and/or microevolution of the calling behaviors may be at play. Population genomic work at the local and regional scales can reveal new insights into their microevolution and behavioral plasticity and how they are impacted by human activities (be it during or after the COVID-19 crisis), but similar research is hitherto limited to birds (e.g., Gordo et al. 2020) and a few cricket species (e.g., Shaw 1996, Lewkiewicz and Zuk 2004).

The alteration of human pressures has elicited response in some components of the acoustics communication in the lebinthine crickets, but not their exploratory behaviors (i.e., total exploration duration and emergence time; Appendix S2; Table S1). For these crickets that utilize both exploration and acoustics communication to find mates, it is intriguing that we did not observe similar patterns for both sets of behaviors. We speculate that increasing call and trill durations may be considered less risky than becoming more exploratory, hence crickets would change their acoustic properties

more readily. Another plausible deduction is that changes in acoustic properties are more detectable than changes in exploratory behaviors because acoustic properties, particularly the dynamic traits, are typically more plastic than exploratory behaviors that tend to reflect intrinsic behavioral characteristics such as personality (Naguib et al. 2010). That the exploratory behaviors may reflect personality were supported by significant estimates of repeatability by intraclass correlation coefficient ($ICC_{\text{emergence time}} = 0.28 \pm 0.08$; $ICC_{\text{total exploration time}} = 0.35 \pm 0.08$; Appendix S2; Table S1). However, studies on the link between exploratory and singing behaviors in these crickets are still in their infancy. Therefore, further investigation using these crickets as models can shed new light on selection and evolution of multimodal communication in studies where invertebrates are often neglected (Higham and Hebets 2013, Partan 2013). For example, population genomics may help advance our understanding evolution of multimodal communication, and how it may facilitate speciation.

In conclusion, while humans are still trying to adapt to the COVID-19 pandemic, we are only starting to learn how it is impacting wildlife with the limited studies available. We recommend that more studies on different taxa, especially the often-overlooked invertebrates, in different parts of the world should be conducted. In situ observations of both human visitorship and cricket behavior, including using automatic recorders to monitor calling patterns at a large scale across the region, could also provide more direct evidence for our inferences and complement our ex situ observations, although it was not possible during this COVID-19 crisis itself. We hope that our study can inspire more concerted investigation into the impact of human activities on animal behaviors. Along with long-term studies addressing how the acoustic properties and exploratory behaviors of crickets (and other invertebrates) change, we can then open up new avenues on the adaptive capability of different invertebrates to human activities as the world heads towards a new normal and/or more lockdowns; and advance our knowledge on the dynamics of human-invertebrate interactions especially in this era of uncertainty and rapid changes due to pandemics, global climate change, and impacts of deforestation and pesticide use.

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