Title: Inter-individual differences of calling and exploratory behaviour in a lebinthine cricket species hint at different mate-finding strategies Running title: Repeatability of acoustic display and exploration

Ming Kai Tan, Stefan Schöneich, Tony Robillard

Title: Inter-individual differences of calling and exploratory behaviour in a lebinthine cricket species hint at different mate-finding strategies

Running title: Repeatability of acoustic display and exploration

Authors: Ming Kai Tan [1, 3], Stefan Schöneich [2] & Tony Robillard [1]

[1] Institut de Systématique, Evolution et Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, SU, EPHE, UA, 57 rue Cuvier, CP 50, 75231 Paris Cedex 05, France

[2] Friedrich-Schiller-University Jena, Institute for Zoology and Evolutionary Research, Erbertstraße 1, 07743 Jena, Germany

[3] Corresponding author: orthoptera.mingkai@gmail.com

Summary

Individual fitness can be boosted by behavioural strategies that maximise mate-finding probability while minimising predation risk. Animals that use acoustics to find mates may benefit from using both stationary calling and active exploration, but these also expose them to different types of predators. Studying calling and searching behaviours concurrently allows us to understand their evolutionary trade-offs between survival and reproduction. Unlike most other crickets, lebinthine males alternate between singing and exploration to find females, which offer a unique and excellent opportunity to test

for inter-individual differences and behavioural syndrome between call properties and exploratory behaviours. Our data demonstrate that call properties and exploratory behaviour were repeatable. We did not, however, find that call properties correlate with exploration as some consistently exploratory individuals produce longer calls while others produce shorter calls. Our study suggests that lebinthine males use different combinations of calling and exploratory behaviours to cope with unpredictable risk–benefit scenarios.

Key words: acoustic communication, exploratory behaviour, lebinthine crickets, animal personality, behavioural syndrome

Introduction

Behavioural strategies for mate finding, foraging behaviour and predator avoidance have strong impacts on the reproductive success (Hoy, 1991; Hunt et al., 2004; Rodriguez-Munoz et al., 2010). In most animals using acoustic communication in the context of pair formation, males produce calling songs to advertise themselves to conspecific females, but may also actively explore their habitat to increase the chances of finding potential mating partners and other resources like food (Wilson et al., 2010). While calling and exploration can both benefit the fitness of males, these behaviours are also costly with respect to energy and time consumption, and can attract attention of visually and/or acoustically hunting predators (Sakaluk & Belwood, 1984; Torsekar et al., 2019; Geipel et al., 2020).

An individual's behavioural strategies are expected to be shaped by natural and sexual selection to balance their survival and reproductive needs (Sakaluk, 1990; Zuk & Kolluru, 1998; Hedrick & Kortet, 2006; Dobbs et al., 2020). For instance, a high tendency to explore can be beneficial for individuals under low predator-risk conditions while a low tendency to explore might be more advantageous when predation risk is high (Hedrick, 2000; Römer et al., 2010; Symes et al., 2020). With relatively persistent risk–reward conditions, conspecific behaviours will be adapted to fit particular ecological niches (Honegger, 1981; Fergus & Shaw, 2013). However, consistent inter-individual differences in behavioural expression may also reflect variation of the behavioural phenotype within a population (Rose et al., 2017; Balsam & Stevenson, 2020, 2021). This may consequently improve both survivability and reproductive

success of different individuals within a population under fluctuating selection pressures over time (Smith & Blumstein, 2008; Wey et al., 2019).

Consistent inter-individual behavioural differences across time and context has been coined animal 'personality' (Sih et al., 2004; Biro & Stamps, 2008; Bell et al., 2009). A prominent and well-studied example of a personality trait is exploration which refers to the likelihood of an individual to spontaneously explore a novel environment (Dingemanse et al., 2007; Biro & Stamps, 2008; Wilson et al., 2010). Different species have been reported to show consistent inter-individual differences in exploration under different ecological conditions, including anti-predation, mate choice, foraging and learning (e.g., Wilson & Godin, 2009; Guillette et al., 2009; Mazué et al., 2015; Wat et al., 2020). Exploration can also be heritable and may have significant consequences for individual's fitness (Dingemanse et al., 2004, 2007; Sih et al., 2004; Réale et al., 2007; Smith & Blumstein, 2008). A meta-analysis by Smith & Blumstein (2008) indicated that exploration is in general tightly linked with increased survival but not necessarily also to reproductive success. In the context of acoustic mate-finding in crickets, however, behavioural evolution from male calling and female phonotaxis (field cricket strategy: Schöneich, 2020) to male calling and male searching (lebinthine strategy: ter Hofstede et al.2015) will most likely involve a significant shift of the predation risk towards the male side (e.g., Heller 1992). Nonetheless, a male which has higher exploration level may have a more active coping strategy and would be more likely to search around its environment to find females than a male with lower exploratory tendency and rather passive coping strategy (Dingemanse et al., 2004; Garamszegi et al., 2008).

Multidimensional acoustic signals used for attracting mates can vary within and between individuals, populations and species (Gerhardt & Huber, 2002). The extent of this variation can be broadly categorised into ‘static’ or ‘dynamic’ call properties (Gerhardt, 1991) based on the level of within-male variability and corresponding female preference functions. Static call properties are relatively consistent within and between the males’ calls, and females can use them to differentiate conspecific from heterospecific males (Gerhardt, 1991). In contrast, dynamic properties are generally more variable between males, and to some extent, within each male’s calls. Females may potentially use this information to discriminate the qualities of the singing male regarding body size, fertility, age and health conditions (e.g., Wagner & Hoback, 1999; Scheuber et al., 2003; Bertram et al., 2012; Rodiguez et al., 2014). In the context of pair formation, the acoustic communication signals may be used by the receiver to recognise and locate, as well as to select between, potential mates. These objectives—species recognition and mate choice—can impose different selection pressures on the variably of signal parameters (Gerhardt, 1991Gerhardt & Huber, 2002), implying that both inter- and intra-individual variation in these properties are crucial for studying evolution of acoustic communication.

One main finding of the studies on static and dynamic call properties in different species is that individuals exhibit different degrees of repeatability in their call properties (Gerhardt, 1991; Nityananda & Balakrishnan, 2008; Bertram et al., 2012; Deb et al., 2012; Nandi & Balakrishnan, 2013). To date, studies in anurans and orthopteran insects have demonstrated that static properties tend to exhibit higher

repeatability and usually include carrier frequency and pulse rate (e.g., Gerhardt & Huber, 2002; Gerhardt, 2008; Nandi & Balakrishnan, 2013). On the other hand, dynamic properties, which may include temporal parameters such as chirp rate and call duration, are usually less repeatable within the males' calls (Gerhardt, 1991; Nityananda & Balakrishnan, 2008; Nandi & Balakrishnan, 2013). High repeatability in call parameters are often attributed to morphological features responsible for sound production (Montealegre-Z et al., 2009, 2011) while lower repeatability can apply to features depending mostly on the neuronal control of behaviour (Schöneich & Hedwig, 2012, 2017), which can be significantly affected by internal body condition and external environment (e.g., temperature, duration of day light, disturbance by rainfall or background noise).

Since multiple behavioural traits can be correlated, it is likely that behavioural syndrome might exist between calling and other behaviour associated with finding mates (e.g., exploration) (Garamszegi et al., 2008). A behavioural syndrome is defined as the correlation of inter-individual differences of two or more different behaviours (Sih, 2004; Hertel et al., 2020). It provides a more holistic view of behaviour, in which selection affecting one behaviour can influence how other behaviours are expressed across different contexts (Sih et al., 2004; Kortet & Hedrick, 2007; Wilson et al., 2010). To date, only a handful of studies investigated inter-individual differences in mate-finding strategies by examining how variation in acoustic signalling traits correlate with other fitness-influencing behavioural traits complementing acoustic signalling (Nityananda & Balakrishnan, 2008; Naguib et al., 2010).

Crickets have been frequently utilised to examine neurophysiological mechanisms and evolutionary processes related to their behaviours (Huber et al., 1989; Horch et al., 2017; Schöneich, 2020). Nevertheless, studies of repeatability in the call properties of their calling songs and potential correlations with other mate-finding behaviours are still scarce (Wilson et al., 2010; Fitzsimmons & Bertram, 2013; Shaw & Herlihy, 2000). There is also a need for more comparative studies to diversify the study subjects to avoid making general statements based only on very few and phylogenetically constrained model species. The majority of studies on cricket personality (but see Tan et al., 2018; Tan & Tan 2019), particularly in the context of acoustic mate finding, and on the static and dynamic traits in cricket calls are focused on only a handful of field cricket species (e.g., Bailey and Zuk, 2008; Zuk et al., 2008; Bertram et al., 2012; Stahlschmidt et al., 2014; Santostefano et al., 2016). Field crickets (Gryllinae) are often used as model species (Horch et al., 2017), but male's call at low frequencies while remaining at the same location on the ground and while relying on female phonotaxis (Simmons, 1988; Bennet-Clark, 1989; Schöneich and Hedwig 2010). On the other hand, the Lebinthini crickets—a speciose tribe of the subfamily Eneopterinae possess diverse high-frequency calls (Robillard et al., 2007; Tan et al., 2021)—live on bushes in a three-dimensional habitat. More importantly, lebinthine males actively search for female's vibratory responses to their high-frequency calls by alternating between calling and walking around (ter Hofstede et al., 2015), a behaviour that is generally not observed in field crickets. The crickets of the tribe of Lebinthini crickets provides a unique and excellent opportunity to study evolutionary trade-offs between calling and searching behaviour in the context of mate finding.

We used a lebinthine cricket species (*Lebinthus bitaeniatus* Stål, 1877) to investigate if males exhibit consistent inter-individual differences in call properties and exploratory behaviour, and whether they correlate. We hypothesise that a highly exploratory individual should also be more eager to acoustically advertise itself to females or against other males, thus having the tendency to produce songs with longer call duration and/or shorter syllable period (Garamszegi et al., 2008; Wilson et al., 2010). Although this strategy might increase male mating opportunities it could also be more costly as it increases male conspicuousness to acoustically orienting predators (Garamszegi et al., 2008). Alternatively, individuals that produce songs with longer call duration and/or shorter syllable period could be less exploratory, suggesting a trade-off between the two activities.

Materials and methods

Study animals

A species of Southeast Asian lebinthine crickets was used for the experiments: *L. bitaeniatus* from the Philippines (Figure 1a). *L. bitaeniatus* can be found living in secondary forests, usually among plant foliage or on top of leaf litter (Robillard & Tan, 2013). It is a medium-sized (male hind femur length = 11.6 mm) species and the males' call has a broadband frequency spectrum at high frequency (12–30 kHz). Calls are emitted mostly from early morning to dusk, and the echeme consists of two parts (Figure 1b): initial well-spaced syllables (hereafter referred to as clicks) followed by a short trill (Robillard & Tan, 2013). Breeding colonies in the lab were established with cricket eggs collected during fieldwork from 2014 in Luzon, Philippines. The cricket

colonies were housed and maintained at a temperature-controlled insect rearing room of the Muséum national d'Histoire naturelle, Paris (MNHN). The animals were kept at 25–27ºC in large tanks with soil as substrate and living foliage to simulate natural environment and maintain high humidity. The colonies were subjected to 13:11 hours light:dark cycle. The crickets were fed with European ivy (*Hedera helix* Linnaeus) and Affinity ULTIMA Mini Adult dog pellets food and BJORG Muesli whole grain cereals without added sugar *ad libitum*. Adult males and females, as well as juveniles, were kept together as they would usually be in their natural environment. Moist cotton balls were provided for females to lay eggs.

Individual males were isolated from the colonies about 24 hours before the start of the experiments, each placed in a separate container (6.5 cm in diameter and 8.5 cm high). Each container was cleaned daily and food and water (wet cotton ball) replaced at least every second day. We used individuals from the same colony to control for population differences, and only healthy and intact individuals were selected for the experiments. Fresh body weight was measured using a precise weighing balance with 0.1 mg accuracy (Mettler Toledo GmbH [MS304TS/00], Switzerland). We were careful not to harm the crickets during the collection, housing and experiments. After the experiments, the crickets were euthanised in a freezer and pinned for vouchering in the MNHN. Pronotum length of the dried specimen was measured. Body condition was calculated by using Peige and Green's (2009) scaled mass index (SMI), which accounts for the covariation between body mass and body size when calculating a standardised condition score. We used pronotum length as a proxy for body size in our calculations of SMI.

Sound recording and analysis of call properties

To test for consistent inter-individual differences in the calling properties, we placed an isolated male in a cage with nylon netting (considered as a novel environment) in a temperature-controlled sound attenuating room in MNHN and recorded the acoustic activity for 24 hours. Recording commenced after the cricket was placed inside the cage. These standardised conditions are aimed at minimising the influence of noise from the environment and other males on the singing activity. As temperature can influence the call properties, we used a HOBO 8K Pendant® Temperature logger (model: UA-001-08, Onset, Bourne, MA) to track the room ambient temperature once every hour. Temperature was kept at around 25–27ºC; high humidity was maintained with a cotton ball soaked in water; light:dark hours followed that in the insect rearing room.

Singing activity was recorded using a Condenser Capsule microphone CM16 (Avisoft Bioacoustics, Berlin, with a flat frequency response from 3 to 150 kHz), which was placed next to the nylon cage. Automatic recordings were made at a sampling rate of 96 kilo-samples per second (16 bit) using a suitable sound card (8-Pre MOTU) and Avisoft software (Triggering Harddisk Recorder version 2.97). All sound 5 s prior to the trigger was recorded and saved, and the recording continued for 30 s after the last sound had been detected. In total, we recorded the calls of 18 male *L. bitaeniatus*.

From the recordings, we considered each song as a unit of replication and analysed the following parameters to examine repeatability in the call properties: call duration, number of clicks, trill duration and syllable period of the trill part and dominant frequency. This was done using Raven Lite 2.0 for visualisation of sound files, and then

"autodetec" function in R package WarbleR version 1.1.14 (Araya-Salas & Wright, 2017) to identify the starts and ends of sound signals and the number of syllables for each song. For individuals that sang continuously, we randomly selected and analysed a subset of eight sound files between 0800–1400 hours during which the cricket was most active (Tan & Robillard, 2021a) and that the video recording was done (see below), but ensured that there were at least five analysed calls per individual. This also ensured that the data used for downstream analyses was not unbalanced among the different individuals. To extract the dominant frequency, we used the "specan" function in R package WarbleR version 1.1.14 (Araya-Salas & Wright, 2017).

Video recording and analysis of the exploratory behaviour

To assess repeatability of exploratory behaviour in a new environment, a behavioural assay was conducted in a temperature-controlled room (30±2ºC), isolated from other crickets. This was done usually between 08:00 to 14:00 daytime hours. The testing arena (Figure 1c) was an empty 34 cm length, 23 cm wide, 10 cm tall plastic container (RAD1068) and was covered with a glass plate on top. The bottom surface of the arena was covered with filter paper, which was replaced after each trial to minimise effect of chemical traces introduced by crickets during previous trials. About 30 min prior to the start of assay, the individual was placed in a tumbler (7.7 cm in diameter and 7.5 cm tall) covered with a piece of cardboard to allow for habituation. This glass jar with the cricket inside was then randomly placed in one of the eight segments of the arena (i.e., zones) to avoid systematic spatial biases. The trial commenced upon removal of the cardboard covering the jar. The exploratory behaviour of the cricket in the test arena was video recorded for 40 min using a Sony HD AVCHD Progressive HandyCam

HDR-CX240, 9.2 mega pixels. After the trial, the cricket was returned to its individual container. The glass jar was also cleaned using Diversity FandB Divosan ETHA-plus after each trial to remove chemical traces of the previous crickets. For each individual, the trial was repeated five times, once every day (about 24 hours gap between trials). In total, we video-recorded repeated assays for 19 male *L. bitaeniatus*.

From the video files, we used the animal-tracking software EthoVision XT version 15.0 (Noldus Information Technology, the Netherlands) to determine the following measures: 1) number of zones within the testing arena explored by the cricket and 2) total distance covered by the cricket. The pixels representing the cricket was detected using grey scaling and the position of the centre of mass of each cricket was tracked.

Testing repeatability of call properties and behavioural traits

Repeatability is defined as the intraclass correlation coefficient (ICC), which is calculated as the ratio of inter- group variance and the sum of inter- and within-group variance (Nakagawa & Schielzeth, 2010), where 'group' refers to individual crickets when determining repeatability. To assess repeatability, we followed the mixed effect modelling approach by Nakagawa & Schielzeth (2010) and Dingemanse & Dochtermann (2013). In all models, the individual cricket identity was fitted as a random effect, so as to allow partitioning of phenotypic variation into between- and within-individual components, for even non-Gaussian data, as compared to traditional ANOVA-based methods. To assess repeatability of the call properties, we fitted four univariate linear mixed-effects models (LMMs), one for call duration, dominant frequency, trill duration and syllable period each using the "lmer" function from the R

package “lme4” (Bates et al., 2014). We also fitted an univariate generalised linear mixed-effect model (GLMM) with negative binomial error distribution for the number of clicks using the “glmer.nb” function from “lme4” (Bates et al., 2014). For continuous variables (e.g., call duration), gaussian error distribution was used for modelling, hence the use of LMMs. We also log-transformed call duration and syllable period to improve model performance. For count data (i.e., number of clicks), negative binomial error distribution was preferred over poisson because overdispersion was detected via the ‘dispersion_glmer’ function from ‘blmeco’ (Korner-Nievergelt et al., 2015). Included as fixed effects were: 1) ambient temperature at the time of calling to control for temperature effect on the call properties (Walker, 1962), 2) scaled body index of cricket to control for body condition of cricket and 3) the time (i.e., hour of the day) during which the song was recorded. All fixed effects were centred on their means to facilitate model fitting (Schielzeth, 2010). Dispersion, outliers, heterogeneity of residuals and variable collinearity were checked to ensure that the assumptions of the models were not violated (Zuur et al., 2010, 2016). The marginal and conditional R^2 (i.e., R^2_m and R^2_c respectively) were also reported for each model.

To assess repeatability of exploratory behaviour in each individual, we fitted an univariate GLMM with negative binomial error distribution (to account for overdispersion) for the total number of zones within the testing arena that were explored, as well as an univariate LMM for total distance covered using the same functions of the same R package described previously. To control for potential spatio-temporal biases in parameter estimates caused by the experimental setup, arena location in a test platform (1–3; three levels, categorical) was considered as a fixed effect. To

299 control for potential habituation to the novel environment of the testing arena, trial
300 number was also considered as a fixed effect. Moreover, scaled body index of cricket to
301 control for body condition of cricket (found to be correlated to the total number of
302 singing bouts over 24 hours) was also included as fixed effects.
303
304 To calculate repeatability estimate, we used the functions “rpt” and “rptPoisson”
305 functions from the R package “rptR” (Stoffel et al., 2017) for call duration, trill duration
306 and syllable period, as well as, total distance covered; and for number of clicks and
307 number of zones explored, respectively. We reported the standard errors of the
308 repeatability estimates and performed 500 parametric bootstraps to obtain the 95%
309 confidence intervals (CIs) for the random effect. Repeatability was calculated after
310 controlling for variation due to covariates. For the number of clicks and number of
311 zones explored, we accounted for overdispersion and the repeatability approximated
312 using an original scale was used. Since the R package “rptR” uses algorithms that do
313 not converge if repeatability is zero or negative, we concluded that repeatability is zero
314 only if CIs and p- values were shown as NA (Schuster et al., 2017). The “rpt” R-
315 package applies parametric bootstrapping for CI estimation, but randomisation for
316 inference testing (p-values) which may lead to non- congruent conclusions.
317 Nonetheless, effect sizes in combination with the CIs were also considered during
318 interpretation. Repeatability estimates larger than 0.1 were considered as weak
319 evidence, even if the estimated CI included zero; and repeatability estimates smaller
320 than 0.1 as not repeatable, even if the p-value suggested significance (Schuster et al.,
321 2017).
322

Correlations between call properties and exploratory behaviour

To investigate whether the call properties and exploratory behaviour correlate, multivariate mixed effects models are preferred to extracting individual point estimates from random effects (also known as best linear unbiased predictor, BLUP). This is because BLUP overlooks the errors inherited in the estimates, and using BLUP extracted from univariate models tends to lead to false positive results and hence (erroneous) conclusion (Houslay & Wilson, 2017). We fitted multivariate mixed effects models with call properties and exploratory behaviours as response variables using the 'MCMCglmm' package (Hadfield, 2010). To avoid overfitting the model with correlated call properties, we first used a principal component analysis (PCA) to summarise the variations of the multivariate call properties and visualise collinearity among the call properties. Only males with data sets for both exploratory behaviour and call properties were used for the correlation analysis. If two or more call properties were correlated, we used only one of them for the multivariate mixed effects models. Response variables were scaled to facilitate model fitting. As we had much greater number of repeats for song data than for exploration data, we randomly selected five songs from each individual to be fitted as a response in the models (since each individual had five repeats of emergence time and/or total exploring duration). We added as fixed effects the parameters, which are considered important in explaining each trait based on the results from the repeatability estimation. We used the MCMCglmm default prior for the fixed effects and an inverse-gamma prior for the residuals ($V = 1$, $\nu = 0.002$); an uninformative, parameter-expanded prior for the random effect ($V= 1$, $\nu = 3$, $\alpha\mu = 0$, $\alpha V = 625$). We ran the model for 750,000 MCMC iterations with a burn-in of 50,000 and a thinning-interval of 175. Estimated model

coefficients and credible intervals were based on 4,000 effective samples. A Bayesian 95% credible interval that crosses zero indicates that there is no evidence of a statistically significant correlation, and one with the lower bound close to zero indicates weak evidence. To assess the strength and direction of correlation, we followed the approach by Houslay & Wilson (2017): we calculated the mean for the correlation between the variances of the singing and exploring behaviour. This was done by dividing the covariance between an exploratory trait with a singing property by the product of the square roots of their variances.

Results

Repeatability of call properties

Of the 19 *Lebinthus bitaeniatus* males used for the experiments, one died (ID # 19) before the sound recording was completed, and was therefore excluded from the analyses. Another male (ID # 9) did not call, despite the exploratory assay was completed, and was also therefore also excluded from the analyses. The remaining data (17 animals; n = 675 calls) showed that *L. bitaeniatus* males showed consistent inter-individual differences in the following call parameters: call duration (ICC = 0.26±0.09, p-value <0.001, 95 % CI [0.09, 0.43], R^2_m = 0.00, R^2_c = 0.26), number of clicks per call (ICC = 0.24±0.08, p-value <0.001, 95 % CI [0.05, 0.37], R^2_m = 0.00, R^2_c = 0.20), trill duration (ICC = 0.32±0.10, p-value <0.001, 95 % CI [0.14, 0.51], R^2_m = 0.03, R^2_c = 0.34) and syllable period (ICC = 0.32±0.10, p-value <0.001, 95 % CI [0.12, 0.50], R^2_m = 0.11, R^2_c = 0.39) (Figure 2). None of the fixed effects predicted call duration or number of clicks (Table 1). Syllable period correlated negatively only with ambient temperature (estimate = −0.008±0.004, 95% CI [−0.015, −0.001]) (Table 1). *L.*

bitaeniatus also showed consistent inter-individual differences in dominant frequency (ICC = 0.90±0.04, p-value <0.001, 95 % CI [0.78, 0.94], R^2_m = 0.06, R^2_c = 0.90) (Figure 2). Dominant frequency correlated negatively with the time of the recording (estimate = −0.002±0.001, 95% CI [−0.003, −0.001]) and increased with higher temperature (estimate = 0.004±0.002, 95% CI [0.001, 0.007]) (Table 1).

Repeatability of the exploratory behaviours

Of the 19 *L. bitaeniatus* males used for the experiments, one (ID # 19) died before exploratory assays were completed, and was therefore excluded from the analyses. *L. bitaeniatus* (n = 90 videos, 18 males) showed weak consistent inter-individual differences in the number of zones explored within the testing arena (ICC = 0.15±0.11, p-value < 0.001, 95 % CI [0.03, 0.41], R^2_m = 0.01, R^2_c = 0.57) (Figure 3), but showed stronger consistent inter-individual differences in the total distance covered in the arena (ICC = 0.25±0.12, p-value = 0.005, 95 % CI [0.02, 0.48], R^2_m = 0.10, R^2_c = 0.33) (Figure 3). The *L. bitaeniatus* males did not show evidence of habituation to the novel environment in both number of zones explored (estimate = −0.01±0.18, 95% CI [−0.36, 0.34]) and total distance covered (estimate = 30.0±26.5, 95% CI [−21.8, 81.6]) (Table 2). Individuals with better body conditions tend to cover a greater distance (estimate =91.3±43.6, 95% CI [7.3, 175.7]) but did not explore more or less zones (estimate = 0.22±0.43, 95% CI [−0.74, 1.16]) than individuals with poorer body conditions (Table 2).

Correlations between call properties and exploratory behaviours

394 The first two components of the principal component analysis explained 63.9% of
395 variance (PC1 41.0% and PC2 22.9% of variances, respectively). PC1 summarises the
396 number of clicks and call duration whereas PC2 summarises dominant frequency and
397 syllable period, which are in both cases positively correlated with one another) (Figure
398 6). Then, we fitted a multivariate mixed effects model using call duration, syllable
399 period and total distance covered as the response variables. We added fixed effects that
400 were previously important in predicting the respective response variables: Body
401 condition of the cricket was added as a fixed effect for total distance covered; and
402 ambient temperature was added as a fixed effect for syllable period. There was no
403 evidence of correlation between exploratory behaviours and call properties: individuals
404 that consistently produced longer call duration and syllable period did not consistently
405 cover either a longer or shorter distance in the arena during the tests of exploratory
406 behaviour (Table 3).
407
408
409 **Discussion**
410 *Repeatability in call properties*
411 Our results demonstrate that male *L. bitaeniatus* crickets exhibit inter-individual
412 differences and repeatability in their calls. Specifically, we were able to quantify
413 consistent inter-individual differences in all measured call properties: call duration,
414 dominant frequency, number of clicks, trill duration and syllable period of the trill part.
415 These suggest that some individuals consistently produce longer calls (longer call and
416 longer trill durations) or with shorter syllable periods than others. These differences

417 may allow females to detect these males more readily, but having longer calls can also
418 increase exposure to eavesdropping predators or rival males.
419
420 In the lebinthine species studied here, call duration, trill duration and syllable period
421 tend to be less repeatable than dominant frequency. Our findings are therefore similar to
422 previous studies in other crickets, which also demonstrated that the properties with
423 lower repeatability estimates are usually found as dynamic rather than static call
424 properties (e.g., dominant frequency) (Nityananda & Balakrishnan, 2008; Deb et al.,
425 2012; Nandi & Balakrishnan, 2013).
426
427 A separate study using similar methodology demonstrated that the same call properties
428 as examined in this study are also repeatable in the sister species, *Lebinthus luae*
429 Robillard & Tan, 2013 (Tan & Robillard, 2021b). However, the call properties of *L.*
430 *luae* were more repeatable than that of *L. bitaeniatus* in this study. We postulate that the
431 differences may be attributed to the fact that while the *L. bitaeniatus* males used in this
432 experiment come from lab colonies that are more acclimatised to human disturbance, *L.*
433 *luae* used in Tan & Robillard (2021b) were obtained from wild populations. The
434 different wild populations of *L. luae* faced different levels of predation risks and
435 dangers (Fung et al., 2018) leading to population differences in the call properties (Tan
436 & Robillard, 2021b), compared to our *L. bitaeniatus* population that was nursed and
437 bred for several generations under the unique and safe conditions as a lab colony.
438 Besides species-specific differences, this may also explain why consistent inter-
439 individual differences in the call properties were more prominent among the wild-
440 caught individuals of *L. luae*.

We found that the call properties that exhibit most consistent inter-individual differences in the two *Lebinthus* species are also temporal parameters in other gryllid crickets of the genera *Acheta*, *Gryllus* and *Plebeiogryllus*, as shown in previous studies (see Bertram et al., 2012; Nandi & Balakrishnan, 2013). These call properties include chirp length (analogous to call duration in *Lebinthus*) and syllables per chirp (approximating the number of click per call). Other orthopterans, however, such as the *Mecopoda* bush-crickets and *Oecanthus* tree crickets did not necessarily exhibit clear repeatability in their call properties (Nityananda & Balakrishnan, 2008; Deb et al., 2012). This suggests that whether a call property is repeatable may differ among species and taxonomic groups, probably as a consequence of differences in terms of selection pressures, phylogenetic relatedness or different acoustic mate finding strategies. This illustrates the importance of broadening the study systems across more species.

Studying individuality in the calling behaviours of lebinthines is still in its infancy. Further studies could record the calls of each male over repeated trials, rather than one 24-hour recording, to examine individuality in the call properties over longer time periods (see: Bertram et al., 2012; Nandi & Balakrishnan, 2013). Calls recorded within one day can produce inflated repeatability estimates compared to those when recorded over a few days, because the former can be confounded by inflated between-individual differences attributed condition (e.g., health, mating status, motivation, energy level, food and water consumed). Consequently, even if we have considered scaled body index in our models, estimating the repeatability across numerous trials might better reflect personality than statistically controlling for internal state in the models.

Repeatability of the exploratory behaviours

Unlike most gryllines, male lebinthines are not just passive callers, but instead they actively search for females' vibrational responses between their calling bouts and walking around on plant branches (ter Hofstede et al., 2015). As such, merely examining the call properties in lebinthines may not be sufficient to understand how males find females. The repeatability in the exploratory behaviour of the males also needs to be examined to better understand how the lebinthines' communication system influences behavioural strategies to optimise the mate-finding success.

In line with our hypothesis that male lebinthines exhibit different 'personality' types regarding their exploratory behaviours, we identified consistent inter-individual difference in the two investigated exploratory traits of *L. bitaeniatus*. Some males consistently covered a greater distance and visited more zones within the testing arena than others, which suggests that individuals of this species exhibit different 'personalities' in terms of exploration behaviour. Our data thus add more evidence for widespread occurrence of inter-individual behavioural differences (animal 'personality') in orthopteroid insects. Specifically, Eneopterinae represents another orthopteran lineage to exhibit behavioural personality types previously reported for Gryllinae by Stahlschmidt et al. (2014), DiRienzo et al. (2016), Santostefano et al. (2016) and others, as well as for Tettigoniidae by Tan et al. (2018) and Tan & Tan (2019).

The inter-individual differences in exploratory behaviours of male *L. bitaeniatus* suggests that both strategies, high and low tendency to actively explore may benefit

males under different unforeseeable situations. Since male lebinthines explore among vegetation and actively search for potential mates (ter Hofstede et al., 2015), males with a higher tendency to explore will improve their chances to find and be heard by females, which can be advantageous under low predator-risk conditions. Under high predation pressure, being less exploratory can be more advantageous as it reduces the risks of predation (Hedrick, 2000; Römer et al., 2010; Symes et al., 2020). Depending on the circumstances, benefits of avoiding predation may outweigh the reduced chance of finding mates among these less exploratory males. Furthermore, more stationary males may have the additional advantage to better perceive the female's vibratory response transmitted via the plant substrate, hence being more likely to advance from responses of females if they sit on a remote branch or even different plant nearby.

Correlations between call properties and exploratory behaviours

Both call properties and exploratory behaviours are subjected to pressures applied by natural and sexual selection, which can consequently shape behavioural strategies that balance survival and reproductive needs. The fact that call properties as well as exploratory behaviour of the individuals are repeatable—although the former was repeatable within a day and the latter between days—allowed us to tentatively explore whether call properties and exploratory behaviour may correlate. However, contrary to our predictions, we did not detect any correlation between call properties and exploratory behaviour, which suggests that the inter-individual differences of call properties and exploratory behaviour might be independent. This result contrasts with studies on other cricket species and birds where such correlations were found (e.g.,

512 Garamszegi et al., 2008; Naguib et al., 2010, 2016; Wilson et al., 2010; Guillette &
513 Sturdy, 2011).
514
515 Our different results might reflect the unique communication system in lebinthine
516 crickets. Instead of remaining stationary, as typical gryllines do, male lebinthines
517 usually alternate between calling and walking (ter Hofstede et al., 2015). It is thus likely
518 that the chance of finding mates under unpredictable predation risk can involve multiple
519 strategies, and that more than a single suite of traits might be successful in different
520 circumstances. As such, we speculate that individual males might therefore employ
521 different strategies: although males can either stay stationary (less exploratory) until
522 receiving positive feedback from a nearby female or move around (more exploratory) to
523 actively find females, males at both ends of the exploration continuum could produce
524 more or fewer acoustic signals (i.e., longer or shorter syllable period and/or call
525 duration), blurring any attempt to detect a simple correlation between the two trait
526 categories. Our interpretation that different lebinthine males might employ different
527 strategies should be taken with some caution owing to our small sample size. Although
528 a larger number of crickets would permit the use of multivariate mixed effects
529 modelling (see: Dingemanse & Dochtermann, 2013), it is difficult to obtain large
530 numbers of individuals from the same colony and generation under laboratory
531 conditions.
532
533 Using different calling and exploration strategies can be crucial for increasing the
534 survival of individuals in a population experiencing unpredictable conditions (e.g.,
535 sparsity or abundance of potential mates, parasites and predators). For example,

536 acoustically-orientated parasitoids of crickets (e.g., *Ormia* species) are generally
537 effective in attacking a wide variety of calling songs in *Gryllus* (e.g., Sakaguchi &
538 Gray, 2011; Gray et al., 2019) and could possibly also attack lebinthine males with
539 different call properties (e.g., longer call duration or syllable period or fewer number of
540 clicks). Having individuals that use different strategies can therefore help to spread the
541 risk of predation and parasitism (Pascoal et al., 2014; Rayner et al., 2019). One
542 possibility is that, when the parasitoid abundance is high, individuals which are either
543 highly exploratory but produce shorter calls or *vice versa*, may be favoured because
544 they are less likely to encounter, and be detected by, predators and parasitoids with
545 different hunting strategies. Under a different selection pressure where parasitoid
546 abundance is low, males which are both more exploratory and produce longer calls may
547 be favoured instead, because they can find mates more readily. Nevertheless, no
548 acoustically -orientated parasitoid is known to attack lebinthines thus far, and detailed
549 studies on the predator–lebinthine cricket dynamics are hitherto lacking. As we may
550 expect that their dynamics can be different from field crickets owing their different
551 modes of mate-finding in a different habitat (ter Hofstede et al. 2015), investigating
552 personality traits and call properties in the context of parasitoid–lebinthine crickets
553 dynamics could further validate our hypothesis.
554
555
556 **Conclusions**
557 New evidences from a lebinthine cricket species for consistent inter-individual
558 differences in call properties and exploratory behaviour demonstrates that animal
559 'personality' is more widespread than currently known and highlights its importance for

560 the individual's fitness. The lack of a clear correlation between call properties and
561 explorative behaviour in our study suggests that lebinthine crickets may cope with
562 unpredictable risk–benefit scenarios by different individual males using different
563 combinatoric strategies. Although our study is limited by sample size and recording
564 periods, it is the first to investigate how inter-individual differences in exploratory and
565 calling behaviours in this behaviourally-unique lebinthine cricket.
566
567
568 **Acknowledgments**
569 The work of MKT was supported by the Fyssen Foundation Postdoctoral Fellowship on
570 "From Individuality to Species: Personality and Evolution of Acoustics Communication
571 in Eneopterinae Crickets". The field work by TR in Luzon, Philippines (2014) was
572 organised by TR (MNHN) and Sheryl Yap (University of Philippines Los Baňos
573 Museum of Natural History), funded by grants from the MNHN's Action Transversale
574 du Muséum. In the final stages of the project Stefan Schöneich was supported by the
575 German Research Foundation (DFG Grant: SCHO 1822/3-1). The authors are thankful
576 to Marion Guillaume who helped with the husbandry of the crickets and Julia Balsam
577 for her help and advice with the visualisation of exploration paths.
578
579
580 **Author contributions**
581 **Ming Kai Tan:** Conceptualisation, Methodology, Investigation, Formal analysis,
582 Writing (both Original Draft and Review & Editing). **Stefan Schöneich:**
583 Conceptualisation, Methodology, Formal analysis, Writing (both Original Draft and

584 Review & Editing). **Tony Robillard:** Conceptualisation, Methodology, Formal
585 analysis, Writing (both Original Draft and Review & Editing), Supervision.
586
587
588 **References**
589 Araya- Salas, M. & Smith- Vidaurre, G. (2017). warbleR: an R package to streamline
590 analysis of animal acoustic signals. – Methods Ecol. Evol 8(2):184-191.
591 Bailey, N.W. & Zuk, M. (2008). Acoustic experience shapes female mate choice in field
592 crickets. – Proc. Royal Soc. B 275(1651):2645-2650.
593 Balsam, J.S. & Stevenson P.A. (2021). Agonistic experience during development
594 establishes inter-individual differences in approach-avoidance behaviour of
595 crickets. – Sci. Rep. 11(1):16702.
596 Balsam, J.S. & Stevenson P.A. (2020). Pre-adult aggression and its long-term
597 behavioural consequences in crickets. – PLoS ONE 15(3): e0230743.
598 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H. &
599 Dai, B. (2014). lme4: linear mixed-effects models using Eigen and S4 (Version 1.1-
600 7). – J. Stat. Softw 67 (1):1-48.
601 Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009). The repeatability of behaviour: a
602 meta-analysis. – Anim. Behav. 77(4):771-783.
603 Bennet-Clark, H.C. (1989). Songs and the physics of sound production. – In: Cricket
604 behaviour and neurobiology (Huber, F., Moore, T.E. & Loher, W., eds.). Cornell
605 University Press, Ithaca, p. 227-261.

606 Bertram, S.M., Fitzsimmons, L.P., McAuley, E.M., Rundle, H.D. & Gorelick, R.
607 (2012). Phenotypic covariance structure and its divergence for acoustic mate
608 attraction signals among four cricket species. – Ecol. Evol 2(1):181–195.
609 Biro, P.A. & Stamps, J.A. (2008). Are animal personality traits linked to life-history
610 productivity? – Trends Ecol. Evol. 23(7):361-368.
611 Deb, R., Bhattacharya, M. & Balakrishnan, R. (2012). Females of a tree cricket prefer
612 larger males but not the lower frequency male calls that indicate large body size. –
613 Anim. Behav. 84(1):137-149.
614 Dingemanse, N.J. & Dochtermann, N.A. (2013) Quantifying individual variation in
615 behaviour: mixed-effect modelling approaches. – J Anim Ecol 82(1):39-54.
616 Dingemanse, N.J., Wright, J., Kazem, A.J., Thomas, D.K., Hickling, R. & Dawnay, N.
617 (2007). Behavioural syndromes differ predictably between 12 populations of
618 three- spined stickleback. – J Anim Ecol 76:1128-1138.
619 Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. (2004). Fitness consequences
620 of avian personalities in a fluctuating environment. – Proc. Royal Soc. B
621 271(1541):847-852.
622 DiRienzo, N., Niemelä, P.T., Hedrick, A.V. & Kortet, R. (2016). Adult bacterial
623 exposure increases behavioural variation and drives higher repeatability in field
624 crickets. – Behav. Ecol 70(11):1941-1947.
625 Dobbs, O.L., Talavera, J.B., Rossi, S.M., Menjivar, S. & Gray, D.A. (2020). Signaller–
626 receiver–eavesdropper: Risks and rewards of variation in the dominant frequency of
627 male cricket calls. – Ecol. Evol. https://doi.org/10.1002/ece3.6866
628 Fergus, D.J. & Shaw, K.L. (2013). Circadian rhythms and period expression in the
629 Hawaiian cricket genus *Laupala*. – Behav. Genet. 43(3):241-253.

630 Fitzsimmons, L.P. & Bertram, S.M. (2013). Signalling effort does not predict
631 aggressiveness in male spring field crickets. – Behav. Ecol 67(2):213-220.
632 Fung, T.K., Tan, M.K. & Sivasothi, N. (2018). Orthoptera in the scat content of the
633 common palm civet (*Paradoxurus hermaphroditus*) in Pulau Ubin, Singapore. –
634 Nat. Singap 11:37-44.
635 Garamszegi, L.Z., Eens, M. & Török, J. (2008). Birds reveal their personality when
636 singing. – PLoS One 3(7):0002647
637 Geipel, I., Kernan, C.E., Litterer, A.S., Carter, G.G., Page, R.A. & ter Hofstede, H.M.
638 (2020). Predation risks of signalling and searching: bats prefer moving katydids. –
639 Biol. Lett. 16(4):20190837.
640 Gerhardt, H.C. (1991). Female mate choice in treefrogs: static and dynamic acoustic
641 criteria. – Anim. Behav. 42(4):615-635.
642 Gerhardt, H.C. & Huber, F. (2002). Acoustic Communication in Insects and Anurans:
643 Common Problems and Diverse Solutions. – University of Chicago Press, Illinois.
644 Gerhardt, H. C. (2008). Phonotactic selectivity in two cryptic species of grey treefrogs:
645 effects of differences in pulse rate, carrier frequency and playback level. – J. Exp.
646 Biol. 211(16):2609-2616.
647 Guillette, L.M., Reddon, A.R., Hurd, P.L. & Sturdy, C.B. (2009). Exploration of a novel
648 space is associated with individual differences in learning speed in black-capped
649 chickadees, *Poecile atricapillus*. – Behav. Processes 82(3):265-270.
650 Guillette, L.M. & Sturdy, C.B. (2011). Individual differences and repeatability in vocal
651 production: stress-induced calling exposes a songbird's personality. –
652 Naturwissenschaften 98:977-981.

653 Hadfield, J.D. (2010). MCMC methods for multi-response generalised linear mixed
654 models: the MCMCglmm R package. – J. Stat. Softw 33(2):1-22.
655 Hedrick, A.V. (2000). Crickets with extravagant mating songs compensate for predation
656 risk with extra caution. – Proc. Royal Soc. B 267(1444):671-675.
657 Hedrick, A.V. & Kortet, R. (2006). Hiding behaviour in two cricket populations that
658 differ in predation pressure. – Anim. Behav. 72:1111-1118.
659 Heller, K.G. (1992). Risk shift between males and females in the pair-forming
660 behaviour of bushcrickets. – Naturwissenschaften 79:89-91.
661 Hertel, A.G., Niemelä, P.T., Dingemanse, N.J. & Mueller, T. (2020). A guide for
662 studying among-individual behavioural variation from movement data in the wild.
663 – Mov. Ecol. 8(1):1-18.
664 Honegger, H.W. (1981). Three different diel rhythms of the calling song in the cricket,
665 *Gryllus campestris*, and their control mechanisms. – Physiol. Entomol 6:289-296.
666 Horch, H.W., Mito, T., Popadić, A., Ohuchi, H. & Noji, S. (2017). The cricket as a
667 model organism-development, regeneration, and behaviour. – Springer Japan,
668 Tokyo.
669 Houslay, T.M. & Wilson, A.J. (2017). Avoiding the misuse of BLUP in behavioural
670 ecology. – Behav. Ecol. 28(4):948-952.
671 Hoy, R.R. (1991). Signals for survival in the lives of crickets. – Am. Zool. 31:297–305.
672 Huber, F., Moore, T.E. & Loher, W. (1989). Cricket behaviour and neurobiology. –
673 Cornell University Press, New York.
674 Hunt, J., Brooks, R., Jennions, M.D., Smith, M.J., Bentsen, C.L. & Bussiere, L.F.
675 (2004). High-quality male field crickets invest heavily in sexual display but die
676 young. – Nature 432:1024-1027.

677 Korner-Nievergelt, F., Roth, T., Von Felten, S., Guélat, J., Almasi, B. & Korner-
678 Nievergelt, P. (2015). Bayesian data analysis in ecology using linear models with
679 R, BUGS, and Stan. – Academic Press, Cambridge.
680 Kortet, R. & Hedrick, A. (2007). A behavioural syndrome in the field cricket *Gryllus*
681 *integer*: intrasexual aggression is correlated with activity in a novel environment. –
682 Biol J Linn Soc Lond 91(3):475-482.
683 Mazué, G.P., Dechaume-Moncharmont, F.X. & Godin, J.G.J. (2015). Boldness–
684 exploration behavioural syndrome: interfamily variability and repeatability of
685 personality traits in the young of the convict cichlid (*Amatitlania siquia*). – Behav.
686 Ecol. 26(3):900-908.
687 Montealegre-Z, F., Jonsson, T. & Robert, D. (2011). Sound radiation and wing
688 mechanics in stridulating field crickets (Orthoptera: Gryllidae). – J. Exp. Biol.
689 214:2105-2117.
690 Montealegre-Z, F., Windmill, J.F.C., Morris, G.K. & Robert, D. (2009). Mechanical
691 phase shifters for coherent acoustic radiation in the stridulating wings of crickets:
692 the plectrum mechanism. – J. Exp. Biol. 212(2):257-269.
693 Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non- Gaussian
694 data: a practical guide for biologists. – Biol. Rev. 85(4):935-956.
695 Naguib, M., Kazek, A., Schaper, S.V., Van Oers, K. & Visser, M.E. (2010). Singing
696 activity reveals personality traits in great tits. – Ethology 116(8):763-769.
697 Naguib, M., van Rooij, E.P., Snijders, L. & Van Oers, K. (2016). To sing or not to sing:
698 seasonal changes in singing vary with personality in wild great tits. – Behav. Ecol.
699 27(3):932-938.

Nandi, D. & Balakrishnan, R. (2013). Call intensity is a repeatable and dominant acoustic feature determining male call attractiveness in a field cricket. – Anim. Behav. 86(5):1003-1012.

Nityananda, V. & Balakrishnan, R. (2008). Leaders and followers in katydid choruses in the field: call intensity, spacing and consistency. – Anim. Behav. 76(3):723-735.

Pascoal, S., Cezard, T., Eik-Nes, A., Gharbi, K., Majewska, J., Payne, E., Ritchie, M.G., Zuk, M. & Bailey, N.W. (2014). Rapid convergent evolution in wild crickets. – Curr. Biol. 24:1369-1374.

Peig, J. & Green, A.J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – Oikos 118(12):1883-1891.

R Core Team (2018). R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna.

Rayner, J.G., Aldridge, S., Montealegre, Z.F. & Bailey, N.W. (2019). A silent orchestra: convergent song loss in Hawaiian crickets is repeated, morphologically varied, and widespread. – Ecology 100(8):e02694.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. – Biol. Rev. 82 (2):291-318.

Robillard, T., Grandcolas, P. & Desutter-Grandcolas, L. (2007). A shift toward harmonics for high-frequency calling shown with phylogenetic study of frequency spectra in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae). – Can. J. Zool. 85(12):1264-1275.

723 Robillard, T. & Tan, M.K. (2013). A taxonomic review of common but little known
724 crickets from Singapore and the Philippines (Insecta: Orthoptera: Eneopterinae). –
725 Raffles Bull. Zool. 61(2):705-725.
726 Rodriguez-Munoz, R., Bretman, A., Slate, J., Walling, C.A. & Tregenza, T. (2010).
727 Natural and sexual selection in a wild insect population. – Science 328:1269-1272.
728 Rodríguez, R.L., Araya-Salas, M., Gray, D.A., Reichert, M.S., Symes, L.B., Wilkins,
729 M.R., Safran, R.J. & Höbel, G. (2015). How acoustic signals scale with individual
730 body size: common trends across diverse taxa. – Behav. Ecol. 26(1):168-177.
731 Römer, H., Lang, A. & Hartbauer, M. (2010). The signaller's dilemma: A cost–benefit
732 analysis of public and private communication. – PLoS ONE 5(10):e13325.
733 Rose, J., Cullen, D.A., Simpson, S.J. & Stevenson, P.A. (2017). Born to win or bred to
734 lose: aggressive and submissive behavioural profiles in crickets. – Anim. Behav.
735 123:441-450.
736 Sakaluk, S.K. (1990). Sexual selection and predation: balancing reproductive and
737 survival needs. – In: Insect defences: Adaptive mechanisms and strategies of prey
738 and predators (Evans, D.L. & Schmidt, J.O., eds.). State University of New York
739 Press, New York, p. 63-90.
740 Sakaluk, S.K. & Belwood, J.J. (1984). Gecko phonotaxis to cricket calling song – a case
741 of satellite predation. – Anim. Behav. 32:659-662.
742 Santostefano, F., Wilson, A.J., Araya-Ajoy, Y.G. & Dingemanse, N.J. (2016).
743 Interacting with the enemy: indirect effects of personality on conspecific aggression
744 in crickets. – Behav. Ecol. 27(4):1235-1246.

745 Scheuber, H., Jacot, A. & Brinkhof, M.W. (2003). Condition dependence of a
746 multicomponent sexual signal in the field cricket *Gryllus campestris*. – Anim.
747 Behav. 65(4):721-727.
748 Schielzeth, H. (2010). Simple means to improve the interpretability of regression
749 coefficients. – Methods Ecol. Evol 1(2):103-7113.
750 Schöneich, S. (2020). Neuroethology of acoustic communication in field crickets - from
751 signal generation to song recognition in an insect brain. – Prog. Neurobiol.
752 194:101882
753 Schöneich, S. & Hedwig, B. (2010). Hyperacute directional hearing and phonotactic
754 steering in the cricket (*Gryllus bimaculatus* DeGeer). – PLoS ONE 5(12):e15141.
755 Schöneich, S. & Hedwig, B. (2010). Cellular basis for singing motor pattern generation
756 in the field cricket (*Gryllus bimaculatus* DeGeer). – Brain Behav. 2(6):707-725.
757 Schöneich, S. & Hedwig, B. (2017). Neurons and networks underlying singing
758 behaviour. – In: The cricket as a model organism (Horch, H.W., Mito, T., Popadić,
759 A., Ohuchi H. & Noji, S., eds.). Springer Japan, Tokyo, p. 141-153.
760 Schuster, A.C., Carl, T. & Foerster, K. (2017). Repeatability and consistency of
761 individual behaviour in juvenile and adult Eurasian harvest mice. – Sci. Nat. 104(3-
762 4):1-14.
763 Shaw, K.L. & Herlihy, D.P. (2000). Acoustic preference functions and song variability
764 in the Hawaiian cricket *Laupala cerasina*. – Proc. Royal Soc. B 267(1443):577-
765 584.
766 Sih, A., Bell, A. & Johnson, J.C. (2004). Behavioural syndromes: an ecological and
767 evolutionary overview. – Trends Ecol. Evol. 19(7):372-378.

768 Simmons, L.W. (1988). The calling song of the field cricket, *Gryllus bimaculatus* (De
769 Geer): constraints on transmission and its role in intermale competition and female
770 choice. – Anim. Behav. 36(2):380-394.
771 Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: a meta-
772 analysis. – Behav. Ecol. 19(2):448-455.
773 Stahlschmidt, Z., O'Leary, M.E. & Adamo, S. (2014). Food limitation leads to risky
774 decision making and to tradeoffs with oviposition. – Behav. Ecol. 25(1):223-227.
775 Stahlschmidt, Z.R. & Chang, E. (2021). Body condition indices are better surrogates for
776 lean mass and water content than for body fat content in an insect. – J. Zool.
777 315(2):131-137.
778 Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and
779 variance decomposition by generalised linear mixed- effects models. – Methods
780 Ecol. Evol 8:1639-1644.
781 Symes, L.B., Martinson, S.J., Kernan, C.E. & ter Hofstede, H.M. (2020). 'Sheep in
782 wolves' clothing: prey rely on proactive defences when predator and non-predator
783 cues are similar. – Proc. Royal Soc. B 287(1933):20201212.
784 Tan, M.K., Chang, C.-C. & Tan, H.T.W. (2018). Shy herbivores forage more efficiently
785 than bold ones regardless of information-processing overload. – Behav. Processes
786 149:52-58.
787 Tan, M.K. & Robillard, T. (2021). Highly diversified circadian rhythms in the calling
788 activity of eneopterine crickets (Orthoptera: Grylloidea: Gryllidae) from Southeast
789 Asia. – Bioacoustics. https://doi.org/10.1080/09524622.2021.1973562
790 Tan, M.K. & Robillard, T. (2021). Population divergence in the acoustic properties of
791 crickets during the COVID-19 pandemic. – Ecology 102(7):e03323.

792 Tan, M.K., Malem, J., Legendre, F., Dong, J., Baroga-Barbecho, J.B., Yap, S.A.,
793 Wahab, R.A., Japir, R., Chung, A.Y.C. & Robillard, T. (2021). Phylogeny,
794 systematics and evolution of calling songs of the Lebinthini crickets (Orthoptera,
795 Grylloidea, Eneopterinae), with description of two new genera. – Syst. Entomol..
796 https://doi.org/10.1111/syen.12510
797 Tan, M.K. & Tan, H.T.W. (2019). Individual- and population-level personalities in a
798 floriphilic katydid. – Ethology 125(2):114-121.
799 ter Hofstede, H.M., Schöneich, S., Robillard, T. & Hedwig, B. (2015). Evolution of a
800 communication system by sensory exploitation of startle behaviour. – Curr. Biol.
801 25(24):3245-3252.
802 Torsekar, V.R., Isvaran, K. & Balakrishnan, R. (2019). Is the predation risk of mate-
803 searching different between the sexes? – Evol. Ecol 33(3):329-343.
804 Wagner, W.E. & Hoback, W.W. (1999). Nutritional effects on male calling behaviour in
805 the variable field cricket. – Anim. Behav. 57(1):89–95.
806 Walker, T.J. (1962). Factors responsible for intraspecific variation in the calling songs
807 of crickets. – Evolution 16(4):407-428.
808 Wat, K.K., Banks, P.B. & McArthur, C. (2020). Linking animal personality to problem-
809 solving performance in urban common brushtail possums. – Anim. Behav. 162:35-
810 45.
811 Wey, T.W., Réale, D. & Kelly, C.D. (2019). Developmental and genetic effects on
812 behavioural and life- history traits in a field cricket. – Ecol. Evol, 9(6):3434-3445.
813 Wilson, A.D. & Godin, J.G.J. (2009). Boldness and behavioural syndromes in the
814 bluegill sunfish, *Lepomis macrochirus*. – Behav. Ecol. 20(2):231-237.

Wilson, A.D., Whattam, E.M., Bennett, R., Visanuvimol, L., Lauzon, C. & Bertram, S.M. (2010). Behavioural correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, *Acheta domesticus*. – Behav. Ecol 64(5):703-715.

Zuk, M. & Kolluru, G.R. (1998). Exploitation of sexual signals by predators and parasitoids. – Q Rev Biol 73(4):415-438.

Zuk, M., Rebar, D. & Scott, S.P. (2008). Courtship song is more variable than calling song in the field cricket *Teleogryllus oceanicus*. – Anim. Behav. 76(3):1065–1071.

Zuur, A.F., Ieno, E. N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol 1:3–4.

Zuur, A.F. & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. – Methods Ecol. Evol 7:636–645.

827

828 **Table 1.** Model summaries on the inter- and intra-individual variations in different

829 measures of call properties for *L. bitaeniatus*. R^2_m = marginal R^2, R^2_c = conditional R^2. *

830 denotes a strong effect.

Responses	**Covariates**	**Parameters**	**SE**	***t/Z* - values**
Call duration (R^2_m = 0.00, R^2_c = 0.26)	*Fixed effect*	*Estimate*		
	Intercept	0.716	0.038	18.99*
	Time (hour of the day)	0.004	0.016	0.27
	Ambient temperature	−0.020	0.033	−0.58
	Scaled body index	0.006	0.046	0.14
Number of clicks R^2_m = 0.00, R^2_c = 0.20	*Fixed effect*	*Estimate*		
	Intercept	2.59	0.10	25.6
	Time (hour of the day)	0.051	0.051	0.98
	Ambient temperature	−0.031	0.108	−0.29
	Scaled body index	0.006	0.130	0.05
Trill duration (R^2_m = 0.03, R^2_c = 0.34)	*Fixed effect*	*Estimate*		
	Intercept	1.54	0.04	41.2*
	Time (hour of the day)	0.006	0.014	0.40

Responses	Covariates	Parameters	SE	*t/Z* - values
	Ambient temperature	−0.028	0.030	−0.94
	Scaled body index	0.056	0.044	1.27
Syllable period (R^2_m = 0.11, R^2_c = 0.39)	*Fixed effect*	*Estimate*		
	Intercept	1.54	0.004	341.4*
	Time (hour of the day)	−0.003	0.002	−1.81
	Ambient temperature	−0.008	0.004	−2.07*
	Scaled body index	−0.003	0.005	−0.54
Dominant frequency (R^2_m = 0.06, R^2_c = 0.90)	*Fixed effect*	*Estimate*		
	Intercept	1.27	0.01	186.0*
	Time (hour of the day)	−0.002	0.000	−2.71*
	Ambient temperature	0.004	0.002	2.49*
	Scaled body index	0.004	0.007	0.56

831

832 **Table 2.** Model summaries on the inter- and intra-individual variations in different
833 measures of explorative behaviours for *L. bitaeniatus*. R^2_m = marginal R^2, R^2_c =
834 conditional R^2. * denotes a strong effect.

Responses	Covariates	Parameters	SE	*t/Z* - values

Responses	**Covariates**	**Parameters**	**SE**	***t/Z* - values**
Number of zones explored (R^2_m = 0.01, R^2_c = 0.57)	*Fixed effect*	*Estimate*		
	Intercept	0.38	0.53	0.72
	Position of arena within platform	−0.25	0.49	−0.51
	Scaled body index	0.22	0.43	0.51
	Trial number	−0.01	0.18	−0.06
Total distance covered (R^2_m = 0.10, R^2_c = 0.33)	*Fixed effect*	*Estimate*		
	Intercept	221.7	61.0	3.64*
	Position of arena within platform	−72.2	72.2	−1.00
	Scaled body index	91.3	43.6	2.10*
	Trial number	30.0	26.5	1.13

835

836 **Table 3.** Summary of the mean and credible intervals (in brackets) of the correlations
837 between the explorative behaviours and call properties in *L. bitaeniatus* (N = 17 males)
838 based on a multivariate mixed effects model of these traits.

	Total distance covered	Call duration	Syllable period
Total distance covered	—	−0.18 (−0.49, 0.82)	−0.39 (−0.89, 0.19)
Call duration		—	−0.26 (−0.85, 0.35)
Syllable period			—

839

Figure legends

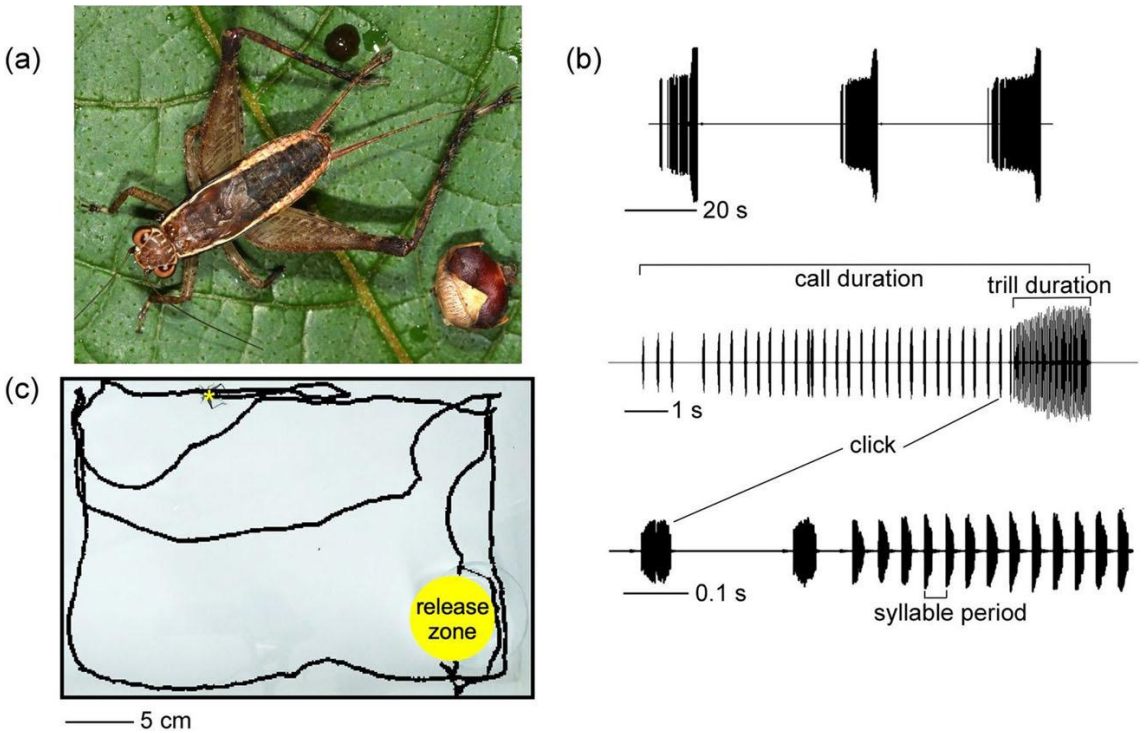


Figure 1. *Lebinthus bitaeniatus*. (a) Photograph of an adult male. (b) Microphone recording of the calling song (top: three echemes, middle: one echeme, bottom: a section of an echeme). (c) Top-view of the test arena for video-recordings of exploration behaviour is shown with an example trace of the movement track for one individual over 40 min each (yellow circle: release zone; yellow star: cricket position at the end of the test).

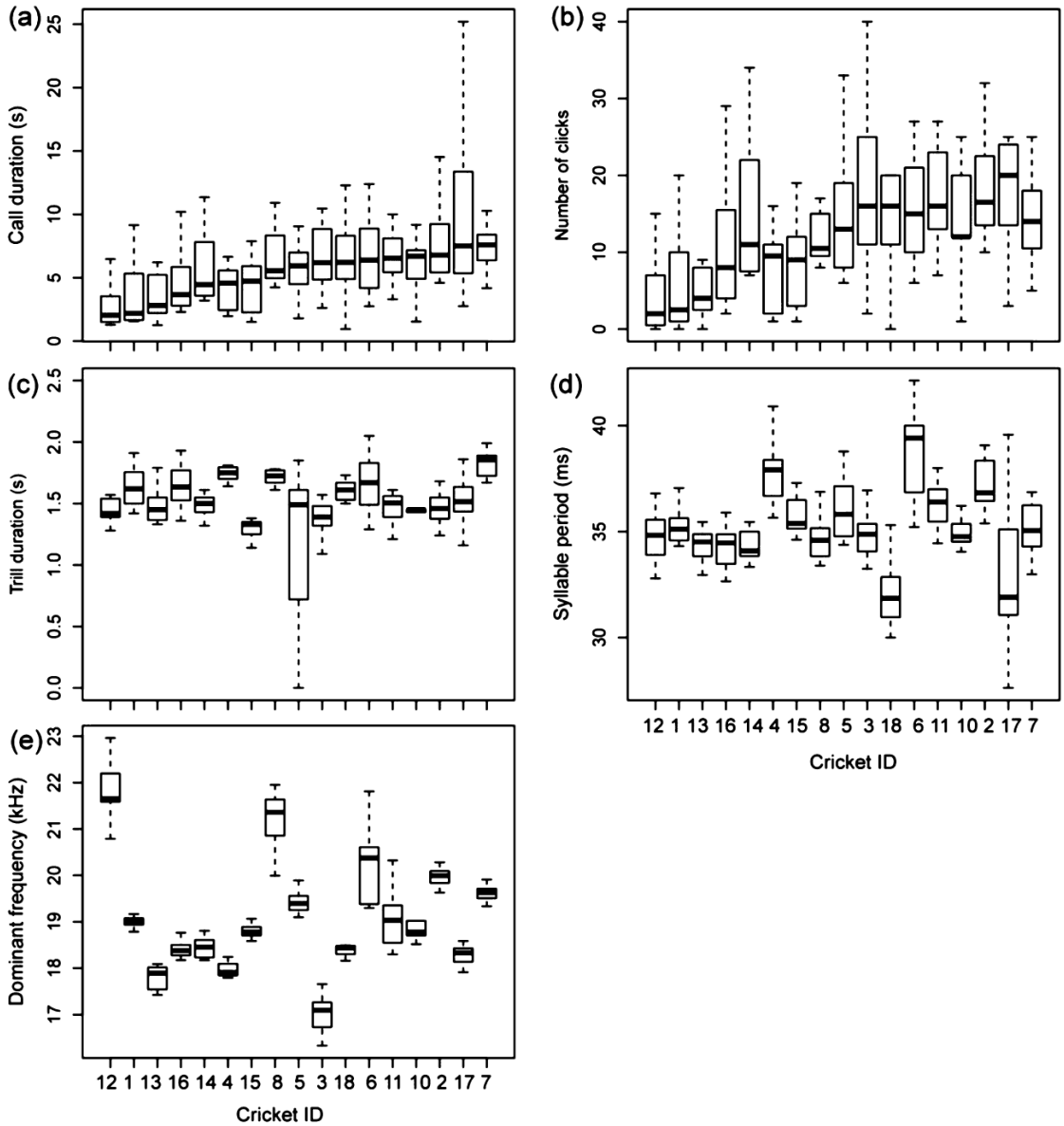
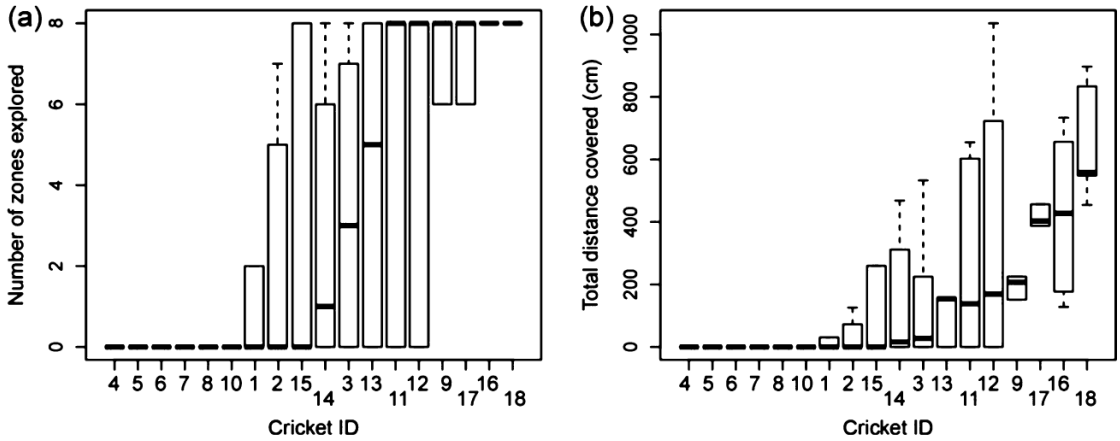
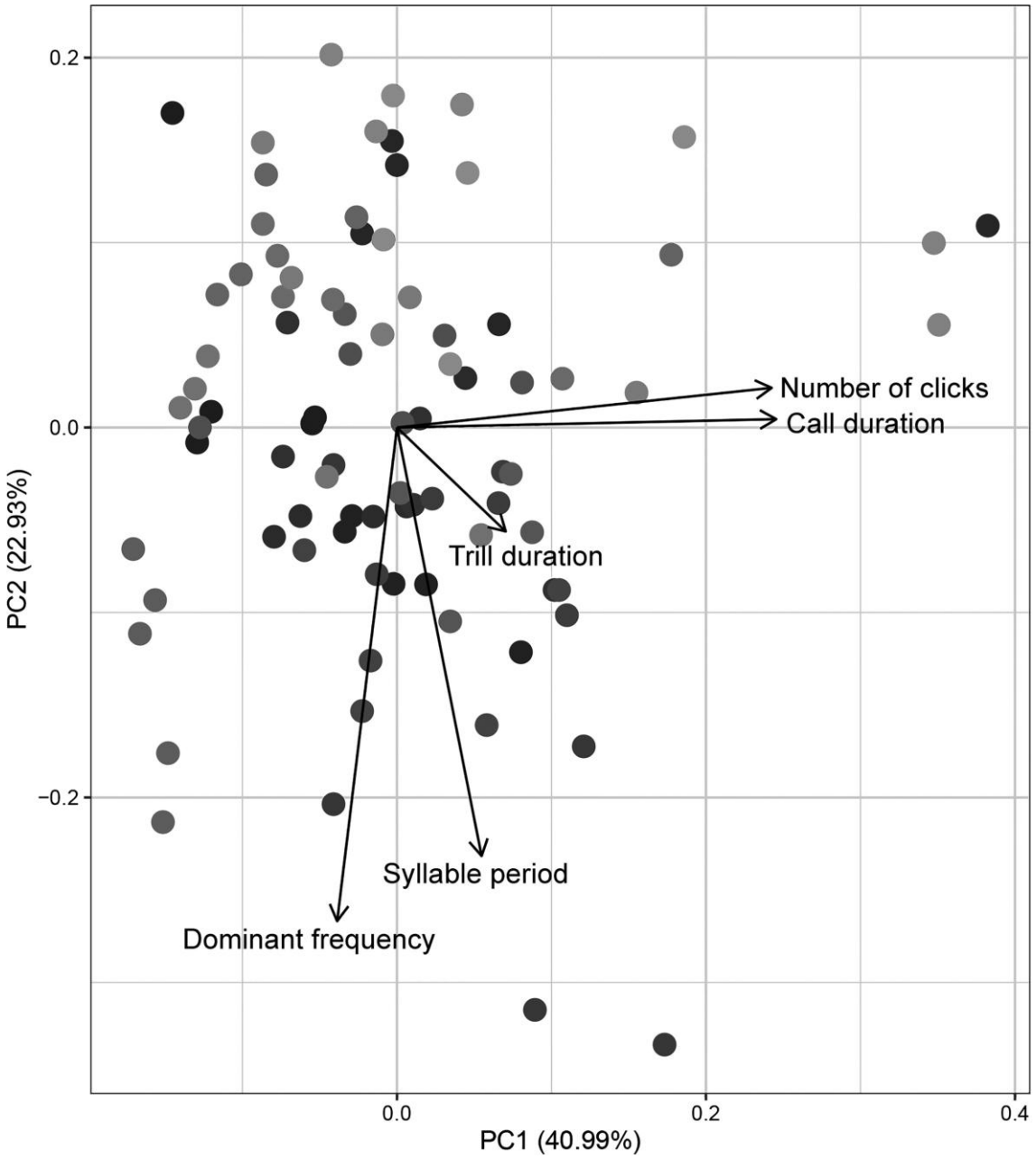


Figure 2. Boxplots show differences in the call properties of individual *L. bitaeniatus* males. Thick horizontal bar shows the median; lower and upper margin of the box indicate the inter-quartile range and whiskers refer to minimum and maximum data points.



855 **Figure 3.** Boxplots show differences in the exploratory behaviour between individual *L.*
856 *bitaeniatus* males. Thick horizontal bar shows the median; lower and upper margin of
857 the box indicate the inter-quartile range and whiskers refer to minimum and maximum
858 data points.
859



860 **Figure 4.** Principal component analysis of the five repeatable call properties for *L.*
861 *bitaeniatus* males shows that number of clicks and call duration are strongly correlated
862 and can be summarised along the first component (PC1). Dominant frequency and
863 syllable period can be explained along the second component (PC2). Data for different
864 cricket individuals are represented with points of different shades of grey.