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Effects of Anthropogenic Noise on Mating Behavior and Fitness

Abstract

When environments change rapidly, adaptive phenotypic plasticity can ameliorate negative effects of environmental change on survival and reproduction. Recent evidence, however, suggests that plastic responses to human induced environmental change are often maladaptive or insufficient to overcome novel selection pressures. Anthropogenic noise is a ubiquitous and expanding disturbance with demonstrated effects on fitness-related traits of animals like stress responses, foraging, vigilance, and pairing success. Elucidating the lifetime fitness effects of noise has been challenging because long-lived vertebrate systems are typically studied in this context. In both chapters described herein, I reared field crickets, *Teleogryllus oceanicus*, in masking traffic noise, traffic noise from which we removed frequencies that spectrally overlap with the crickets' mate location song (non-masking), or silence. In chapter 1, I tested female mate location ability at reproductive maturity under one of the same three acoustic conditions (masking, non-masking, silence). We found that exposure to noise during rearing hindered female location of mates, regardless of the acoustic environment at testing. Females reared in masking noise took 80% longer than females reared in silence to locate a simulated singing male who was < 1m away. In chapter 2, I follow noise stressed invertebrates throughout their lives, assessing a comprehensive suite of life history traits, and ultimately, lifetime number of surviving offspring, for the first time. I found that exposure to noise extended development time (delaying maturity) and reduced adult lifespan; crickets exposed to masking noise spent 23% more time in juvenile stages and 13% less time as reproductive adults than those exposed to no traffic noise. Chronic lifetime exposure to noise, however, did not affect lifetime reproductive output (number of eggs or surviving offspring), perhaps because mating provided females a substantial longevity benefit. Impaired mate location ability and changed life histories can be added to a growing list of fitness costs associated with anthropogenic noise, alongside reductions in pairing success, nesting success, and offspring survival. I encourage researchers to consider effects of anthropogenic disturbances on growth, survival, and reproductive traits simultaneously because plastic responses of different traits are likely to amplify or nullify one another, influencing fitness.

Document Type

Thesis

Degree Name

M.S.

Department

Biological Sciences

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Keywords

Anthropogenic noise, Impaired mate location ability, *Teleogryllus oceanicus*

Subject Categories

Behavior and Ethology | Entomology | Other Ecology and Evolutionary Biology

Publication Statement

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Effects of Anthropogenic Noise on
Mating Behavior and Fitness

A Thesis

Presented to

the Faculty of Natural Sciences and Mathematics

University of Denver

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Gabrielle A. Gurule-Small

June 2018

Advisor: Dr. Robin Tinghitella

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Abstract

When environments change rapidly, adaptive phenotypic plasticity can ameliorate negative effects of environmental change on survival and reproduction. Recent evidence, however, suggests that plastic responses to human induced environmental change are often maladaptive or insufficient to overcome novel selection pressures. Anthropogenic noise is a ubiquitous and expanding disturbance with demonstrated effects on fitness-related traits of animals like stress responses, foraging, vigilance, and pairing success. Elucidating the lifetime fitness effects of noise has been challenging because long-lived vertebrate systems are typically studied in this context. In both chapters described herein, I reared field crickets, *Teleogryllus oceanicus*, in masking traffic noise, traffic noise from which we removed frequencies that spectrally overlap with the crickets' mate location song (non-masking), or silence. In chapter 1, I tested female mate location ability at reproductive maturity under one of the same three acoustic conditions (masking, non-masking, silence). We found that exposure to noise during rearing hindered female location of mates, regardless of the acoustic environment at testing. Females reared in masking noise took 80% longer than females reared in silence to locate a simulated singing male who was <1m away. In chapter 2, I follow noise stressed invertebrates throughout their lives, assessing a comprehensive suite of life history traits, and ultimately, lifetime number of surviving offspring, for the first time. I found that exposure to noise extended development time (delaying maturity) and reduced adult

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Acknowledgments

I would like to first and most importantly thank my advisor, Robin Tinghitella for trusting in me as a Masters student, helping me conceptualize this project, aiding in procuring funding for this project, and the compilation of this manuscript as well as being an incredibly brilliant and supportive mentor. Additionally, my committee, Shannon Murphy, Anna Sher, and Erica Larson, has been essential in providing input that has led to the success of these projects and publication of these chapters. The DU Ecology and Evolutionary Biology (DUEEB) group has given amazing feedback on both of these chapters. I would like to extend thanks to my fellow graduate students for extensive advice on the preparation of these chapters, specifically Whitley Lehto and Mayra Vidal. I thank the three undergraduate researchers for their help in collecting project data, Anne Bowen, Jared Smith, and Caroline Smith. Finally, I want to acknowledge the groups responsible for funding this thesis: the University of Denver, Sigma Xi, and the Orthopterists' Society.

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CHAPTER 1: Developmental experience with anthropogenic noise hinders adult mate location in an acoustically signaling invertebrate

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Introduction

Adult traits, including behaviour, are shaped by ecological and social environments experienced during development and beyond (Snell-Rood 2013). When adaptive, behavioural plasticity can reduce negative impacts of environmental change on individual fitness and enhance population persistence. Mating preferences and decisions are particularly plastic, varying, for instance, with risk encountered (Godin & Briggs 1996) and social experience (Bailey & Zuk 2008). Developmental experience alters adult mating behaviour in ways that likely reshape evolutionary trajectories (e.g. Kasumovic et al. 2012, Gillespie et al. 2014). Here we ask how developmental experience with anthropogenic noise impacts reproductive components of fitness at adulthood (Lampe et al. 2014), because noise transforms the mating environment (Barber et al. 2009).

Anthropogenic noise is a major and expanding human-induced global pollutant that can have dramatic physiological (reviewed in Wright et al. 2007, Kight & Swaddle 2011, Kunc et al. 2016) and behavioural [reviewed in Barber et al. 2009, Wright et al. 2007, Kunc et al. 2016, Morley et al. 2014) impacts on animals. Noise could influence

reproductive success through effects on signals and signaling strategies (e.g. Lampe et al. 2014, Orci et al. 2016), contest behaviour, location of mates and mate preferences (e.g. Cunnington & Fahrig 2013), nesting or pairing success (e.g. Habib et al. 2007, Francis et al. 2011A), and parental investment (e.g. Nedelec et al. 2017). Much research has focused on whether signallers can improve detection in noisy environments (reviewed in Roca et al. 2016), but less attention has been paid to effects of noise on receivers (Simpson et al. 2016, Kern & Radford 2016, McMullen et al. 2014). Anthropogenic noise may impede receivers' ability to locate signallers if it impacts hearing development, distracts mate searchers, masks acoustic cues, or induces stress responses. Given this, we might expect receiver behaviour to depend on, and perhaps compensate for, experience with anthropogenic noise.

The taxonomic focus on vertebrate study systems in noise research (Morley et al. 2014, Roca et al. 2016, Shannon et al. 2015) limits our understanding of the effects of anthropogenic noise on reproductive success (but see Habib et al. 2007, Francis et al. 2011A, Simpson et al. 2016, Nedelec et al. 2017); this is likely because of logistical difficulties measuring their fitness. Yet, mating behaviour is key to the evolution of male signals, and to fitness more generally. Switching the focus to invertebrates offers advantages: invertebrates comprise most of the biodiversity on earth, are often small, have short generations, and can be lab-maintained under experimental conditions (Morley et al. 2014). We use a field cricket study system to ask 1) does pre-reproductive exposure to anthropogenic noise impact adults' ability to locate mates, and, if so, 2) does developing in noise improve performance in noisy environments?

Teleogryllus oceanicus lives in habitats ranging from urban lots in Australia to undisturbed fields on sparsely populated Pacific Islands. Traffic noise overlaps with the frequency of the calling and courtship songs males use to attract mates from afar and to entice them to mate once in close proximity (4-6kHz). Females are locomotory and search for stationary calling males <1m to >20m away in a matrix of grass and rocks. We manipulated pre-reproductive experience with traffic noise, rearing female *T. oceanicus* under masking noise (traffic noise that overlaps spectrally and temporally with male calling song; Appendix Figure 1), non-masking noise (traffic noise that does not overlap spectrally with male calling song), or silence, and then tested adult female location of mates under the same three acoustic environments in a fully factorial design.

Methods

To produce masking and non-masking traffic noises, we recorded traffic noise at five Denver, Colorado, USA locations using a Marantz (PMD620MKII) digital recorder and Shure SM58 microphone. Locations captured varied vehicular types, volumes, and speeds. We compiled two representative 30s clips from each of the five locations into a single continuous five-minute track (Appendix Figure 1A). We produced a non-masking traffic noise by filtering out frequencies from 3-6kHz using the “filter” command in RavenPro14 (Appendix Figure 1B).

We pulled females from our lab stock (established in 2014 from Mo'orea, French Polynesia) when sex could be reliably identified and the hearing organs are apparent, and randomly assigned them to one of three acoustic rearing environments: masking (n = 44),

non-masking (n = 43), or silence (n = 42). We broadcast the masking or non-masking noise inside the incubators (Percival I36VLC8) crickets were reared in for 14 hours a day (1 hour pre-dawn to 1 hour post-dusk, mimicking traffic patterns) from EcoXBT wireless speakers. We rotated treatments among incubators every two weeks and rotated container positions within incubators during cleanings. Because incubators produce background noise (76-92dBA), we kept them off during the entire experiment, but maintained a photo-reversed 12 hour light-dark cycle. The temperature fluctuated between light and dark phases (21.2°C-30.5°C at the light source) but did not exceed those experienced in nature. We reared females in 64oz Tupperware containers until sexual maturity with rabbit food *ad lib*, egg carton shelters and fresh water (Bailey & Zuk 2008). Females spent 15.5 ± 0.7 days in their rearing treatment prior to eclosion, regardless of treatment ($F_{2,126} = 2.58$, $p = 0.08$, Appendix Figure 2).

We conducted phonotaxis (mate location) trials in a randomly assigned acoustic environment (masking, non-masking, or silent) when females were seven days post-eclosion. Phonotaxis trials took place inside of a square arena 1.45m^2 in size, with a 10cm grid on its floor, located within a 2.3m x 2m room with acoustic foam-lined walls. We conducted phonotaxis trials 0-7.5 hours post-dusk (mean = 2.9 ± 0.2 hours). Time of testing did not differ among rearing ($F_{2,126} = 1.81$, $p = 0.17$) or phonotaxis environments ($F_{2,126} = 1.50$, $p = 0.23$). In each trial we placed the focal female at the centre of the arena under an inverted plastic cup for 2 minutes, after which we simultaneously released the female and projected 1) a strongly preferred *T. oceanicus* calling song (Appendix Figure 3) from a speaker in one randomly assigned corner and 2) the noise treatment from a

speaker suspended 141cm above the arena. Both the song and noise treatment were broadcast at realistic volumes (70dBA from the female's starting point) using EcoXBT wireless speakers. We measured the time to first movement, whether or not a female contacted the speaker broadcasting song, contact time (the difference between start of trial and touching the speaker), search time (the difference between time to first movement and contact time), and the number of grid lines females crossed (as a measure of search path). Trials lasted 5 minutes. Females who did not contact the speaker were assigned the maximum contact time.

We tested if experience with noise alters location of mates and whether developing in noise prepares females for mate searching in noisy environments using 2-way ANCOVAs in JMP Pro 13.0. Rearing environment, phonotaxis environment, and their interaction were main effects, and female pronotum width (size) was a covariate. Size did not differ across rearing environments ($p = 0.76$). We also considered whether females reared under noise shifted their mate searching behaviour temporally using ANCOVAs that included rearing environment, phonotaxis testing time (time post dusk) and their interaction as main effects, and size as a covariate. Continuous outcome variables were natural log transformed to meet assumptions of normality. We ran logistic regressions (size = covariate) to address whether rearing or phonotaxis environments affected likelihood of contacting the speaker because the parameter estimates in the full model were unstable.

Results

Rearing environment was the most important predictor of adult female mate location behaviour (Table 1). Differences in contact time (Figure 1A) were due to the time it took females to initially move (Figure 1B), rather than the search time or search path (grids crossed) (Table 1). Females reared in masking noise took 209% longer to begin searching (Figure 1B), and 81% longer to reach the signalling male than females reared without traffic noise (Figure 1A). Surprisingly, the acoustic environment experienced during phonotaxis never influenced mate location behaviour (Table 1; Appendix Figure 4), and we found no interactions between rearing environment and phonotaxis environment (Table 1). Females who were larger were slower to begin moving and crossed fewer grids during the search (Table 1; Appendix Figure 5). Female mate location behaviour did not depend on phonotaxis testing times (time post dusk; all $p > 0.39$), nor did the interaction between rearing environment and phonotaxis testing times (all $p > 0.11$, Table S1). Of the 129 females, 120 contacted the speaker. Whether or not females contacted the speaker did not depend on rearing environment ($\chi^2_2 = 5.77$, $p = 0.12$) or phonotaxis environment ($\chi^2_2 = 3.21$, $p = 0.36$). All data have been deposited in Dryad (Gurule-Small & Tinghitella 2018b).

Table 1. ANCOVAs testing effects of rearing and phonotaxis noise environments on female location of mates.

Outcome Variable	Effect	F	d.f.	p
Time to first movement	Rearing Environment	3.38	2,126	0.038
	Phonotaxis Environment	0.52	2,126	0.596
	Rearing x Phonotaxis	0.61	4,120	0.658
	Pronotum Width	5.30	1,128	0.023
Time to contact speaker	Rearing Environment	3.18	2,126	0.045
	Phonotaxis Environment	1.42	2,126	0.247
	Rearing x Phonotaxis	1.12	4,120	0.353
	Pronotum Width	0.60	1,128	0.808
Search time	Rearing Environment	1.50	2,126	0.226
	Phonotaxis Environment	0.81	2,126	0.445
	Rearing x Phonotaxis	1.12	4,120	0.351
	Pronotum Width	3.21	1,128	0.076
Grids crossed (search path)	Rearing Environment	2.49	2,126	0.087
	Phonotaxis Environment	1.22	2,126	0.299
	Rearing x Phonotaxis	0.60	4,120	0.662
	Pronotum Width	4.26	1,128	0.041

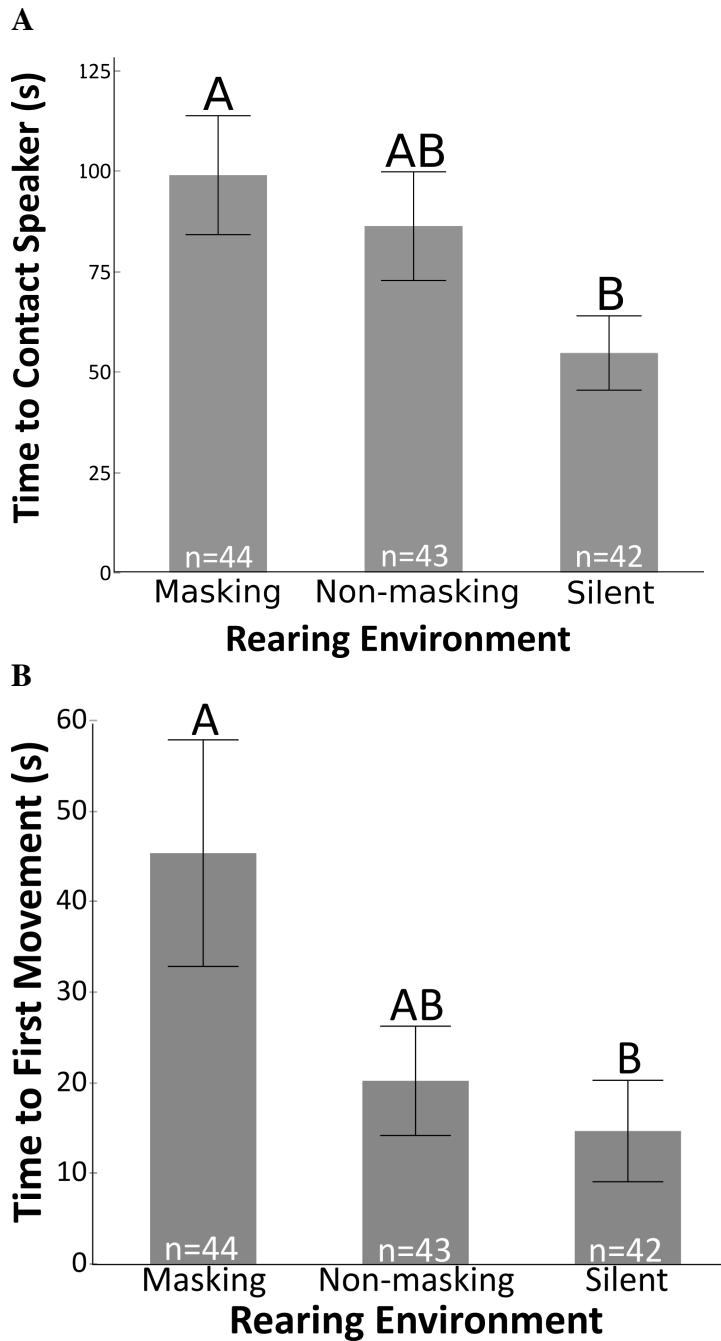


Figure 1: Adult female mate location responses by rearing environment. A) Time to first movement and B) Total time to contact the speaker from the start of the trial. Non-transformed means and standard errors are shown for ease of interpretation. Letters indicate statistically significant differences according to a Tukey's test ($P < 0.05$).

Discussion

Anthropogenic noise experienced prior to sexual maturity hindered adult mate location behaviour, regardless of the acoustic environment encountered at the time of searching. Females reared in masking noise took >200% as long to move and >80% longer to contact a simulated calling male than females reared in silence. Effects of previous and sub-adult exposure to noise may be underappreciated because studies often test for immediate behavioural responses (i.e., vigilance or foraging) to projected noise or make comparisons across habitats that are regularly exposed to more or less anthropogenic noise (Shannon et al. 2015, but see Radford et al. 2016). While certainly valuable, such studies can miss effects of prior exposure altogether or confound previous and current experience. In general, we expect masking noise to affect both signals and receiver responses (Costello & Symes 2014), but organisms like singing insects that cannot alter their signal frequency plastically (Bennet-Clark 1998) or quickly leave undesired areas (Francis et al. 2011B) may suffer greater costs in noise, unless receiver behaviour can compensate.

Similar to our results (Figure 1; see also appendix), noise that masks a focal signal often elicits greater plastic and evolutionary change in signals and signalling behaviour than non-masking noise (Roca et al. 2016, Slabbekoorn & Peet 2003). The mechanism underlying reduced mate location ability of females reared in masking noise is currently unknown, but we are testing several possibilities. There are strong effects of juvenile experience with sexual signals (or lack thereof) on adult mating decisions in this species (Bailey & Zuk 2008), and masking noise might decrease signal detection during

development, limiting learning opportunities, for instance. Alternative explanations for our results include generalized stress responses, physiological damage, or impaired hearing development stemming from juvenile experience with masking noise (Barber et al. 2009).

We were surprised to find no effect of phonotaxis environment on female location of mates, though there is precedent for this in the literature (e.g. Bennet-Clark 1998). Nearly all females eventually located the speaker broadcasting song, which lends support to the hypothesis that juvenile exposure to masking noise produced a more generalized physiological or learning affect that hindered location of mates, but that the broadcast noise did not completely eliminate females' ability to localize song.

With repeated adult exposure to noise, females may become tolerant, reducing the costs of developing in noise. However, our experimental design minimized factors other than noise that might impede female mate location. Animals searched for a highly preferred simulated mate who was <1m away and experienced noise during their inactive period (daylight hours) for roughly two weeks prior to sexual maturity. Costs of developing in noise might be magnified by longer-term exposure, a search environment that includes males of varying attractiveness at more realistic (longer) search distances, and/or unpredictable onset and cessation of noise disturbances.

CHAPTER 2: Life history consequences of developmental experience with anthropogenic noise

Introduction

Experience-mediated plasticity can provide a buffer that allows organisms to survive and reproduce when adaptive evolution cannot keep pace with environmental change (Tuomainen & Candolin 2011, Van Buskirk 2012). However, recent evidence suggests that responses of animals to human-induced change are often maladaptive (e.g. ecological and evolutionary traps; Schlaepfer et al. 2002, Battin 2004) or insufficient to overcome novel selection pressures (Van Buskirk 2012, van Baaren & Candolin 2018), perhaps because human-induced selection pressures are often stronger than, and do not resemble, those experienced historically (Ghalambor et al. 2007, Hendry et al. 2008). The inability to adequately respond to rapid and novel environmental change through plasticity or rapid evolution can lead to reductions in population size causing conservation concerns and even local extinction (Battin 2004, Parmesan 2006, Schwartz et al. 2006).

Anthropogenic disturbances lead to changes in life-history and reproductive traits that directly affect fitness. In some cases, plasticity increases fitness (e.g. Sol 2003, Levey et al. 2009), while in others plastic responses are maladaptive (e.g. Yamane & Gilman 2009, Gross et al. 2010). In still others, there is evidence that different traits

respond in different directions, to varying degrees, and interact with one another (e.g. Crispo et al. 2010). Plastic responses of multiple traits expressed over an individual's lifetime may be additive or multiplicative, compounding one another, or may act in different directions and to different degrees (as might be expected with trade-offs) resulting in less predictable fitness outcomes. For instance, anthropogenic change could reduce lifespan as well as reproductive opportunities and investment, making fitness effects compounding and negative. Conversely, environmental change could lead to compounding positive effects if it consistently increases survival and reproductive components of fitness. Another alternative is that anthropogenic stressors may nullify one another, if, for instance, they reduce adult lifespan, but increase reproductive investment. Thus, we would gain a more complete understanding of how, and the extent to which, animals respond adaptively to anthropogenic stressors if we understood how multiple fitness components interact with one another following environmental change.

Anthropogenic noise is a global pollutant with expansive reach; more than 83% of land in the continental United States is exposed to vehicular noise, for instance, including locations we might superficially consider to be protected from anthropogenic influence such as national parks and other areas with low human disturbance and population (Barber et al. 2009, Buxton et al. 2017). Human-created noise decreases environmental quality by degrading natural acoustic environments and changes community composition by excluding noise-sensitive species (Francis et al. 2009, Shannon et al. 2015). Recent work has shown that anthropogenic noise disrupts animal behavior, linking noise to alterations in foraging (e.g. Lagardere 1982, Luo et al. 2015; Shannon et al. 2014),

parental care (e.g. Picciulin et al. 2010), hormonal stress responses (e.g. Evans et al. 2001, Anderson et al. 2011), vigilance (e.g. Shannon et al. 2014), and offspring hatching success (e.g. Nedelec 2017). Noise is also implicated in changes to reproductive traits like sexual signals (e.g. Lampe et al. 2012), mate location ability (e.g. Gurule-Small and Tinghitella 2018a), and mate preferences or choosiness (e.g. Des Aunay et al. 2014, Reichert and Ronacher 2014) in acoustically signaling organisms. All of these changes in behavior and physiology may affect fitness, but despite recent progress, the mechanisms by which noise impacts animal survival and reproduction remain unclear (Kleist et al. 2018).

Some responses to noise increase fitness in noisy environments. For example, house sparrows exposed to noise have increased anti-predatory behavior (Meillere et al. 2015) and male grasshoppers that develop in relatively noisy environments produce calling songs with a frequency (or pitch) that is more detectable to females in those noisy environments (Lampe et al. 2014). Anurans (e.g., Cunnington & Fahrig 2013) and birds (e.g., Slabbekoorn & Peet 2003, Slabbekoorn 2013) have similar adaptive signaling responses that enhance mating success in noise. Conversely, some animal responses to noise are maladaptive. Developing in noise increases embryo mortality and slows growth rates of zebra finches (Potvin & MacDougall 2015), and signaling male tree crickets (Orci et al. 2016) and frogs (Kaiser et al. 2011) reduce calling effort under noisy conditions. Some effects are more clearly related to fitness. For instance, ovenbirds have reduced pairing success near human-created noise (Habib et al. 2007), and western bluebirds have reduced hatching success closer to compressor engines (Kleist et al.

2018). Frequently, however, researchers have investigated changes in fitness-related traits in isolation from other such traits or at a single ontogenetic stage, which can be misleading if such changes have consequences for other related traits and processes.

Until now, the overwhelming majority of noise research (>96%) has used vertebrate study systems and less than 2% has directly measured fitness consequences of anthropogenic noise (Shannon et al. 2016). We have learned some about the fitness effects of anthropogenic noise from vertebrate study systems (e.g. Habib et al. 2007, Halfwerk et al. 2011, Nedelec et al. 2017, Kleist et al. 2018), but our understanding is limited because it is difficult to measure multiple interacting components of fitness in long-lived vertebrates studied in the field. We are unaware of any work that follows noise stressed individuals throughout their entire lives, which is necessary to measure lifetime reproductive success, assess impacts of early life exposure, and make inferences about the population-level evolutionary consequences of noise (Kight and Swaddle 2011). Thus, we ask how anthropogenic noise affects a suite of interacting life history traits that affect fitness in an acoustically signaling invertebrate. The Pacific field cricket, *Teleogryllus oceanicus*, is an ideal study system as it is easily reared under manipulated laboratory conditions, has a 3-4 month adult lifespan, has high fecundity, and low frequency traffic noise masks (overlaps spectrally and temporally) the crickets' long distance mate location signal (Gurule-Small and Tinghitella 2018b). Previously, we assessed the impacts of developmental and adult experience with masking noise (which overlaps and non-masking traffic noise on mate location ability in this study system (Gurule-Small and Tinghitella 2018a). Masking noise overlapped spectrally and

temporally with the crickets' long-distance mate location song, and we digitally manipulated traffic recordings to remove the frequencies that overlap with the crickets' song in order to produce the non-masking traffic noise. In that study, we found that early life experience with masking traffic noise hindered adult females' mate location ability regardless of the noise environment in which mate location was tested, suggesting that developmental behavioral plasticity may be insufficient to overcome the negative effects of developing in traffic noise.

Our previous work demonstrated that developmental experience with noise strongly impacted adult reproductive behavior; thus, we focus here on how developing in noise influences lifetime reproductive success (fitness) through a comprehensive suite of interacting life history traits. We reared crickets in chronic masking traffic noise, non-masking traffic noise, or silence from the 2nd instar through death, and assayed growth and survival-related life history traits of both sexes (development time, survival to adulthood, adult size, adult lifespan) plus female reproductive characteristics (mating success, number of eggs laid, proportion eggs hatching). Our ultimate measure of fitness is lifetime number of surviving offspring. Assessing the impacts of both masking and non-masking noise on fitness allows us to determine whether any effects of noise on fitness stem from traffic noise overlapping spectrally with the crickets' sexual signal or more generally from noise (e.g., through distraction, stress etc). We ask 1) does developing in masking or non-masking anthropogenic noise alter cricket life history strategies through changes in growth, survival, and reproductive traits and 2) if so, how do these traits interact to amplify or nullify one another resulting in overall fitness

effects? To our knowledge, this is the first investigation of the impacts of noise that extends throughout the organisms' lifetime, rather than focusing on particular life stages. We hypothesize that fitness is negatively affected by chronic exposure to noise during development and beyond, and that different contributing traits will be differentially affected by anthropogenic noise, owing to underlying life history trade-offs.

Methods

To comprehensively assess the fitness consequences of traffic noise, we reared crickets in one of three alternative acoustic environments: masking traffic noise, non-masking traffic noise, or silence. The traffic noises broadcast in these environments were identical to those used in Gurule-Small & Tinghitella (2018a). In short, to produce masking and non-masking traffic noises, we recorded traffic noise at five Denver, Colorado, USA locations with varied traffic densities, amplitudes, and speeds using a Marantz (PMD620MKII) digital recorder and Shure SM58 microphone. We compiled two representative 30s recordings from each of the five locations into a single continuous five-minute track that was looped during treatment. We used the “filter” command in RavenPro14 to filter out frequencies that overlap with the crickets' song (from 3-6kHz) to produce the non-masking traffic noise.

We assigned juvenile crickets from an outbred population (established in 2014 from Mo'orea, French Polynesia) randomly to one of the three acoustic environments as early as can be done without causing mortality (2nd of 9 instars): masking ($n = 79$), non-masking ($n = 82$), or silence ($n = 73$). We assigned 2nd instar crickets from our

laboratory population to acoustic environments six times between June and December of 2017. We reared crickets inside of Percival I36VLC8 incubators, in which we broadcast one of the three acoustic treatments continuously from EcoXBT wireless speakers at 68-72 dBA 1m from the speaker, exposing animals to chronic traffic noise. To prevent incubator effects, we rotated treatments among the incubators every two weeks. Because they produce background noise (76-92 dBA), we kept the incubators off for the entire experiment, but maintained a 12 hour light-dark cycle using 40 watt lights on timers. The temperature fluctuated some between light and dark phases of the day (21.2°C-30.5°C at the light source), but did not exceed temperatures experienced by the animals in their natural habitats. We reared juvenile crickets in groups of 15-25 in 64oz Tupperware containers until they could be sexed, and provided them Fluker's cricket chow *ad lib*, egg carton shelters and fresh water. When the animals could be sexed, we isolated them, and housed each in an individual 16oz deli container with rabbit food *ad lib*, egg carton shelter, and water. We checked crickets daily in order to measure development time (number of days between being placed into an acoustic treatment and eclosion to sexual maturity), survival to adulthood (yes or no), size at adulthood (pronotum width), and adult lifespan (number of days between sexual maturity and death) for all crickets of both sexes.

To assess mating success, reproductive investment, and lifetime reproductive success under alternative noise treatments, we also paired a haphazardly chosen subset of adults from each treatment in no choice mating trials, giving each pair the opportunity to mate or not. We confirmed that females paired in mating trials did not differ from those

not paired in terms of development time (Student's t-test; $t = -1.467$, $df = 111$, $p = 0.15$). One week post-eclosion (when animals were sexually mature), we placed a focal female into a 16oz deli container with a randomly assigned male who was reared under the same acoustic environment, and placed the pair into the incubator broadcasting the same acoustic environment in which they were reared. We allowed the pair 48 hours to mate before the male was removed. After the mating opportunity, we provided females with moist cotton in which to lay eggs (egg pads) and replaced the egg pads weekly until the female's natural death. We determined whether a pair mated by assessing the presence of fertilized eggs in the egg pads, and we counted total number of eggs laid in the female's lifetime (across all of her egg pads) and determined how many of those eggs hatched by counting first instar offspring. This allowed us to capture each female's mating success, lifetime number of eggs laid (fecundity), the proportion of eggs that hatched, and lifetime number of surviving (first instar) offspring, which is our measure of overall fitness.

Statistical Analysis

We first addressed whether chronic exposure to masking or non-masking noise affected growth, survival, and reproduction related life history traits using mixed-effects ANCOVAs and binomial generalized linear mixed models (GLMM). We conducted separate mixed-effects ANCOVAs with each continuous measure (development time, adult lifespan, size at adulthood, number of eggs, proportion eggs hatching, lifetime number of surviving offspring) as an outcome variable. Models with development time, survival to adulthood, adult lifespan, or size at adulthood as outcome variables were

conducted on all crickets. The number of eggs, proportion eggs hatching, and lifetime number of surviving offspring models only applied to females who successfully mated during mating trials (see below). In the mixed-effects ANCOVAs addressing development time, adult lifespan, and adult size, the fixed effects included acoustic environment (masking, non-masking, or silence), sex, and the interaction between sex and acoustic environment. In the mixed-effects ANCOVAs addressing number of eggs, and proportion eggs surviving, the fixed effect was acoustic environment. The random effect in all mixed-effect ANCOVAs was a blocking variable, the date on which the 2nd instar crickets were randomly assigned to acoustic treatments (hereafter treatment date). For models examining effects on adult lifespan, number of eggs, proportion eggs surviving, and lifetime number of surviving offspring, we also included size (pronotum width) as a covariate. To meet assumptions of normality, we natural log-transformed number of eggs laid, proportion surviving offspring, and lifetime number of surviving offspring. There were four females who laid ≤ 20 eggs overall who were clear outliers on normal quantile plots and we removed these four from all models investigating female reproductive characteristics. When models yielded a significant fixed effect of acoustic environment, we performed post hoc pairwise comparisons of least square means using Tukey's HSD. We used binomial GLMMs to test for differences in survival to adulthood and mating success (mate or not) across noise treatments. Each model included acoustic environment as a fixed effect and the treatment date blocking variable as a random effect. We compared each binomial GLMM to a reduced null model that had no fixed effect, and determined statistical significance using chi-squared tests.

Having found effects of acoustic experience on both development time and adult lifespan, we became interested in whether adult lifespan was directly affected by noise, or if the effect of noise on adult lifespan was mediated by an effect of development time on adult lifespan (Figure 2). We used mediation modeling to address this question. Our mediation analysis included the mixed-effects ANCOVAs for development time and adult lifespan described above, a third model investigating effects of development time on adult lifespan (fixed = development time, sex; covariate = pronotum width; random = treatment date blocking variable), plus a final model that simultaneously considered the effects of acoustic experience and development time on adult lifespan (fixed = acoustic environment, development time, sex; covariate = pronotum width; random = treatment date). We were interested in the effect of acoustic environment, and in the mixed-effects ANCOVAs, the masking treatment was significantly different from the silent treatment with respect to both development time and adult lifespan. Thus, we report the parameter coefficients for masking versus silence. If the effect of experience with traffic noise on adult lifespan is fully mediated through changes in development time, we should find no significant effect of acoustic environment on adult lifespan, but an effect of development time in the model that contains both development time and acoustic environment as predictors. If the effect of experience with traffic noise is partially mediated through changes in development time, both effects should be significant when modeled together. And, if effects of noise on adult lifespan are independent of changes in development time, only acoustic environment should be a significant predictor of adult lifespan in a model that includes both acoustic environment and development time.

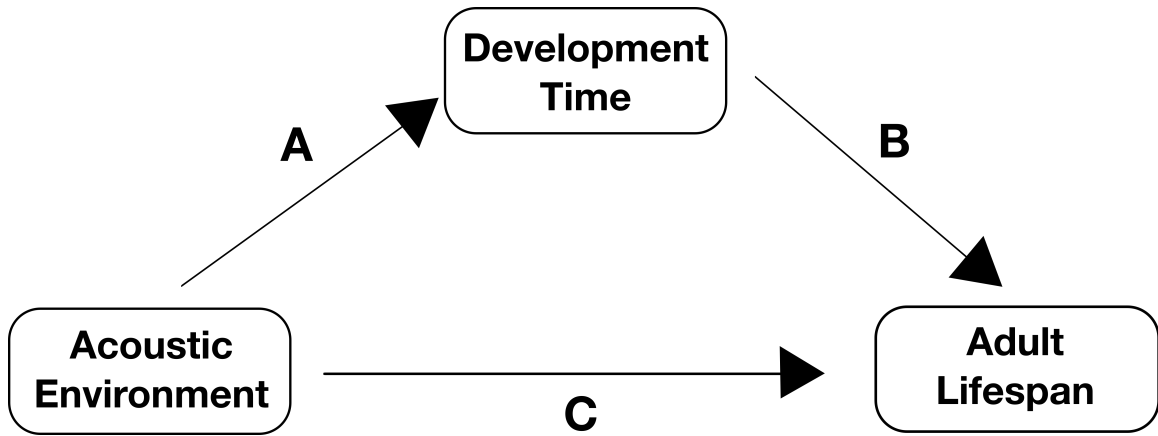


Figure 2: A conceptual model of how adult lifespan may be affected by acoustic experience with noise indirectly through changes in development time (path A), which then affect adult lifespan (path B) or directly (path C).

Finally, given that both development time and adult lifespan were significantly affected by acoustic environment, to determine whether these characteristics interacted with treatment to affect number of eggs laid, proportion of surviving eggs, and lifetime surviving offspring, we also ran two additional mixed model ANCOVAs per measure. The first ANCOVA included development time, acoustic environment, and their interaction as fixed effects, adult size as a covariate, and the blocking variable (treatment date) as a random effect. The second ANCOVA included adult lifespan, acoustic environment, and their interaction as fixed effects, adult size as a covariate, and the blocking variable (treatment date) as a random effect.

We performed mixed effects ANCOVAs and Tukey's HSD using JMP Pro 13.0. Binomial generalized linear mixed models were conducted in R (R Core Team, 2013, version 2.1.2) using the 'glmer' function in the 'lme4' library (Bates et al. 2013).

Results

Anthropogenic noise alters life history measures of both sexes but not reproductive investments of females who successfully mated. We found large effects of acoustic environment on two of four growth-related life history traits that we measured in both sexes: development time and adult lifespan. However, traits related to female reproductive investment were not affected by experience with traffic noise. Crickets reared in masking noise took 23% longer (11 more days) than those reared in silence to reach adulthood (Table 2A; Tukey's HSD with $\alpha = 0.05$; Figure 3A) and spent 13% less time (9 fewer days) as an adult (Table 2A; Tukey's HSD with $\alpha = 0.05$; Figure 3B).

Crickets reared in non-masking noise took 15% longer to reach adulthood than those reared in silence (Table 2A; Tukey's HSD with $\alpha = 0.05$; Figure 3A). Non-masking noise did not reduce adult lifespan relative to the silent treatment (Table 2A, Figure 3B). In our mediation analysis, we found that the effects of acoustic environment on adult lifespan are not mediated through changes in development time (Figure 4). When both acoustic environment and development time were included in a model together, the effect of acoustic environment on lifespan was significant, while development time became a non-significant effect (Figure 4). In other words, both increased development time and masking traffic noise independently reduced adult lifespan. We also found that adult lifespan differed between the sexes (Table 2A), with males living 37% longer than females. Acoustic environment did not affect size at adulthood (Table 2A) nor did it impact survival to adulthood ($X^2 = 1.63$, $df = 2$, $p=0.44$).

Table 2: Model summary for the effect of traffic noise on six life history and reproductive characteristics of Pacific field crickets. Bold values indicate model effects that were significant at $p < 0.05$.

A. Growth and survival-related life history traits of both sexes

<i>Fitness Characteristic</i>	<i>Model Effect</i>	<i>F</i>	<i>d.f.</i>	<i>p</i>
Development Time	Acoustic Environment	13.75	2, 199.1	<0.001
	Sex	1.22	1, 198.4	0.363
	Acoustic Environment x Sex	0.69	2, 198.1	0.503
Adult Lifespan	Acoustic Environment	5.57	2, 176.4	0.005
	Sex	24.01	1, 179.2	<0.001
	Pronotum width	5.33	1, 105.8	0.025
	Acoustic Environment x Sex	1.12	2, 176.5	0.328
Adult Size	Acoustic Environment	2.30	2, 209.0	0.103
	Sex	5.02	1, 208.7	0.026
	Acoustic Environment x Sex	0.162	2, 208.4	0.850

B. Female reproductive investment traits

<i>Fitness Characteristic</i>	<i>Model Effect</i>	<i>F</i>	<i>d.f.</i>	<i>p</i>
Ln(Number of Eggs)	Acoustic Environment	0.29	2, 38.4	0.606
	Pronotum width	0.39	1, 40.4	0.687
Ln(Proportion Eggs Surviving)	Acoustic Environment	0.43	2, 38.7	0.618
	Pronotum width	0.41	1, 39.8	0.701
Ln(Lifetime surviving offspring)	Acoustic Environment	0.18	2, 31.9	0.785
	Pronotum width	0.13	1, 36.8	0.613

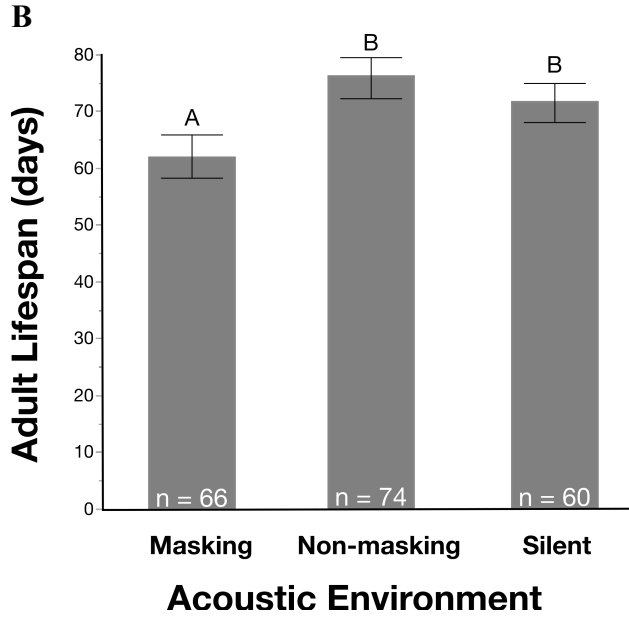
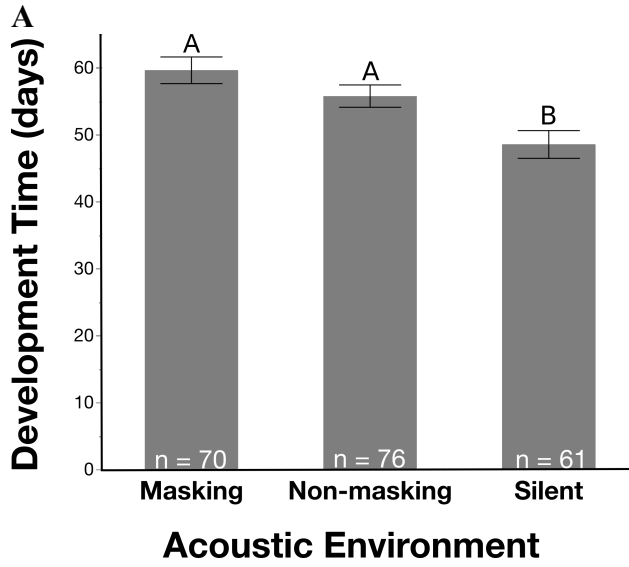


Figure 3: Acoustic experience with noise has strong effects on development time (a) and adult life span (b). Error bars indicate a single standard error from the mean. Letters indicate significant differences among treatments (post-hoc Tukey HSD test, adjusted $P < 0.05$).

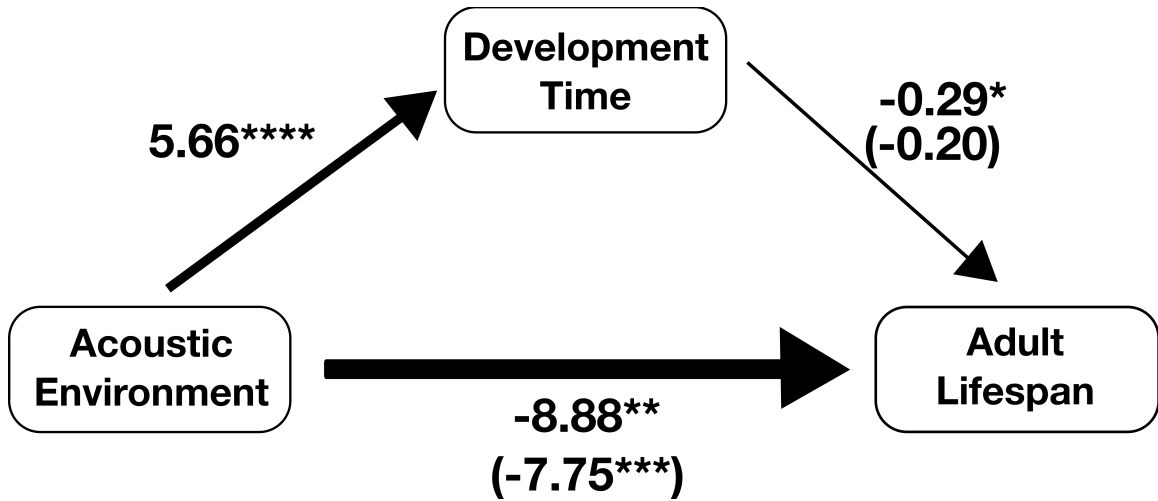


Figure 4: Mediation analysis of acoustic environment, development time, and adult lifespan of crickets. We found responses to masking noise were significantly different from silence, so numbers indicated are model coefficients when comparing masking versus silence. Coefficients in parentheses are from the model that considers both acoustic environment and development time simultaneously. Asterisks indicate significant effects at * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$.

Mating rates were high overall (>90%) and females reared in masking traffic noise, non-masking traffic noise, and silence were equally likely to mate over a 48 hour period ($X^2 = 0.49$, $df = 2$, $p = 0.78$). Unlike development time and adult lifespan, life history traits related to reproduction (lifetime number of eggs, proportion eggs surviving, and lifetime surviving offspring) were unperturbed by noise experienced in the three acoustic environment treatments (Table 2B). Similarly, interactions between acoustic environment and development time and acoustic environment and adult lifespan did not impact female reproductive traits (number of eggs, proportion surviving eggs, lifetime surviving offspring; Table 3, 4). However, females who lived longer as adults laid more eggs (Table 3B; Figure 5A) and there was a strong trend toward females who lived longer also having more surviving offspring (Table 3B; Figure 5B). Finally, because we found that adult lifespan affects the number of eggs laid, but found no effect of acoustic environment on number of eggs laid nor the interaction of acoustic environment and adult lifespan on number of eggs laid, we asked whether females who mated and did not mate differed in adult lifespan. We ran a mixed model ANCOVA with mating (yes or no) and size as fixed effects and treatment date (the blocking variable) as a random effect. Females who successfully mated lived 32% longer than those who did not ($F_{1,76.3} = 7.25$, $p = 0.009$).

Table 3A: Model summary for the interacting effects of traffic noise (acoustic environment) and development time on reproductive investment of Pacific field crickets.

<i>Reproductive Outcome</i>	<i>Model Effect</i>	<i>F</i>	<i>d.f.</i>	<i>p</i>
Ln(Number of Eggs)	Acoustic Environment	0.55	2, 24.3	0.582
	Development Time	0.01	1, 36.4	0.937
	Acoustic Environment*Development Time	0.69	2, 34	0.509
	Pronotum width	0.79	2, 34.5	0.381
Ln(Proportion eggs surviving)	Acoustic Environment	0.50	2, 36.3	0.611
	Development Time	3.99	1, 36.2	0.048
	Acoustic Environment*Development Time	2.04	2, 35.9	0.144
	Pronotum width	0.86	1, 36.5	0.359
Ln(Lifetime surviving offspring)	Acoustic Environment	2.81	2, 38.0	0.072
	Development Time	0.20	1, 38.0	0.654
	Acoustic Environment*Development Time	2.37	2, 38.0	0.107
	Pronotum width	0.41	1, 38.0	0.525

Table 3B: Model summary for the interacting effects of traffic noise (acoustic environment) and adult lifespan on reproductive investment of Pacific field crickets.

<i>Reproductive Outcome</i>	<i>Model Effect</i>	<i>F</i>	<i>d.f.</i>	<i>p</i>
Ln(Number of Eggs)	Acoustic Environment	0.33	2, 34.0	0.722
	Adult Lifespan	6.10	1, 38.0	0.018
	Acoustic Environment*Adult Lifespan	2.03	2, 36.8	0.146
	Pronotum width	2.07	2, 36.3	0.159
Ln(Proportion eggs surviving)	Acoustic Environment	0.39	2, 35.7	0.680
	Adult Lifespan	0.40	1, 34.9	0.534
	Acoustic Environment*Adult Lifespan	1.56	2, 34.8	0.224
	Pronotum width	0.01	1, 36.9	0.920
Ln(Lifetime surviving offspring)	Acoustic Environment	0.09	2, 33.5	0.915
	Adult Lifespan	3.99	1, 37.8	0.053
	Acoustic Environment*Adult Lifespan	2.42	2, 35.8	0.103
	Pronotum width	1.27	1, 36.5	0.266

Table 4: Mean±SE for reproductive investment measures of female Pacific field crickets reared in alternative acoustic environments.

	<i>Acoustic Environment</i>		
	<i>Masking</i>	<i>Non-masking</i>	<i>Silent</i>
Ln(Number Eggs)	5.28±0.38	6.04±0.19	5.41±0.26
Ln(Proportion Eggs Surviving)	-0.71±0.10	-0.69±0.14	-0.78±0.08
Ln(Lifetime Surviving Offspring)	4.58±0.42	5.35±0.13	4.63±0.29

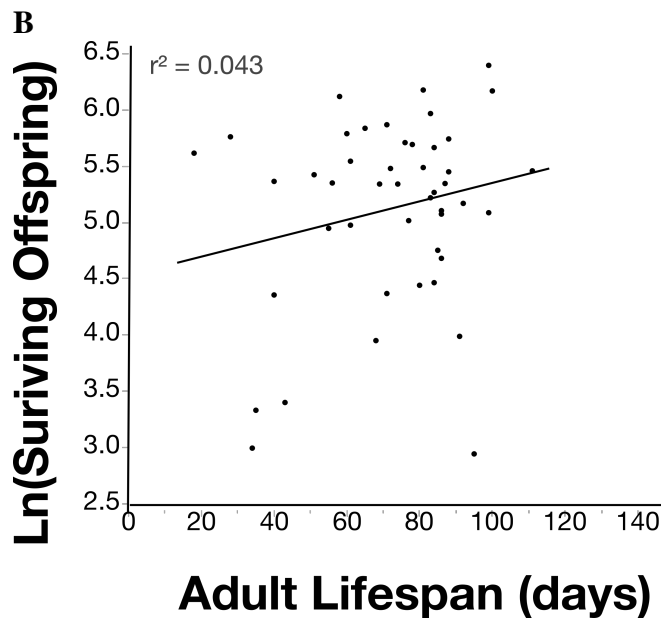
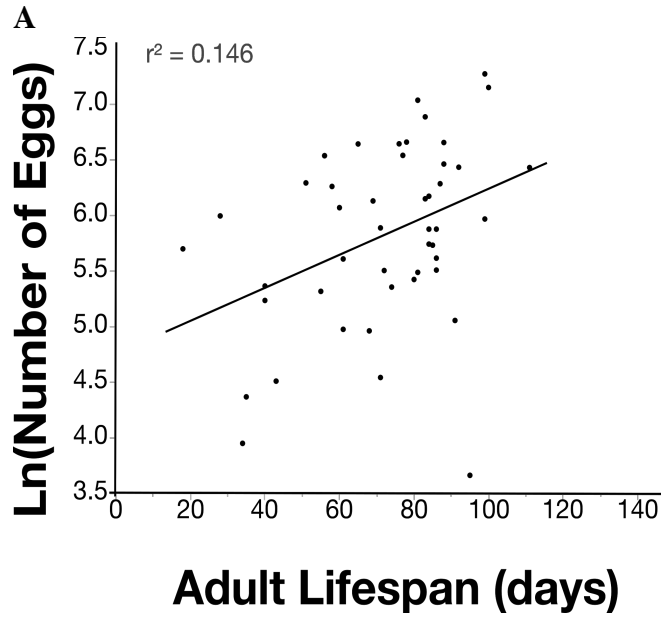


Figure 5: The relationships between female adult lifespan and lifetime number of eggs laid (a) and lifetime surviving offspring (b). Each point represents an individual female who successfully mated and black lines are the linear regression lines from the models.

Discussion

How traffic noise affects fitness and the likely evolutionary consequences of noise exposure remain elusive, in part because following noise stressed individuals throughout their lives is prohibitively difficult in many study systems. Life histories are particularly plastic (Stearns 1992, Roff 1992), and that plasticity may facilitate survival and reproduction in anthropogenically disturbed environments (Van Buskirk 2012, van Baaren & Candolin 2018). Here we show that chronic lifetime exposure to masking traffic noise (that overlaps temporally and spectrally with cricket song) in the lab shifts cricket life history strategies through changes in development time (age at maturity) and adult lifespan, but apparently not through changes in lifetime reproductive investment. Crickets took 23% longer (11 more days) to reach adulthood (development time) in masking traffic noise relative to silence, and spent 13% less time (9 fewer days) as adults than those reared in silence. Crickets exposed to non-masking noise had similar delays in development, but no reduction in adult lifespan. Conversely, we found no difference in the number of eggs laid, proportion eggs hatching, or lifetime surviving offspring (our ultimate measure of fitness) among noise treatments, or through interactions of noise treatment and growth-related life history measures.

Our first main finding is that individuals experiencing chronic masking noise, non-masking noise, and silence are equally likely to live to adulthood (under lab conditions), but spend different amounts of time in juvenile versus adult life stages. We found delayed maturation of crickets exposed to masking and non-masking traffic noise, consistent with work in marine scallop larvae whose development is delayed by exposure

to low frequency noise from geophysical seismic surveys (Aguilar de Soto et al. 2013). Adult lifespan was also affected by chronic exposure to masking noise, but in the opposite direction. We used mediation modeling to show that the effects of noise on adult lifespan are not mediated through effects of development time on adult lifespan; rather, the two are independently affected by exposure to noise. This suggests that non-human animals, including insects, may suffer some of the same mortality costs of noise exposure that have been recently identified in humans (World Health Organization 2011).

Life history theory predicts both costs and benefits of increased development time (Stearns 1992, Nunney 1996, Rantala & Roff 2005). In natural populations, a common cost of extended development time is reduced survival to maturity; individuals who take longer to reach maturity spend more time in vulnerable juvenile stages, risking death through exposure to natural enemies, for instance (Feeny 1976, Price et al. 1980). The cost of extended development time in noise may be amplified by the increased predation rates that have been documented in relatively noisy environments (Simpson et al. 2016). In sum, in natural populations, extended development time and its associated reductions in survivorship could leave fewer individuals to successfully reproduce in noisy populations, and perhaps reduce population growth rates.

Common benefits of increased development time include increased adult size, increased fecundity, reduced adult mortality, and increased offspring quality (Stearns & Crandall 1981). Our second major finding, however, is that crickets exposed to chronic masking and non-masking noise are not larger at adulthood, nor do they differ in reproductive characteristics like lifetime number of eggs or surviving offspring relative to

crickets reared in silence. Further, noise independently reduced adult lifespan, in contrast to the predicted reduction in mortality (extended lifespan) that might accompany increased development time. In other words, noise causes late maturation, but without the concomitant predicted benefits of late maturation. The lack of measurable differences in female reproductive characteristics across noise treatments coupled with shorter adult lifetimes of individuals is puzzling, particularly because we also found a strong positive correlation between adult lifespan and number of eggs laid and a trend toward longer-lived females having more surviving offspring. Females exposed to masking noise (who have shorter adult lifespans) may be compensating for the reduction in lifespan by laying more eggs; the pattern suggests a greater overall rate of egg production by females reared in masking traffic noise or age-specific differences in reproductive investment that were not measured here. Interestingly, consistent with work in other field crickets (Wagner et al. 2001), we found that mated females had longer adult lives than unmated females. Perhaps, then, this longevity benefit is enough to mask any fecundity deficits short-lived females might otherwise have.

Additional costs of reduced adult lifespan might include reductions in time to locate a mate and fewer overall lifetime mates. In species that mate multiply and throughout adulthood, individuals with shorter adult lifespans may mate less overall, limiting offspring production. Female field crickets who mate multiply lay far more eggs (Wagner 2010, Gershman 2010). This, combined with reduced adult lifespans means that females exposed to masking noise may have less time to find mates, find fewer mates per unit time (or not at all), and thus lay fewer eggs overall. Such declines in population level

reproductive output can impact population size and ultimately long-term population persistence.

We previously demonstrated that developmental exposure to traffic noise hinders female mate location ability; female *T. oceanicus* reared in masking traffic noise took 200% longer to begin searching and >80% longer to locate a signaling male than females reared in the absence of traffic noise (Gurule-Small and Tinghitella 2018A), potentially limiting the lifetime number of mates females may encounter in noisy settings, and motivating this study to more comprehensively investigate effects of traffic noise on fitness. Our experimental design in this study eliminated mate location, but the changes in life history we observed here may be amplified by negative consequences of noise for mate location ability in nature. Taken together, crickets exposed to masking noise spend more time in risky developmental/juvenile stages because they mature later in life, and live short adult reproductive lives (this paper) during which their mate location ability is reduced, even if noise is not experienced as an adult (Gurule-Small and Tinghitella 2018a). This may be true even if organisms can leave noisy environments at the adult stage. We previously found that mate location ability was reduced even when noise was not experienced as an adult (Gurule-Small and Tinghitella 2018a). Further, though we found no difference in mating rates across treatments in this study, this may be due to methodological choices. To increase the odds of mating, such that we could measure reproductive investment across noise treatments, we allowed pairs 48 hours to interact and mate in a small confined space. Further study would be required to determine if noise alters females' latency to mate and the direction in which noise alters mating success

under more realistic conditions. Females may be too stressed or distracted by anthropogenic noise to mate, or, conversely, may be less discriminating upon locating a male if traffic noise masks male courtship song or simulates environments in which males are rare (Attwell & Wagner 2014).

Our work has laid the foundation for understanding life history costs of anthropogenic noise. Future work conducted in the field will illuminate the 1) extent to which delayed development and reduced adult lifespan impact survival and reproduction in natural populations experiencing predation and reproductive costs of noise, and 2) whether there are population growth and persistence consequences of the life history changes we observed. We anticipate the effects of noise to be more dramatic in natural populations in part because in a laboratory setting, animals are protected from predation and resource limitation, both of which are exacerbated in anthropogenically disturbed habitats (Simpson et al. 2016). Measuring fitness effects comprehensively in natural populations will also allow researchers to capture the extent to which predation costs, difficulties associated with mate location, and reduced mating rates may compound the delayed maturation and reduced lifespan effects we found here.

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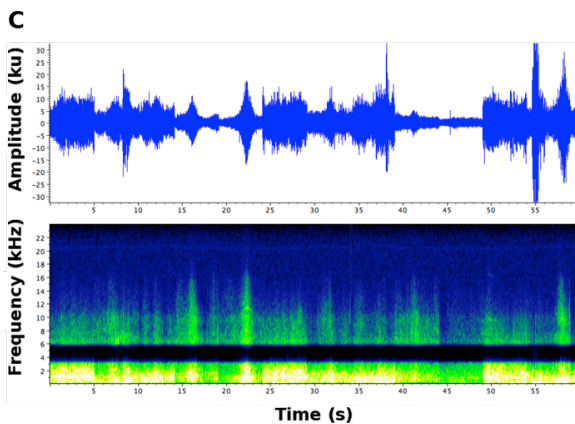
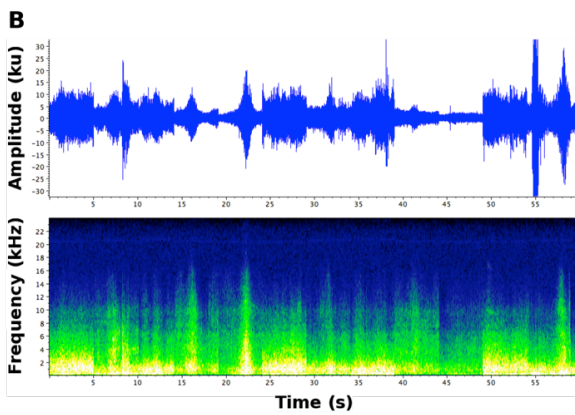
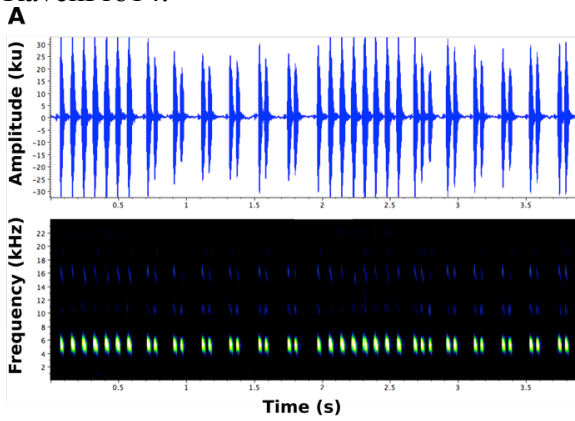
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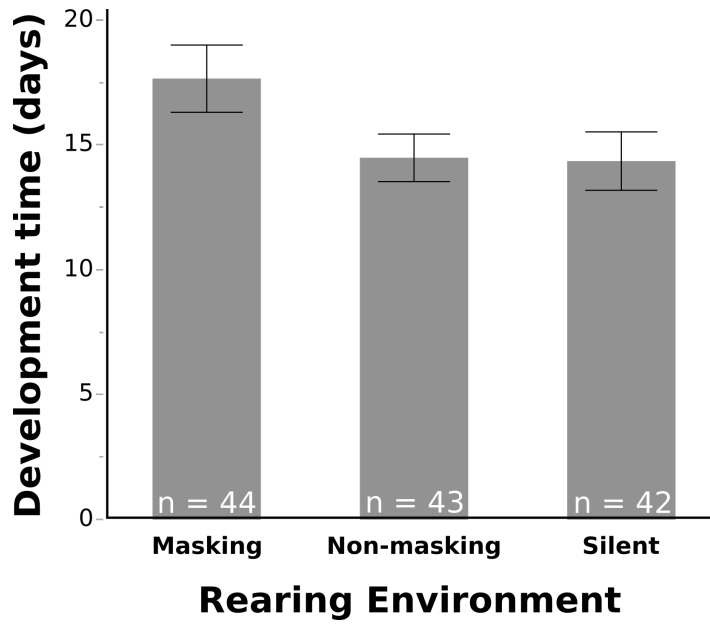
Appendix

Appendix Figure 1: Waveforms (top) and spectrograms (bottom) of *T. oceanicus*' long distance calling song (A), the compiled masking [1] traffic noise (B), and the non-masking traffic noise (C). *T. oceanicus* song has a peak frequency of 4-6kHz. To create the non-masking noise (C), we filtered out the traffic noise from 3-6kHz using RavenPro14.

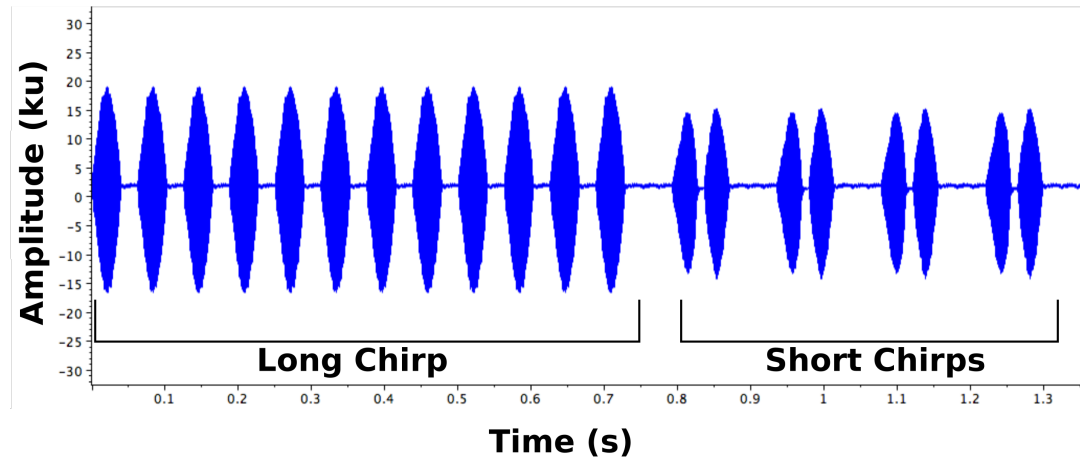


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Appendix Figure 2: Though non-significant, there was a trend toward rearing environment influencing development time (from the time of sexing to eclosion; $F_{2,126}=2.58$, $p=0.08$), suggesting juvenile experience with noise could affect development time.

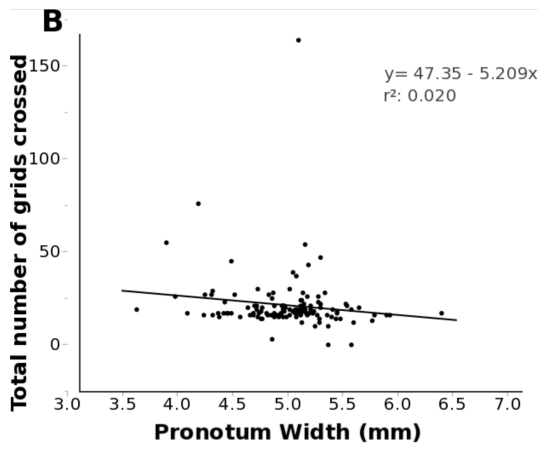
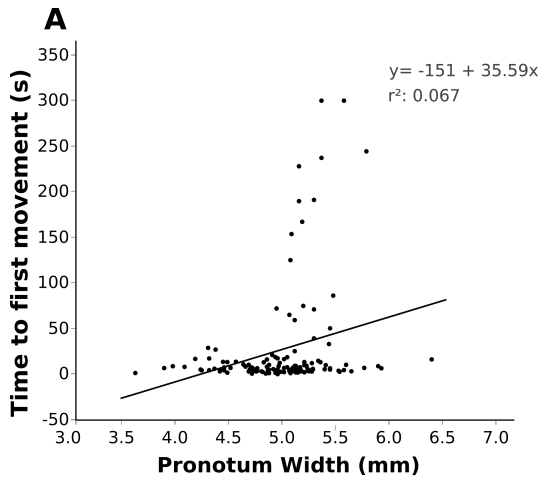


Appendix Figure 3: Female *T. oceanicus* express strong preferences for temporal components of the long distance calling song. *T. oceanicus* calling song consists of a trill-like long chirp followed by a series of paired pulses (the ‘short chirps’). We broadcast a highly preferred (high quality) song in phonotaxis trials. The song was digitally produced using field-recorded chirps and has previously been used by [1-4]. This song variant contains a ratio of 60% long chirp to 40% short chirp.



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Appendix Figure 4: Female size (pronotum width) was associated with time to first movement (A) and the search path taken (number of grid lines crossed; B). Larger females were slower to move and crossed fewer grid lines.



Appendix Discussion: Noise that masks a focal signal often elicits greater plastic and evolutionary change in signals and signalling behaviour than non-masking noise [1-2]. Though we did not find statistically significant effects of developing in non-masking noise on time to contact (Table 1; Figure 1B), visual inspection of the data suggests mate location following development in masking and non-masking noise are similar. We calculated effect sizes (Cohen's d) for time to contact and found effects were of medium size for both development in masking noise (0.54) and development in non-masking noise (0.42) when compared to rearing in silence. The difference in time to contact between masking and non-masking treatments was comparatively small (0.14). This suggests that prior exposure to both types of noise may negatively effect mate location.

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