Parasitoid pressures and silence evolution

Megha R. Suswaram[1*], Justin D. Yeakel[2]
Chaitanya S. Gokhale[3]
[1]Quantitative Systems Biology, University of California Merced,
[2]Life and Environmental Sciences, University of California Merced,
[3]Research Group for Theoretical Models of Eco-evolutionary Dynamics,
Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology
[*]Corresponding author: msuswaram@ucmerced.edu

Abstract

Acoustic signals used by organisms to attract mates are known to attract parasitoid flies. The parasitoid flies lay their eggs inside the host signaler eventually killing the host. We build a host-parasitoid acoustic model to investigate the effect of parasitoid flies on the signaling host's eco-evolutionary dynamics. We used field crickets as a system to build the framework of the model. We explore how the sex-ratio, as well as, the maximum progeny of the parasitoid females impacts the evolution of the acoustic signal and population density of the signaling hosts. We also explore the stability of the host populations with increase in parasitoid load. We find that up to a threshold value, an increase in parasitoid load leads to a thriving yet silent host population. This emergence of silence as an evolutionary strategy is rapid. Our results show that a drastic increase in the parasitoid load quickly pushes the signaling host population towards instability and extinction.

Keywords: acoustic signal, crickets, parasitism, reproduction, eco-evolutionary dynamics

Contents

1 Introduction **2**

2 Model **3**

2.1 Reproductive fitness of the host based on acoustic trait 4

2.2 Search efficiency of the parasitoid based on acoustic trait 5

2.3 Density dependence 6

2.4 Simulation of the eco-evolutionary dynamics 7

3 Results **8**
3.1 Quick transition from conspicuousness to silence 8
3.2 Stability of the system and bifurcation analysis 10

4 Discussion **12**

1 Introduction

Acoustic signaling is the primary mode of communication shared by roughly 8.7 million species ranging from arthropods to mammals [1], inhabiting terrestrial and marine environments. There are several types of acoustically signaling species such as crickets, anurans, birds, and marine organisms. The reproductive fitness can be attributed to the mating success of the individual signalers in many acoustically signaling species [2–4]. A consistent life-history trade-off is the one between reproduction and survival [5]. This trade-off determines the evolution of the signaling trait whether visual [6], chemical [7] or indeed acoustic acoustic [8, 9]. Signaling populations evolve to amplify or diminish their conspicuousness based on their natural chorus, and other environmental pressures [10–13]. Many organisms solely use acoustic signals to secure mates. In most of these systems, the acoustic signals transmit mating opportunities with the females approaching the calling males to copulate [14]. Females cue into the signal, with some species performing phonotaxis, and locate the male. The females assess the song to assess the quality of the male [15].

Conspicuous sexual signallers, however, also garner unwanted attention. The signals risk attracting potential predators and exploiters [16]. Male crickets use stridulation to produce the chirp by rubbing their front wings together against the underneath of their wing, called the scraper [17]. The parasitoid flies locate the signaling males by eavesdropping on their song by cuing in on the sound produced by the stridulation [18, 19]. The female fly then places larvae on the cricket that then burrow into the cricket's body cavity [20]. They develop there for seven to ten days before emerging. Some parasitoid females show specificity to specific hosts species [16]. Studies have shown that with an increased risk of parasitism, males switch their mate securing strategies and resort to alternative mating strategies or can even lose the signaling ability altogether [21]. Both polymorphism and plasticity shown in cricket populations [22, 23]. With increased parasitoid densities, male singing crickets have evolved to become silent [24]. The males develop flat wings which are incapable of producing a song. The silent males still have a chance at reproduction, as they become satellite males of the few signaling males in the population. They steal the mates from these signaling males. Additionally, added ecological pressures, like parasitoid population density, sex ratio and fecundity compound the

effects under this trade-off to change the course of signal evolution [25]. Furthermore, population dynamics create a feedback process that controls the reproduction and mortality rates, thus changing the evolutionary trajectory of sexual signals [26]. As a culmination of all the confounding factors, the process of evolution in losing the signaling traits can be remarkably rapid, in less than twenty generations where largely the population becomes silent with a few signalers and many satellite males [24, 27].

Many studies have focused on the evolutionary significance of parasitoid exploiters and their acoustically signaling insect hosts, such as the above-described crickets [28]. However, a quantitative estimate of the exact parasitoid densities, the proportion of parasitoid females, and other environmental pressures influencing the speed of signal loss are lacking. The existing host-parasitoid models predict the population dynamics as a version of the classical predator-prey cycles. We develop a theoretical model specific to such an extraordinary host-parasitoid system by incorporating reproductive costs and benefits of the acoustic signal produced by the crickets.

Our mechanistic eco-evolutionary model goes beyond classical evolutionary game-theoretic reasoning and investigates the threshold of parasitoid load under which silence emerges in a population. We investigate the parasitoid sex-ratio and the parasitoid fecundity's influence on the host's acoustic signal evolution and the host population density dynamics. We find that there is a threshold parasitoid load at which there is a rapid evolutionary transition from conspicuousness to silence in the hosts. We also find that an increase in the parasitoid load decreases the stability of the host population, and the population enters cycles, chaos and extinction faster. Our model will thus provide insights into the fundamental mechanisms that affect the evolution of acoustic signals in the presence of parasitoids.

2 Model

We begin by recapitulating an existing host-parasitoid insect population model [29]. The population size of the host at a given time t is H_t, and the population size of the parasitoid is P_t. The proportion of parasitoid females in the population is q. Simultaneously, a is the search efficiency of the parasitoid and F_{max} is the maximum fecundity of the parasitoid. The reproductive rate of the host is represented by r. This model assumes that there are i) q proportion of parasitoid females, ii) a parasitoid female can examine area α ("area of discovery") during its lifetime, and iii) there is a maximum parasitoid fecundity, F_{max}. The population dynamics of the host and parasitoid is given by:

$$H_{t+1} = H_t\big(e^{-\frac{\alpha P_t F_{max}}{F_{max}+\alpha H_t}}\big)r$$
$$P_{t+1} = H_t\big(1 - e^{-\frac{\alpha P_t F_{max}}{F_{max}+\alpha H_t}}\big)q \tag{1}$$

Ecologists have extensively used this particular approach to study insect populations that have been parasitised. Host-parasitoid theoretical models typically generate oscillating populations of increasing amplitude and are by themselves unstable [30–32]. However, this does not accurately represent what happens in nature. In nature, additional ecological processes like intraspecific competition and spatial heterogeneity can partially or completely stabilize the system. The model developed by Rogers provides a realistic depiction as compared to Thompson's 1922 model [29] and Nicholson and Bailey's 1935 model [33]. It is a further development of Holling's disc equation [34] because it includes a realized fecundity instead of a potential fecundity [29].

2.1 Reproductive fitness of the host based on acoustic trait

We assume that the signaling host's acoustic trait is represented by a single acoustic character, the syllable rate. While we have considered syllable rate for building the model, it can be any feature of the acoustic signal like amplitude, frequency or intensity. We assume that the syllable rate, z, varies from 0 to 100 units in time. A chorus forms when many individuals signal together with varying syllable rates. The chorus will have a mean syllable rate, $\bar{z}$. A low syllable rate is when an individual has $z < \bar{z}$. A silent individual who does not signal is represented by $z = 0$, and a high syllable rate when $z > \bar{z}$ indicates a conspicuous signaler. Given an environment devoid of acoustic interference, we can assume that the mean syllable rate, $\bar{z}$, sets the reproductive fitness standard for all calling individuals. If the syllable rate of a calling individual is higher than that of the chorus' mean, then the individual stands out from the overall population, is conspicuous, and can be easily distinguished by listening mates. Therefore, it has a higher chance of securing more mates. We can model this as an individual caller, whose syllable rate is higher than that of the chorus' mean, $z > \bar{z}$, having a higher reproductive fitness component. While we assume that securing more mates increases the reproductive component of fitness, there is a maximum reproductive reward within a given time frame. The reproductive fitness at which there is maximum reproductive reward is given by r_{max}. Hence, even when the individual's syllable reaches maximum conspicuousness, the reproductive fitness component saturates at r_{max} (Fig. 1). Similarly, suppose the syllable rate of a calling individual is lower than that of the chorus' mean. In that case, the chorus deafens the individual's signal, and therefore it has a lower chance of securing mates. So, we can model

an individual whose syllable rate is lower than that of the chorus' mean, $z < \bar{z}$, with a lower reproductive fitness component. Nevertheless, we also assume that even if a caller is silent (a non-calling individual), it can encounter a mate by random chance, with its movement within the habitat. This gives the silent individual a minimum reproductive reward value, r_{min}. By β we denote the sensitivity of the reproductive curve, considered to be the phonotactic selectivity of the receiver [35] (Fig. 1). The reproductive component of fitness of an individual signaler is therefore given by:

$$r(z|\bar{z}) = r_{min} + \frac{r_{max} - r_{min}}{1 + e^{-\beta(z-\bar{z})}} \tag{2}$$

2.2 Search efficiency of the parasitoid based on acoustic trait

We then modeled the search efficiency with a type II functional response. Hence, as the syllable rate increases, the more conspicuous the individual is, the parasitoid can better find the signaller. After a certain threshold of the syllable rate, the search efficiency of the parasitoid saturates (Fig. 1). The search efficiency α is

$$\alpha = \frac{z}{1 + z} \tag{3}$$

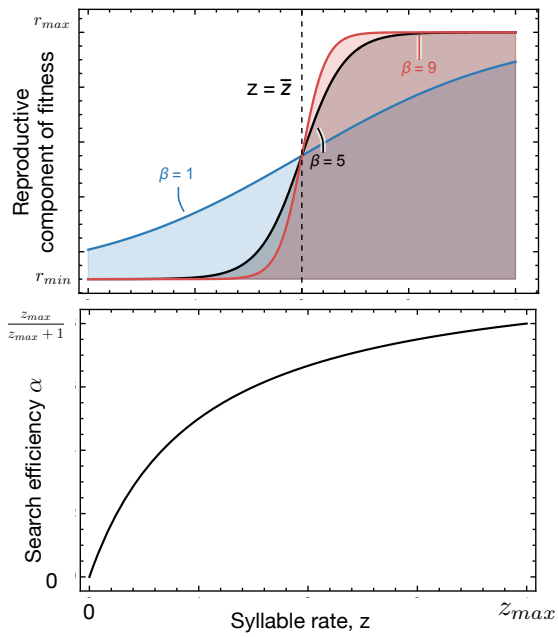

Figure 1: Reproductive component of fitness function of an individual host Eq. (2), Search efficiency (Eq. (3)) of a parasitoid as a function of mean chorus syllable rate. The reproductive component of fitness is dependent on how far the syllable rate of the individual, z is from the population chorus mean $\bar{z}$, and the phonotactic selectivity, β. r_{min} and r_max are the minimum and maximum reproductive rewards respectively. With high phonotactic selectivity there is a larger benefit in reproductive component of fitness. The search efficiency of the parasitoid, α, increases with increase in host syllable rate and saturates at a high syllable rates.

2.3 Density dependence

We add density dependence to the insect population host-parasitoid framework and replace reproduction of the host and search efficiency of the parasitoid with the newly formulated acoustic character based modifications. By substituting Eq. (2) and Eq. (3) in Eq. (1), and adding density dependence with K being the carrying capacity of the habitat, we get:

$$H_{t+1} = H_t \underbrace{e^{\left(r_{min}+\frac{r_{max}-r_{min}}{1+e^{-\beta(z-\bar{z})}}\right)(1-H_t/K)-\left(\frac{\frac{z}{1+z}P_t F_{max}}{F_{max}+\frac{z}{1+z}H_t}\right)}}_{\text{prob. of esc. parasitism (density dependent)}}$$

$$P_{t+1} = H_t \underbrace{\left(1 - e^{-\frac{\frac{z}{1+z}P_t F_{max}}{F_{max}+\frac{z}{1+z}H_t}}\right)}_{\text{prob. of parasitism}} q \tag{4}$$

2.4 Simulation of the eco-evolutionary dynamics

Because an analytical solution for the average fitness of the population $\bar{w}(\bar{z})$ is intractable, we track changes in population abundance and the trait distributions of a cricket population with an individual based model. As such, we numerically track the evolution of the full trait distribution of z, denoted by $f(z)$, over time, in addition to population size $N(t)$. Each time-step represents a generation where all adults are assumed to die at the end of each time-step such that generations are non-overlapping. This is generally the case for cricket populations [36], however this assumption would not hold for many other acoustically signaling organisms including most bird species. Offspring inherit trait values from parents with variability σ such that

$$z_{offspring}(t+1) = z_{parent}(t) + g, \tag{5}$$

where $g \sim \mathrm{N}(0, \phi)$, and we set $\phi = 1$. The number offspring for each individual i with trait z_i is determined by its fitness with respect to the chorus mean, $w_i(z_i|\bar{z})$, where the sum across reproducing individuals determines the future population size $N(t+1)$, such that

$$N(t+1) = \sum_{i=1}^{N(t)} w_i(z_i|\bar{z}). \tag{6}$$

We initiate the host population to be conspicuous $\bar{z}(0) = 90$ with a standard deviation of $\sigma = 10$, and simulate dynamics over the course of 100 generations. We visually confirmed 100 generations to be adequate for calculating steady state conditions. We set $r_{min} = 0.01$, $r_{max} = 2\,\beta = 0.5$, and $K = 1000$. The initial host population is represented in Fig. 2 ($t = 1$).

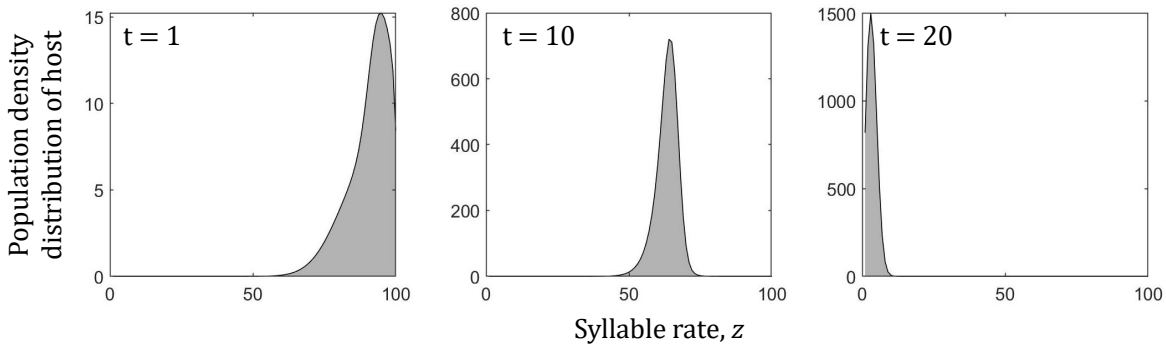

Figure 2: Initial distribution of the host population. With increasing generations, the host population evolves from a conspicuous chorus mean to a silent chorus mean within 20 generations. We see the evolution of silence within 20 generations in a population that has been attacked by parasitoids.The silent population has a higher population density. $H(0) = 500$, $\bar{z}(0) = 90$, $\sigma = 10$, $r_{min} = 0.01$, $r_{max} = 2\,\beta = 0.5$, and $K = 1000$.

3 Results

3.1 Quick transition from conspicuousness to silence

Female biased sex-ratio. As the proportion of parasitoid females increases in the population, the conspicuously signaling population quickly evolves to become silent. The reproductive fitness of the host individual is influenced by the chorus mean, $\bar{z}$. The fitness of the conspicuous individuals is high initially it is are greater than the chorus mean, resulting in reproductive gains as the parasitoid females attack the conspicuous host individuals, mortality increases and the fitness of conspicuous individuals is reduced. In contrast, the silent host individuals escape parasitoid attack, reproduce, and increase the proportion of silent individuals in the host population in next generation, reducing the chorus mean. With increasing proportion of parasitoid females, there are more attacks on the conspicuous hosts, silence accumulates a selective advantage, such that evolution of silence emerges (Fig. 3). This evolutionary transition is rapid and it usually happens within 10 generations. The silent individuals survive and reproduce, increasing the population density to the carrying capacity (Fig. 3). Beyond a certain female parasitoid load, all the host individuals die and the population goes extinct (Fig. 3). Thus a female biased sex ratio of parasitoids influences the signaling trait evolution and drives population extinction of the host.

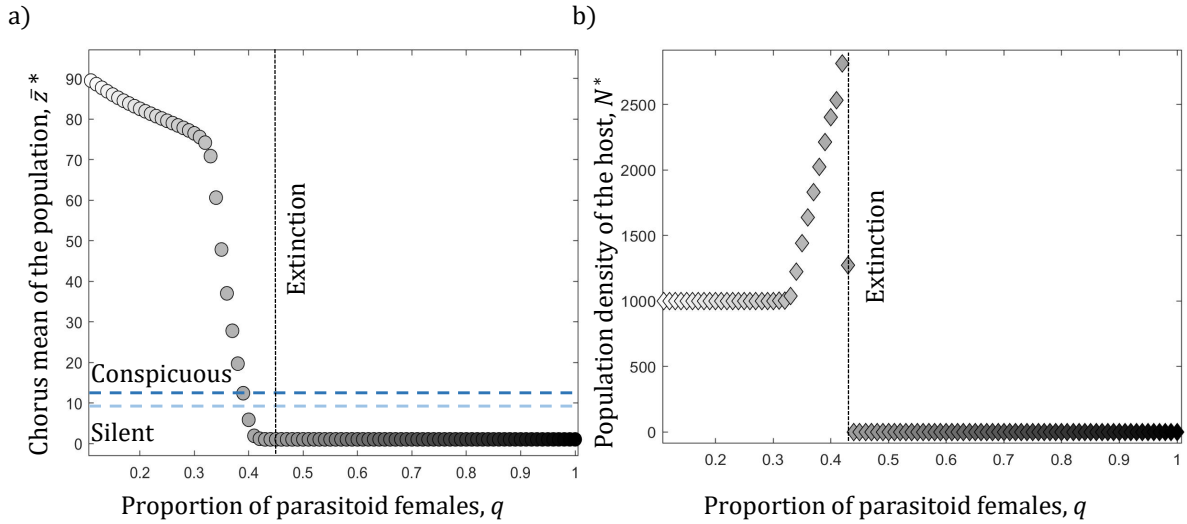

Figure 3: **Quick transition from conspicuous to silence.** a) Change in chorus mean of the host population represented by circle shapes. b) Change in population size of the host population represented by diamond shapes. A more female-biased sex ratio in parasitoid populations results in a host population that is silent and large. Beyond a threshold of female-biased population in the parasitoids, the host population goes extinct. $H(0) = 500$, $\bar{z}(0) = 90$, $\sigma = 10$, $r_{min} = 0.01$, $r_{max} = 2$, $\beta = 0.5$, $F_{max} = 3$ and $K = 1000$.

Parasitoid fecundity influences the signaling trait evolution and drives population extinction of the host As the maximum number of viable offspring of the parasitoid females increase, the conspicuously signaling population abruptly transitions to silence (Fig. 4). The increase in parasitoid fecundity, increases their population density in the next generation. This results in more number of attacks on conspicuous hosts. The conspicuous individuals do not reproduce and die, and proportion of silent individuals increase in the population, driving the chorus mean to silence. This evolutionary transition of the host is rapid and usually happens occurs within 10 generations. Here again, as we further increase the fecundity of parasitoids, the population goes extinct (Fig. 4).

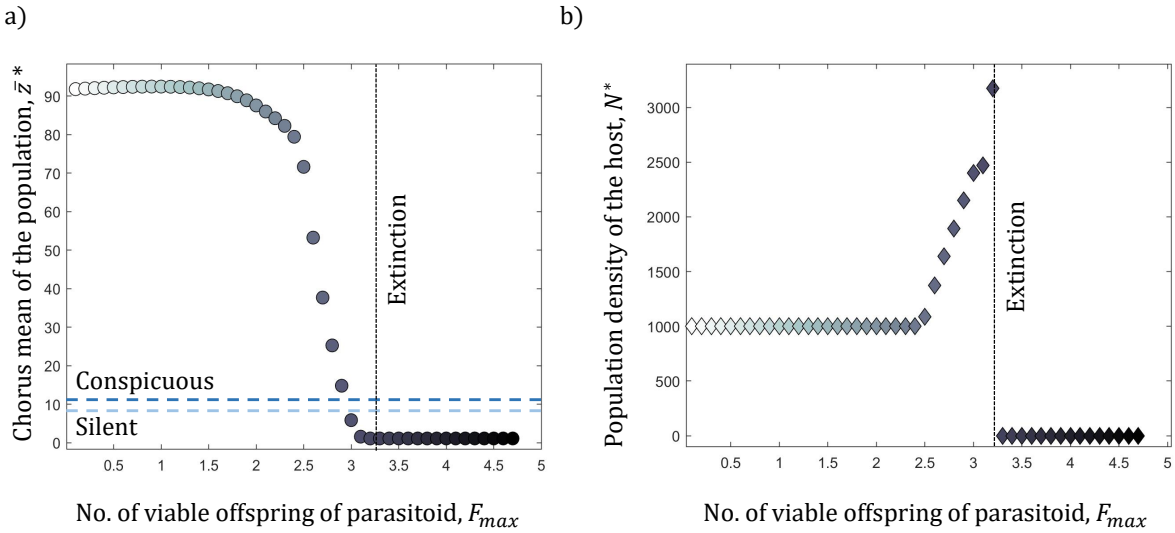

Figure 4: **Quick transition from conspicuous to silence.** a) Change in chorus mean of the host population. b) Change in population size of the host population. Increase in the fecundity of parasitoid females results in a host population that is silent and large. Beyond a threshold of fecundity of the female parasitoids, the host population goes extinct. $H(0) = 500$, $\bar{z}(0) = 90$, $\sigma = 10$, $r_{min} = 0.01$, $r_{max} = 2$, $\beta = 0.5$, $q = 0.4$ and $K = 1000$.

3.2 Stability of the system and bifurcation analysis

The reproductive incentive to signal is given by the difference in the maximum reproductive fitness r_{max} and the minimum reproductive reward r_{min}. Keeping the reproductive reward constant at a low value, $r_{min} = 0.01$, as we increase the maximum reproductive fitness, we increase the reproductive incentive. With the increase in reproductive incentive to signal, multiple population steady-state values emerge, such that, the host population enters cyclic oscillations. We first see period-doubling in the host population density as the reproductive incentive continues to increase. With a high reproductive incentive, the population size is similarly high, there sets in the costs of overpopulation, determined by the carrying capacity, driving the population to go extinct. The stability of the system and the start of period-doubling changes with parasitoid load. As we increase the parasitoid load (increasing fecundity or the proportion of females), the populations go extinct Fig. 5.

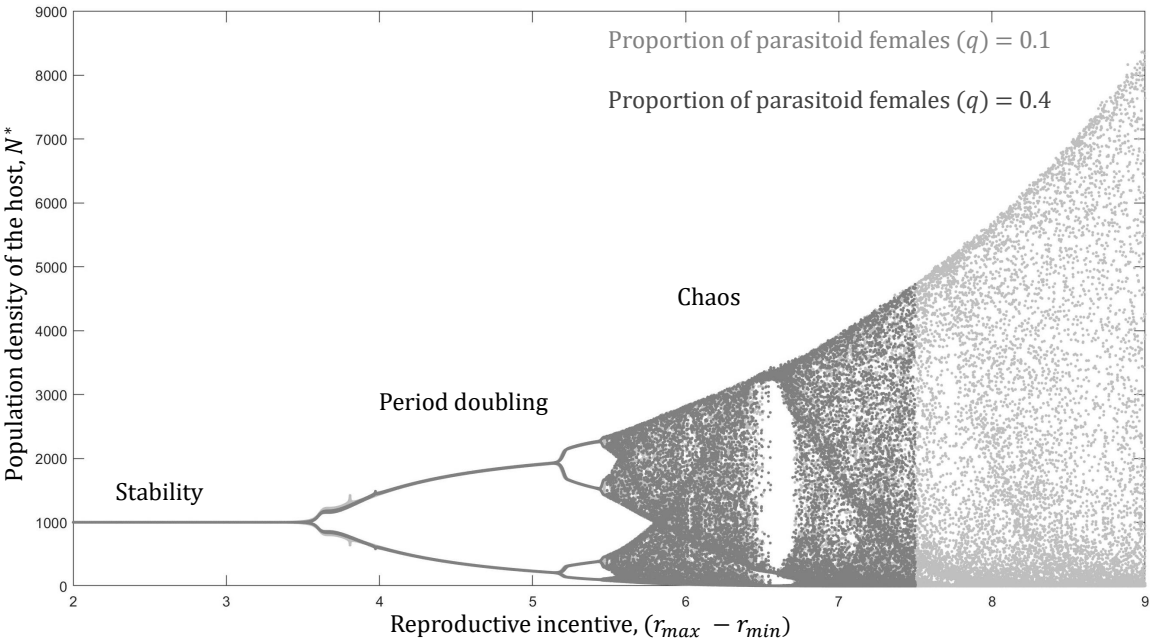

Figure 5: **Bifurcation diagram of the host system.** Outcome of host population when parasitoid population is male-biased shown in light grey and female-biased shown in dark grey. A female-biased parasitoid population causes the host population to be less stable and drive it towards extinction sooner.

Further, we plotted the chorus mean and the size of the host population for a varying sex ratio and fecundity of the parasitoid (Fig. 6). When the parasitoid population is more male-biased and the fecundity of the parasitoid is low, the host population is conspicuous. If the sex ratio relatively is male-biased, but there is high fecundity, then the population is neither conspicuous nor silent but evolves to be at an intermediate signal. Even if the sex ratio is female-biased, but the fecundity of the parasitoid is low, the population is still conspicuous. The host population is pushed towards extinction with a female-biased sex ratio and high fecundity (Table. 1). The system is less stable and pushed towards chaos for a female-biased parasitoid population with high fecundity. When the chaos is very high, the population is driven to extinction.

Parasitoid Condition		Host Outcome	
Sex-ratio	Fecundity	Chorus	Population density
Male-biased	Low	Conspicuous	High
Male-biased	High	Intermediate	Intermediate
Female-biased	Low	Conspicuous	High
Female-biased	High	Silent	Low

Table 1: Effect of parasitoid condition on the host population

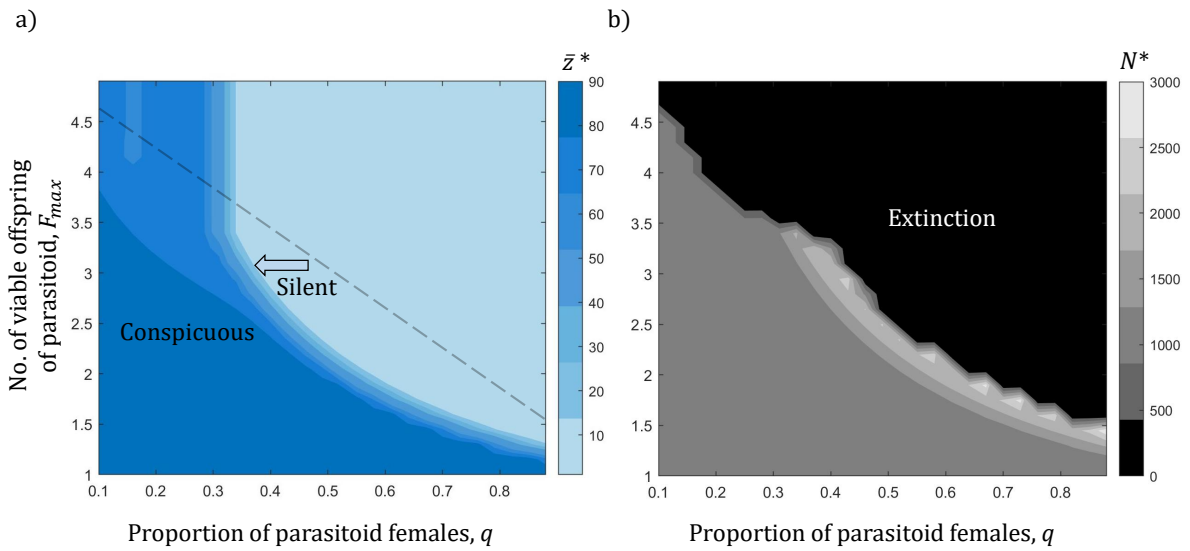

Figure 6: Stability analysis of the host system a) Chorus mean of the host population. Dark blue represents a conspicuous population and light blue represents a silent population. The blue transparent dashed line shows approximate extinction in population. Anything above the line is extinction and not silence. b) Population size of the host population. A high parasitoid load, pushes the host population to silence with a high population density. Beyond, a certain threshold of parasitoid load, the population enters cycles, followed by chaos, and then goes extinct. $H(0) = 500$, $\bar{z}(0) = 90$, $\sigma = 10$, $r_{min} = 0.01$, $r_{max} = 2$, $\beta = 0.5$, and $K = 1000$.

4 Discussion

Acoustic signal evolution has been observed to result from diversification of signal [37], amplification of the existing signal to a conspicuous population [38], diminishing of a signal into a silent population [39] and, loss of signal by a morphological change in the signal producing organ [24], loss of preference for conspicuous signalers from the receiver [40]. This evolu-

tion of the acoustic signal can be a result of population dynamics [41, 42], and environmental pressures [43]. Parasitism is one of the major drivers of the diminishing of acoustic signals in various signaling species [5]. Several empirical studies have shown that with an increase in parasitoid load, the acoustic signal is diminished and lost within a few generations [26, 44, 45]. Various aspects of the effect of parasitoids on host signaling traits and population sizes have been documented [5, 46]. As discussed previously, the existing host-parasitoid models do not predict the host's trait evolution, and only focus on the population densities [29, 32, 33]. We model the parasitoid load and its impacts on both the population densities of the host and their signaling trait evolution. We discuss the key components of the parasitoid load that affect the host population, and show the threshold of this load at which the host population responds by the loss of the signal and evolution of silence.

Our results show that the sex ratio and the fecundity of the of the parasitoid population play a key role in the switch from conspicuousness to silence. We show that the sex ratio and the fecundity in the parasitoid population drive the signaling trait evolution which in turn influences host population dynamics and stability (Fig. 3, Fig. 4, and Fig. 5). The evolution from conspicuousness to silence occurs within 10 generations. These results are corroborated by empirical studies. Among field crickets, it is known that signaling males are more affected by the parasitoid fly of the genus *Ormia* [19]. Female parasitoid flies find a specific cricket host in which deposit their parasitoid offspring. The offspring then grow and feed within the host. Within ten days, the fully grown larvae kill the host as they emerge [47]. Therefore one would estimate that the sex ratio in parasitoid populations and the offspring size play key roles in shaping the host survival and signaling behavior. Our results show that both the increasing female biased sex ratio and fecundity quickly drive the populations to evolve silence. Zuk *et al.* (2006) showed that on the Hawaiian island of Kauai, where there was high parasitoid density, most of the population evolved silence through selection for a flatwing morphology that rendered the males incapable of generating an acoustic signal within twenty generations. To reproduce, they used alternative mating strategies such as increased locomotive behavior to encounter females randomly [46]. That this transition has been observed to occur in such a short period of time is in accordance with the results of our model.

We show that a high reproductive incentive causes population destabilization, period doubling, chaos, and extinction. Population densities of the host can be highly susceptible in nature, and the risk of infection increases with parasitoid density [48, 49]. When subject to varying predator densities, Allee effects or parasitism, fast-growing populations are highly sensitive to initial population densities. Such populations can exhibit chaotic dynamics that may promote extinction risk [50–54]. We show that the reproductive rate drives the population expansion, stability, and ultimately extinction (Fig. 5). Our results support the findings

that in nature, a rapidly growing population which first thrives, soon reach a critical threshold, exhibit chaotic dynamics and then goes extinct [50, 55, 56]. We know that rapid oscillations in population densities can lead to species extinction [57]. These oscillations are dictated by the reproductive incentive, that is in turn set by the parasitoid load. The increase in parasitoid load pushes the system to become unstable much quicker (Fig. 5). This implies that there is a threshold beyond which parasitoid load cannot increase in nature as it drives the host population extinct.

Empirical studies have independently shown that parasitoids cause shifts in host traits [16]. Theoretical models and other empirical findings also point the effects of parasitoids on host populations [29, 32, 33]. We outline the missing link, that is the connection among the parasitoid load, acoustic trait evolution and population density. One would expect the parasitoids to first change the host population density and the evolution of silence to be a response to the population change. Counter-intuitively, we show that it is the parasitoid load that first alters the reproductive rate of the host population, that causes an evolutionary signal adaptation in the host and their population density respond to this evolutionary signal adaptation (Fig. 6).

Our model provides a general framework for organisms that use acoustic signals to secure mates and are exploited by predators or parasitoids. This framework to predict the signal evolution change is applicable to crickets and cicadas, anurans, sparrows, etc. Further, the model can be expanded and developed to understand the effects of parasitism on host sex ratios [58]. The model could also be further developed to understand the evolution of multi-component auditory signals. The acoustic environment is altered by anthropogenic effects [59, 60]. Changes in the environment can cause significant changes in the reproductive incentive of signalers [43, 61, 62]. Changes in the environment can also shift the parasitoid load [63]. At different parasitoid loads, for a given reproductive incentive, we have shown that there are drastic changes in evolutionary adaptations of signaling hosts and their population stability. Taken together, with environmental conditions that alter the reproductive incentive and parasitoid load, the findings our model can provide insight into their reproduction, trait evolution and population densities. In future, with these predictions, we could develop methods for conserving the acoustic communicating populations under changing environmental conditions, by artificially manipulating the parasitoid population size, sex ratios and fecundity.

Acknowledgements. We thank Irina Birskis-Barros, Taran Rallings, and Ritwika VPS for their helpful comments and suggestions. This manuscript benefited from University of California, Merced's School of Natural Sciences Dean Fellowship. Dr. Chaitanya Gokhale acknowledges funding from the Max Planck Society.

Data Availability and Analysis. All code and preliminary plots are available on GitHub at `https://github.com/meghasr92/parasitismsilence`.

Code availability. `https://github.com/meghasr92/parasitismsilence`.

References

[1] Chen, Z. & Wiens, J. J. The origins of acoustic communication in vertebrates. *Nature communications* **11**, 1–8 (2020).

[2] Gerhardt, H. C. & Huber, F. Acoustic communication in insects and anurans: common problems and diverse solutions (2003).

[3] Kumar, A. Acoustic communication in birds. *Resonance* **8**, 44–55 (2003).

[4] Hedwig, B. Insect hearing and acoustic communication (2014).

[5] Kolluru, G. R. *The effects of an acoustically-orienting parasitoid fly Ormia ochracea on reproduction in the field cricket, Teleogryllus oceanicus: a trade-off between natural and sexual selection* (University of California, Riverside, 1999).

[6] Nokelainen, O., Hegna, R. H., Reudler, J. H., Lindstedt, C. & Mappes, J. Trade-off between warning signal efficacy and mating success in the wood tiger moth. *Proceedings of the Royal Society B: Biological Sciences* **279**, 257–265 (2012).

[7] Penn, D. & Potts, W. K. Chemical signals and parasite-mediated sexual selection. *Trends in Ecology & Evolution* **13**, 391–396 (1998).

[8] Stevens, M. *Sensory ecology, behaviour, and evolution* (Oxford University Press, 2013).

[9] Barbosa, F., Rebar, D. & Greenfield, M. D. Reproduction and immunity trade-offs constrain mating signals and nuptial gift size in a bushcricket. *Behavioral Ecology* **27**, 109–117 (2016).

[10] Wollerman, L. & Wiley, R. H. Background noise from a natural chorus alters female discrimination of male calls in a neotropical frog. *Animal Behaviour* **63**, 15–22 (2002).

[11] Vélez, A., Schwartz, J. J. & Bee, M. A. Anuran acoustic signal perception in noisy environments. In *Animal communication and noise*, 133–185 (Springer, 2013).

[12] Parris, K. M., Velik-Lord, M. & North, J. M. Frogs call at a higher pitch in traffic noise. *Ecology and Society* **14** (2009).

[13] Slabbekoorn, H. & Peet, M. Birds sing at a higher pitch in urban noise. *Nature* **424**, 267–267 (2003).

[14] Searcy, W. A. & Andersson, M. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics* **17**, 507–533 (1986).

[15] Otter, K., Chruszcz, B. & Ratcliffe, L. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology* **8**, 167–173 (1997).

[16] Zuk, M. & Kolluru, G. R. Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology* **73**, 415–438 (1998).

[17] Chapman, R. F. & Chapman, R. F. *The insects: structure and function* (Cambridge university press, 1998).

[18] Cade, W. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* **190**, 1312–1313 (1975).

[19] Robert, D., Amoroso, J. & Hoy, R. R. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science* **258**, 1135–1137 (1992).

[20] Adamo, S., Robert, D. & Hoy, R. Effects of a tachinid parasitoid, ormia ochracea, on the behaviour and reproduction of its male and female field cricket hosts (gryllus spp). *Journal of Insect Physiology* **41**, 269–277 (1995).

[21] Heinen-Kay, J. L. & Zuk, M. When does sexual signal exploitation lead to signal loss? *Frontiers in Ecology and Evolution* **7**, 255 (2019).

[22] Rüppell, O. & Heinze, J. Alternative reproductive tactics in females: the case of size polymorphism in winged ant queens. *Insectes Sociaux* **46**, 6–17 (1999).

[23] Ellers, J. & Liefting, M. Extending the integrated phenotype: Covariance and correlation in plasticity of behavioural traits. *Current Opinion in Insect Science* **9**, 31–35 (2015).

[24] Zuk, M., Rotenberry, J. T. & Tinghitella, R. M. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology letters* **2**, 521–524 (2006).

[25] Rotenberry, J. T. & Zuk, M. Alternative reproductive tactics in context: how demography, ecology, and behavior affect male mating success. *The American Naturalist* **188**, 582–588 (2016).

[26] Wilkins, M. R., Seddon, N. & Safran, R. J. Evolutionary divergence in acoustic signals: causes and consequences. *Trends in ecology & evolution* **28**, 156–166 (2013).

[27] Tinghitella, R. Rapid evolutionary change in a sexual signal: genetic control of the mutation 'flatwing'that renders male field crickets (teleogryllus oceanicus) mute. *Heredity* **100**, 261–267 (2008).

[28] Lehmann, G. U. & Lakes-Harlan, R. Adaptive strategies in life-history of bushcrickets (orthoptera) and cicadas (homoptera) to parasitoids pressure on their acoustic communication systems—a case for sociality? *Frontiers in Ecology and Evolution* **7**, 295 (2019).

[29] Rogers, D. Random search and insect population models. *The Journal of Animal Ecology* 369–383 (1972).

[30] Jansen, V. A. The dynamics of two diffusively coupled predator–prey populations. *Theoretical Population Biology* **59**, 119–131 (2001).

[31] Briggs, C. J. & Hoopes, M. F. Stabilizing effects in spatial parasitoid–host and predator–prey models: a review. *Theoretical population biology* **65**, 299–315 (2004).

[32] May, R. M. Stability and complexity in model ecosystems. In *Stability and Complexity in Model Ecosystems* (Princeton university press, 2019).

[33] Nicholson, A. J. & Bailey, V. A. The balance of animal populations.—part i. In *Proceedings of the zoological society of London*, vol. 105, 551–598 (Wiley Online Library, 1935).

[34] Holling, C. S. Some characteristics of simple types of predation and parasitism1. *The canadian entomologist* **91**, 385–398 (1959).

[35] Gerhardt, H. C. Phonotactic selectivity in two cryptic species of gray treefrogs: effects of differences in pulse rate, carrier frequency and playback level. *Journal of Experimental Biology* **211**, 2609–2616 (2008).

[36] Masson, M. V. *et al.* Bioecological aspects of the common black field cricket, gryllus assimilis (orthoptera: Gryllidae) in the laboratory and in eucalyptus (myrtaceae) plantations. *Journal of Orthoptera Research* **29**, 83–89 (2020).

[37] Symes, L., Ayres, M., Cowdery, C. & Costello, R. Signal diversification in oecanthus tree crickets is shaped by energetic, morphometric, and acoustic trade-offs. *Evolution* **69**, 1518–1527 (2015).

[38] Mhatre, N., Pollack, G. & Mason, A. Stay tuned: active amplification tunes tree cricket ears to track temperature-dependent song frequency. *Biology letters* **12**, 20160016 (2016).

[39] Gray, B., Bailey, N. W., Poon, M. & Zuk, M. Multimodal signal compensation: do field crickets shift sexual signal modality after the loss of acoustic communication? *Animal behaviour* **93**, 243–248 (2014).

[40] Bailey, N. W. & Zuk, M. Acoustic experience shapes female mate choice in field crickets. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2645–2650 (2008).

[41] von Helversen, D., von Helversen, O. & Heller, K.-G. When to give up responding acoustically in poecilimon bushcrickets: a clue to population density. *Articulata* **27**, 57–66 (2012).

[42] Reichard, D. G. & Anderson, R. C. Why signal softly? the structure, function and evolutionary significance of low-amplitude signals. *Animal Behaviour* **105**, 253–265 (2015).

[43] Bowen, A. E., Gurule-Small, G. A. & Tinghitella, R. M. Anthropogenic noise reduces male reproductive investment in an acoustically signaling insect. *Behavioral Ecology and Sociobiology* **74**, 1–8 (2020).

[44] Garamszegi, L. Z. Bird song and parasites. *Behavioral Ecology and Sociobiology* **59**, 167–180 (2005).

[45] Rayner, J., Aldridge, S., Montealegre-Z, F. & Bailey, N. W. A silent orchestra: convergent song loss in hawaiian crickets is repeated, morphologically varied, and widespread. *Ecology* (2019).

[46] Balenger, S. L. & Zuk, M. Roaming romeos: male crickets evolving in silence show increased locomotor behaviours. *Animal Behaviour* **101**, 213–219 (2015).

[47] Zukl, M., Simmons, L. W. & Cupp, L. Calling characteristics of parasitized and unparasitized populations of the field cricket teleogryllus oceanicus. *Behavioral Ecology and Sociobiology* **33**, 339–343 (1993).

[48] Anderson, R. M. & May, R. M. Regulation and stability of host-parasite population interactions: I. regulatory processes. *The journal of animal ecology* 219–247 (1978).

[49] Steinhaus, E. A. Crowding as a possible stress factor in insect disease. *Ecology* 503–514 (1958).

[50] Schreiber, S. J. Allee effects, extinctions, and chaotic transients in simple population models. *Theoretical population biology* **64**, 201–209 (2003).

[51] Hastings, A. Transients: the key to long-term ecological understanding? *Trends in ecology & evolution* **19**, 39–45 (2004).

[52] Gokhale, C. S., Papkou, A., Traulsen, A. & Schulenburg, H. Lotka-Volterra dynamics kills the Red Queen: population size fluctuations and associated stochasticity dramatically change host-parasite coevolution. *BMC Evolutionary Biology* **13**, 254 (2013).

[53] Schenk, H., Traulsen, A. & Gokhale, C. S. Chaotic provinces in the kingdom of the Red Queen. *Journal of Theoretical Biology* **431**, 1–10 (2017).

[54] Hastings, A. *et al.* Transient phenomena in ecology. *Science* **361** (2018).

[55] Sinha, S. & Parthasarathy, S. Unusual dynamics of extinction in a simple ecological model. *Proceedings of the National Academy of Sciences* **93**, 1504–1508 (1996).

[56] Schreiber, S. J. Chaos and population disappearances in simple ecological models. *Journal of Mathematical Biology* **42**, 239–260 (2001).

[57] Misra, J. & Mitra, A. Instabilities in single-species and host-parasite systems: period-doubling bifurcations and chaos. *Computers & Mathematics with Applications* **52**, 525–538 (2006).

[58] Venkateswaran, V. R., Roth, O. & Gokhale, C. S. Consequences of combining sex-specific traits. *Evolution* **75**, 1274–1287 (2021).

[59] Laiolo, P. The emerging significance of bioacoustics in animal species conservation. *Biological conservation* **143**, 1635–1645 (2010).

[60] Roca, I. T. *et al.* Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behavioral Ecology* **27**, 1269–1274 (2016).

[61] Nabi, G. *et al.* The possible effects of anthropogenic acoustic pollution on marine mammals' reproduction: an emerging threat to animal extinction. *Environmental science and pollution research* **25**, 19338–19345 (2018).

[62] Lengagne, T. Traffic noise affects communication behaviour in a breeding anuran, hyla arborea. *Biological conservation* **141**, 2023–2031 (2008).

[63] Phillips, J. N., Ruef, S. K., Garvin, C. M., Le, M.-L. T. & Francis, C. D. Background noise disrupts host–parasitoid interactions. *Royal Society open science* **6**, 190867 (2019).