Rising above the noise: The influence of population dynamics on the evolution of acoustic signaling

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Abstract. Acoustic signaling is employed by many sexually reproducing species to select for mates and enhance fitness. However, signaling in dense populations can create an auditory background, or chorus, which may interfere with a signal receiver's phonotactic selectivity, or the ability to distinguish individual signals. Feedback between the strength of an individual's signal, phonotactic selectivity, and population size, may interact in complex ways to impact the evolution of signaling within a population, potentially leading to the emergence of silence. Here we formulate a general model that captures the dynamic feedback between individual acoustic signalers, phonotactic selectivity, and the population-level chorus to explore the eco-evolutionary dynamics of an acoustic trait within a population. We find that population dynamics have a significant influence on the evolutionary dynamics of the signaling trait, and that very sharp transitions separate conspicuous from silent populations. Our framework also reveals that increased phonotactic selectivity promotes the stability of signaling populations, and that transitions from signaling to silence are prone to hysteresis. We suggest that understanding the relationship between factors influencing population size, such as environmental productivity, as well as factors influencing phonotactic selectivity, such as anthropogenic noise, are central to understanding the complex mosaic of acoustically signaling and silent populations.

1. Introduction

Acoustic signaling is the primary mode of communication shared by roughly 8.7 million species ranging from arthropods to mammals [1], inhabiting both terrestrial and marine environments. While acoustic signaling serves many functions, one of central importance is to attract potential mates. Several characteristics of acoustic signaling, such as the length of the signal, repetition rate, frequency, amplitude, pitch, and decibel level can be used to create a meaningful and distinct auditory signal [2, 3, 4]. While acoustic signaling is efficient, it does not come without costs. For instance, conspicuous signalers, or individuals producing acoustic signals far above the population mean, while more easily located by potential mates [5], can also be located by potential predators [6, 7] and parasites [8]. Moreover, conspicuous signaling can be energetically taxing, thus depleting energetic reserves that may otherwise be invested in growing and maintaining somatic tissues or directly invested into offspring [9]. Furthermore, the time spent signaling takes away from time spent foraging [10]. Finding the balance between the reproductive rewards of signaling, while both avoiding predators and maintaining adequate energetic reserves [11, 12], is a central challenge for organisms specializing in this mode of communication.

Signal-producing traits are subject to selection, and depending on the costs and benefits may intensify or diminish over evolutionary time. In some cases, changes in the trade-offs introduced by acoustic signals can lead to both rapid evolution as well as disruptive selection, driving the inherent acoustic diversity within particular phylogenetic groups [13]. Within a population, the signaler interacts not only with potential signal receivers, but with its acoustic environment as well [14, 15, 16, 17]. By producing a signal, the signaler in turn modifies the acoustic environment, which feeds back to affect the costs and benefits associated with signaling among conspecifics. In this sense, acoustic signaling can be thought of as an immediate form of niche construction [14, 18], as signaling behaviors directly alter the acoustic environment, sometimes referred to as the soundscape [19]. As competing signalers must engage this changing environment directly in order to rise above the noise, this feedback may result in further alteration to the acoustic environment. Such feedback serves to alter the fitness benefits of signaling, changing the shape of the fitness landscape for all individuals in the population [20].

The magnitude of the acoustic background produced by local signalers, here and henceforth referred to as the chorus, is influenced by both the traits of individual signalers as well as the number of signalers within the population. If individual signalers are conspicuous, and there are many of them, then the chorus is conspicuous. At the other extreme, if most individuals in the population are silent, so is the chorus. In addition to the influence of individual signalers on the chorus, the size of the population giving rise to the chorus is expected to directly influence the potential reproductive advantage attributed to a small change in an individual's signal. If the population is large, a minor increase in an individual's signal is expected to have negligible effects on the individual's reproductive gain. If the population is small, a minor increase in an individual's signal may carry with it larger reproductive advantages, as it is easier for signal receivers to target and reward the signaler when there are fewer signalers to navigate between [21, 22]. The ability of a receiver to discern between individual signalers, known as phonotactic selectivity, increases the potential reproductive gain given an increase in signal [23, 24]. That phonotactic selectivity is density-dependent means that the eco-evolutionary dynamics of acoustically signaling populations are expected to interact across similar timescales. The potential dynamic outcomes of such a system may thus have consequences with regard to whether signaling traits are reinforced over evolutionary time, or whether they are lost [25].

Here we devise a general model that captures the dynamic feedback between individual acoustic signalers, the population-level chorus, and the eco-evolutionary consequences with respect to a single continuous acoustic trait. Our framework provides insight into *i*) the complex interaction between population density and phonotactic selectivity in determining the fitness landscapes of signaling populations, *ii*) the influence of reproductive rewards on the evolutionary transitions between conspicuous and silent populations, and *iii*) the effects of increasing energetic costs on the evolution of acoustic signaling. Together, we demonstrate how the inherent feedbacks between the reproductive advantages associated with signaling against changes in population density and the strength of the chorus can position some populations to evolve towards signaling and others towards silence. As the benefits of signaling vary across heterogeneous environments, these feedbacks may contribute directly to the complex geographic mosaic of acoustic strategies observed among species.

2. Model Framework

We consider a population of organisms using acoustic signaling to attract potential mates. Individual fitness is thus a trade-off between the reproductive advantages of mate-signaling and survival. We assume that individual fitness is a function of a single quantitative character, which we specify here as the acoustic trait z, scaled to range between $z = 0$ (silence) and $z = 1$ (maximal signaling). The potential reproductive gain of an individual's signal is determined by how well it can be distinguished from the chorus, which in this case is represented by the mean acoustic signal of the population $\bar{z}$, which itself evolves over time. We thus track the eco-evolutionary dynamics of the population by evaluating the fitness of individuals with respect to an evolving chorus of signalers, where energetic investment in an increased acoustic signal relative to that of the chorus is met with an opposing divestment in those behaviors needed to acquire and maintain the organism's energetic stores and avoid a reduction in fitness. We capture the population dynamics and evolution of $\bar{z}$ with a discrete-time individual-based model, where we assume non-overlapping generations. Importantly, this framework is designed to be minimal and generalizable across organisms that signal using alternative acoustic modalities, where the acoustic trait could map onto any aspect of a signal with the only requirement being that there is a trade-off between the reproductive gains associated with signaling and their costs.

2.1. Individual fitness of a signaler

In a sexually-signaling population, reproductive gain is increased when an individual broadcasts a signal that can be distinguished by potential mates from the sensory background. A population of individuals i with variable trait values z_i, when signaling as a group, forms the chorus $\bar{z} = N^{-1} \sum_i z_i$, or the mean acoustic signal across N individuals, setting the acoustic background against which individuals must distinguish themselves. For example, among field crickets (Gryllidae) this trait may represent the syllable rate [26], in which case the chorus represents the conjoined mean syllable rate of the local population. For other species, this trait may represent signal characteristics such as chirp rate or duration in frog calls [27, 15], or even repertoire size or complexity in bird songs [28, 29].

In an environment devoid of external acoustic interference, the mean acoustic trait sets the reproductive standard for all signaling individuals within the population: individuals with $z_i > \bar{z}$ are assumed to have a reproductive advantage over those with $z_i < \bar{z}$ because they are able to attract potential mates. Reproductive gain can thus be described as a sigmoidal function, where $r_{\min}$ represents the minimum per-capita reproductive rate obtained by silent individuals, increasing to the maximum per-capita reproductive rate $r_{\max}$ obtained by individuals with acoustic traits far above the chorus $\bar{z}$. The chorus $\bar{z}$ describes the location of the step transition of the reproductive gain function, which changes dynamically over time as the population evolves (figure 1).

Table 1. Parameter definitions and values

Parameter	Description	Value/Range	Units
z	Acoustic trait	$0:1$	n.s.
$\bar{z}$	Chorus mean of the population	var.	z
N	Population size	var.	inds
N^*	Steady state population size	var.	inds
K	Carrying capacity	10^5	inds
$r_{\min}$	Minimum per-capita reproductive rate	$1:10$	time^{-1}
$r_{\max}$	Maximum per-capita reproductive rate	$1:10$	time^{-1}
$\alpha(N)$	Phonotactic selectivity	var.	ratio
ϕ	Acoustic sensitivity	$1:\mathcal{O}(N^*)$	inds/z
$d_{\min}$	Minimum per-capita mortality rate	0.01	time^{-1}
$d_{\max}$	Maximum per-capita mortality rate	$0:2$	time^{-1}
β	Environmental productivity	0.5	n.a.

n.s. denotes unspecified; var. denotes variable

In sparsely populated habitats where individual calls are more easily distinguished, a small change in an individual's acoustic trait z_i could result in a significant reproductive advantage if it is even slightly above the chorus, which in this case would be the product of a small number of conspecifics. This corresponds to $r(z_i|\bar{z})$ with a steeper slope between $r_{\min}$ to $r_{\max}$ about the chorus mean (solid lines, figure 1). In densely populated habitats, a small change in z_i near or above the chorus would be expected to have a much smaller effect on individual fitness. This corresponds to $r(z_i|\bar{z})$ with a shallower slope from $r_{\min}$ to $r_{\max}$ about the chorus mean (dashed lines, figure 1). The steepness of $r(z_i|\bar{z})$ about $\bar{z}$ describes the 'phonotactic selectivity' of the population, denoted as $\alpha(N)$. Phonotactic selectivity provides a qualitative measure of the auditory discerning ability of the receivers between signalers, where a high value (steep) means that receivers can easily discern between signaling individuals, whereas a low value (shallow) means that receivers cannot easily discern among signaling individuals. The ability to discern between signaling individuals declines with population size, where phonotactic selectivity is inversely proportional to N, such that $\alpha(N) = \phi/N$, where ϕ describes the acoustic sensitivity, or the sensitivity of phonotactic selectivity to changes in the population. Together, the reproductive component of individual fitness is described as

$$r(z_i|\bar{z}) = r_{\min} + \frac{(r_{\max} - r_{\min})}{1 + \exp\left\{-\frac{\phi}{N}(z_i - \bar{z})\right\}}. \tag{1}$$

We note that this framework requires the acoustic sensitivity ϕ to have units of individuals per trait value, such that the phonotactic selectivity $\alpha(N) = \phi/N$ represents the fraction of individuals in the population that are discernable by signal receivers. As $\phi \to \mathcal{O}(N)$, all individuals can be discerned, and the reproductive advantage associated with increasing one's signal above the chorus is maximized. For a given species, ϕ, while expected to arise from a complex array of physiological and neurological attributes [30], could be estimated experimentally, where the recognition of a provided signal relative to an acoustic background is evaluated as a function of the difference between signal and background.

Acoustic signaling entails significant energetic and temporal demands [31, 32]. As more energy and time is invested into signaling, the individual has less to invest in foraging, somatic maintenance, and parasitism/predation avoidance, all of which increase the risk of mortality [33, 34]. As such, we assume that silent individuals are subject to a lower per-capita mortality rate, $d_{\min}$, whereas maximally signaling individuals experience a higher per-capita mortality rate, $d_{\max}$. Mortality as a function of an individual's acoustic trait z_i is then written as

$$m(z_i) = d_{\max} - (d_{\max} - d_{\min})\exp\{-\beta z_i\}, \tag{2}$$

where β determines the steepness with which costs increase with higher z. Changes in β from population to population may capture differences in environmental productivity or predation/parasitsm, where greater energetic investment to survive in environments with scarce resources or more predators or parasites may result in a sharper rise in $m(z)$ above the chorus. Among species with individual variation in mate signaling, β could be estimated by the differential parasitism/predation pressures experienced by those that conspicuously signal compared to those that do not.

The fitness of an individual signaling with trait z_i is computed by its reproductive fitness, modulated by carrying capacity K, minus the fitness costs of mortality, together given by

$$w(z_i|\bar{z}) = r(z_i|\bar{z})\left(1 - \frac{N}{K}\right) - m(z_i). \tag{3}$$

The shape of the fitness function reveals a peak and a plateau, separated by a fitness trough as a function of z (figure 1). The peak emerges at $z = 0$, or silence, while the variable plateau emerges with $z \gg 0$. The fitness plateau at high $z \to 1$ represents the reproductive gains associated with conspicuous signaling, the value of which results from the trade-off between the energetic costs and reproductive rewards. When the

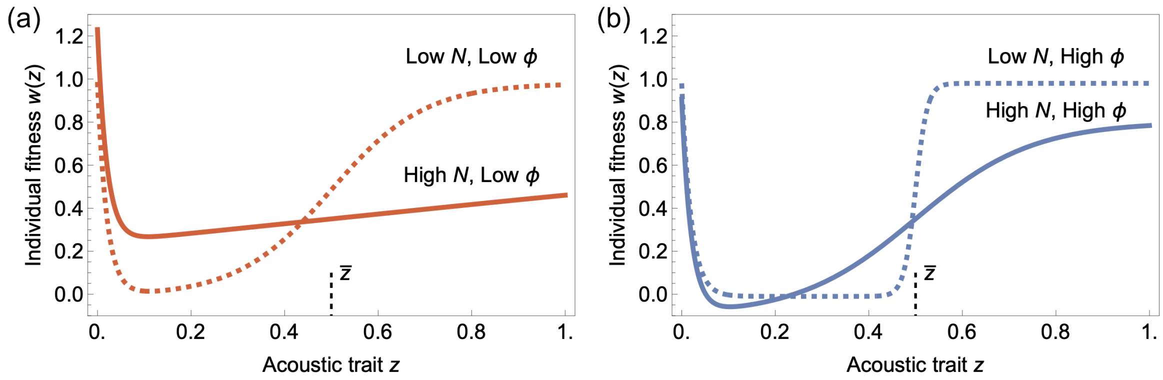

Figure 1. Individual fitness $w(z|\bar{z})$ as a function of low (dashed line) and high (solid line) population densities N, where acoustic sensitivies are either low (a) low (red; $\phi = 100$) and (b) high (blue; $\phi = 1000$). If the acoustic sensitivity ϕ is low, phonotactic selectivity remains limited even at low population sizes, such that a given increase in the acoustic trait z results in a smaller amount of reproductive gain. If acoustic sensitivity ϕ is high, phonotactic selectivity is enhanced at low population sizes, such that a given increase in the acoustic trait z results in a larger amount of reproductive gain. In both cases, the gains are greater when population sizes are low because individuals are more distinguishable against the chorus.

acoustic sensitivity (ϕ) is low, signal receivers cannot easily discern amongst signalers in a population, even if it is very small. This means that there is a smaller amount of reproductive gain associated with signaling above the chorus (figure 1a). As the acoustic sensitivity increases, the effects of phonotactic selectivity become exaggerated, such that smaller population sizes elicit sharper increases in reproductive gains when an individual's signal is slightly above the chorus (figure 1b). In other words, a high value of ϕ indicates that the population is highly sensitive to variations in signaling. Phonotactic selectivity changes with population size over time, dynamically changing the size and steepness of the fitness trough. Together, alongside evolution of $\bar{z}$, the fitness landscape presents a dynamic challenge to individuals, where they must constantly react to the shifting reproductive trade-offs associated with mate signaling.

2.2. Simulation of eco-evolutionary population dynamics

Because an analytical solution for the average fitness of the population $\bar{w}(\bar{z})$ is intractable, we numerically track the evolution of the full trait distribution of z, denoted by $f(z,t)$, over time, in addition to the population size $N(t)$. Throughout, we assume that generations are non-overlapping, where each time-step represents the complete turnover of a generation. The assumption of non-overlapping generations is most appropriate for invertebrate signaling populations, such as field crickets [35]. We start by assuming that the offspring calculated from equation 3 inherit their trait values from their parents with variability σ such that

$$z_{\text{offspring}}(t+1) = z_{\text{parent}}(t) + g, \tag{4}$$

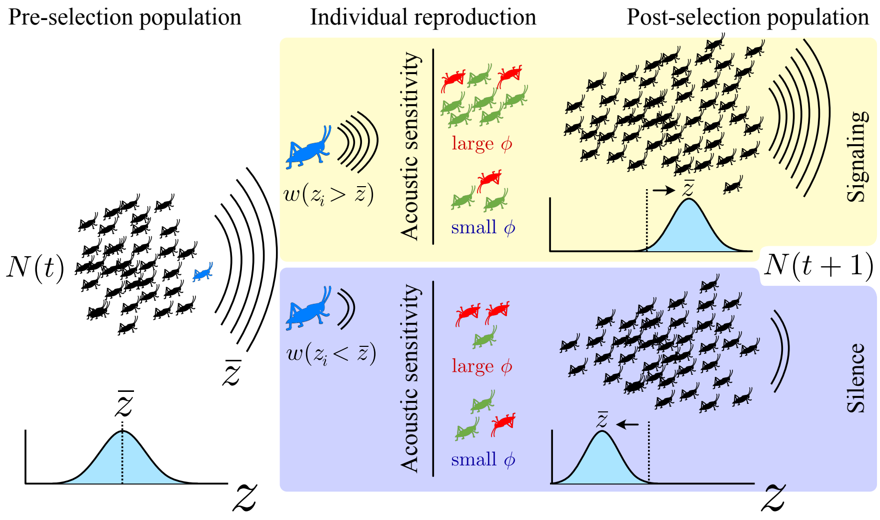

Figure 2. A signaling population $N(t)$ with chorus $\bar{z}$ is composed of individuals, each with an acoustic trait z_i. If individual fitness $w(z_i > \bar{z})$ tends to be relatively higher, the next generation $N(t+1)$ will evolve towards increased signaling. If individual fitness $w(z_i < \bar{z})$ tends to be relatively higher, the next generation $N(t+1)$ will evolve towards diminished signaling, eventually becoming silent. In both cases, evolution of the population is defined by changes to the chorus $\bar{z}$, which alters the selective landscape for individual signalers. Increasing acoustic sensitivity (ϕ) serves to benefit the reproductive output of signalers in relatively larger populations.

where $g \sim \mathrm{Norm}(0, \sigma)$, where we typically set $\sigma = 0.3$. The number offspring attributed to each individual i with trait z_i is given by $w_i(z_i|\bar{z})$, where the sum across reproducing individuals determines the future population size $N(t+1)$, such that

$$N(t+1) = \sum_{i=1}^{N(t)} w_i(z_i|\bar{z}). \tag{5}$$

With the new generation, a change in the trait distribution, from $f(z,t)$ to $f(z,t+1)$ marks the evolution of the population, dynamically altering the chorus $\bar{z}$ and reshaping the fitness landscape given by equation 3. Whether evolution favors conspicuous signaling, silence, or a position in between is therefore a product of the interplay between population size and the trade-offs associated with signaling (figure 2). Model runs were simulated for 1000 generations from an initial population size of $N(t=0) = 1000$ and $\bar{z}(t=0) = 0.5$, where we visually confirmed 1000 generations to be more than adequate for calculating steady state conditions.

3. Results & Discussion

Finding a mate amid the uncertainties and complexities of daily life is a challenge that all sexually reproducing species must overcome. The scale of this challenge grows as individuals within a population become more dispersed [36], particularly in heterogeneous or topologically complex environments [37] such as forest canopies, where encounter rates may be lower. In these situations, the ability to cast a broad signal that could be received by potential mates represents a significant behavioral advance, decreasing the time and energy required to initiate an encounter [36], with possibly large impacts on individual fitness [37]. The advantage of such signaling behaviors is reflected in the incredible diversity of signaling species, and the ways in which they signal. As heretofore mentioned in numerous examples, field crickets generate sound through stridulation, involving the rubbing of a specialized structure called a 'scraper' on one wing against a serrated vein called a 'file' on the other wing [38], emitting an acoustic signal to broadcast their mating potential in complex grassy and shrubby environments where other types of signals may be stifled. Other organisms signal to potential mates by employing different sensory systems. For example, the bodies of male orchid bees are covered in iridescent scales, generating metallic hues that signal to females their species identity and fitness [39]. Olfactory signaling is also commonly used among sexually reproducing species, particularly in systems where the signal must have a lengthy residence time to ensure that it is received by the potential mate, such as the scent deposited by mammals including mandrills, hyenas, many canids and felids, or even the more transitory pheromones emitted by humans [40]. Of course many, if not the majority, of signaling species employ multiple sensory modalities [39], combining their strengths and weaknesses to broadcast as efficiently as possible.

Acoustic signals have the advantage of being relatively long-distance, omnidirectional, effective in light-limited environments, and capable of encoding complex information on mate quality [41]. However, when surrounded by denser populations, individuals must compete against the acoustic background, which includes both signaling conspecifics (the chorus) as well as noise generated from other signaling species and abiotic sources. Among crickets, the mating success of male signalers tends to vary inversely with population size [22], suggesting that a given signal provides greater reproductive gain when there are fewer competitors to cloud the field. The difficulties in both standing apart from the crowd and recieving individually-sourced signals requires organisms to have evolved advanced signaling and receiving anatomies. Acoustic sensitivity, which describes a signal receiver's inate ability to identify a potential mate's signal apart from the noise, is a product of its anatomical signal-receiving equipment, and is known to be physiologically linked to changes in neural responsiveness [42]. Sensitivity to auditory signals is expected to vary from species to species across different environments. For example, among North American gray tree-frogs (*Hyla versicolor*), females more sensitive to external stimuli tend to demonstrate greater selectivity in mate choice [23], translating in our model to increased auditory sensitivity (increased ϕ).

From these specified relationships, we examine the effects of eco-evolutionary feedbacks between population size and the fitness trade-offs associated with conspicuously signaling, or remaining silent. We first describe the qualitative nature of eco-evolutionary steady state conditions, specifying under what regions of parameter space silence or signaling evolves, the effects of signaling on population densities, and the nature of the transition between silent and signaling regimes. We then examine the role of acoustic sensitivity, evaluate how changes in this species-specific characteristic impact the dynamic landscape determining evolutionary outcomes, and consider the role of anthropogenic acoustic disturbances. Finally, we explore how external mortality, whether from parasites co-opting mate signals to target hosts or simply from the effects of the additional energetic costs required to broadcast signals in depleted environments, can influence expected evolutionary trajectories.

3.1. Evolutionary transitions between signaling and silence

Our framework reveals the dynamic emergence of both silent and conspicuous signaling regimes, with sharp transitions separating these divergent evolutionary outcomes. We simulated both the population size $N(t)$ and trait distributions $f(z,t)$ across a range of values for $r_{\rm min}$ and $r_{\rm max}$ to calculate both chorus mean and population steady states, denoted by $\bar{z}^*$ and N^*, respectively. The reproductive incentive associated with signaling, given by $\Delta r = r_{\rm max} - r_{\rm min}$, is of central importance to the potential dynamics of the system. If $r_{\rm max}$ is very large relative to a particular $r_{\rm min}$, the potential reproductive gain of signaling – as long as the signaler can be distinguished from the chorus – is likewise large. If $r_{\rm max}$ is only slightly larger than $r_{\rm min}$, the potential reproductive incentive is similarly slight. Our results reveal that silence is the dominant outcome when $r_{\rm min}$ is relatively high (figure 3a). That silence is the dominant outcome when the reproductive gain associated with silence ($r_{\rm min}$) is large is relatively straightforward: the advantages of signaling do not outweigh the energetic costs when silent individuals receive increasingly attractive reproductive rewards.

Conspicuous signaling emerges as an evolutionary outcome when $r_{\rm min}$ is comparatively lower, and across an intermediate range of $r_{\rm max}$. To understand the emergence of signaling, one must also take into account the influence of population size, which directly influences phonotactic selectivity, or the ability of a signal receiver to distinguish the signaler from the acoustic background. When both $r_{\rm min}$ and $r_{\rm max}$ are low, there are no benefits to signal as Δr is small. Maintaining low $r_{\rm min}$ and increasing $r_{\rm max}$ results in crossing a dynamic threshold, above which the evolution of conspicuous signaling emerges (figure 3a,b) At this transition, the lower population densities emerging from similarly low reproductive rewards enhance the individual fitness associated with conspicuous signaling. This feeds back to increase the chorus, which signalers must surpass to gain the rewards associated with signaling, such that conspicuous signaling becomes the evolutionary outcome.

Because there are two fitness peaks positioned at both silence and signaling (figure 1), the transition from one to the other crosses a parameter region characterized by alternative stable states (dark yellow in figure 3a). This region is much larger than that dominated by signaling alone, where the evolutionary outcome (silence or signaling) is conditioned on the initial state of the population. As implied by the individual fitness function (figure 1), if the population chorus is initiated at a lower value, the evolution of silence is favored; if the poplation chorus is initiated at a higher value, the evolution of

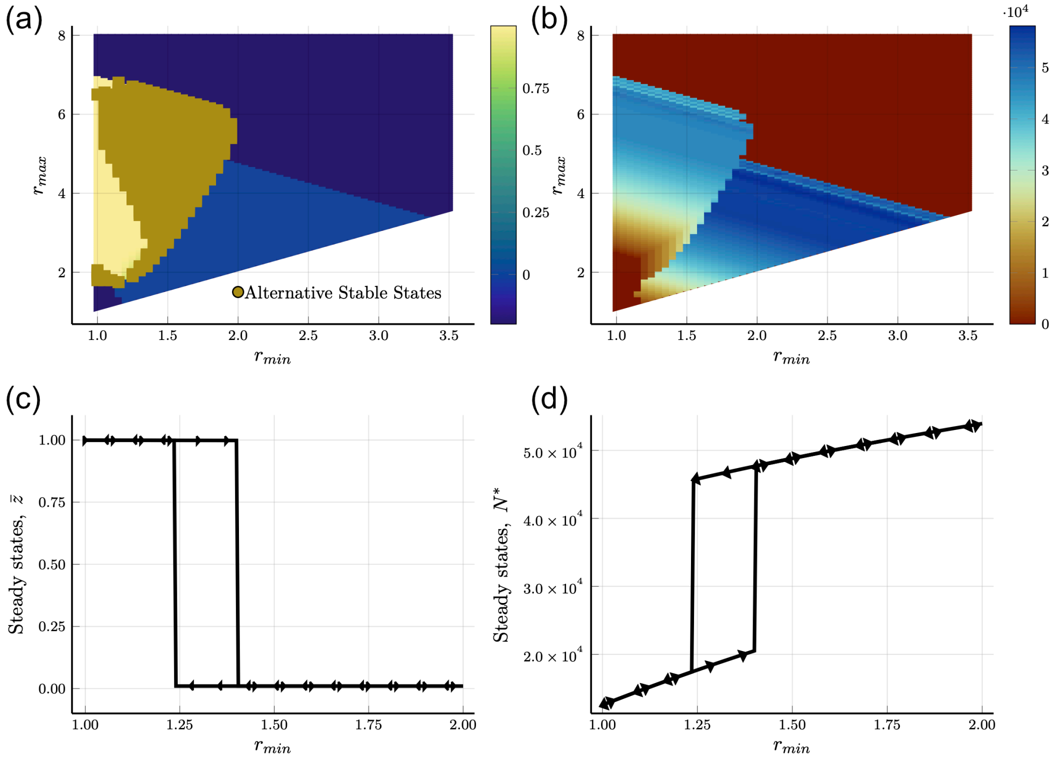

Figure 3. Reproductive incentives drive the evolution of silence or signaling. a) The chorus mean steady states $\bar{z}^*$ and b) population density steady states N^* as a function of minimum r_{min} and maximum r_{max} reproductive rewards. The population densities shown here are those for signaling populations in parameter regions identified as alternative stable states. An increase in r_{min} across the alternative stable state regime reveals hysteresis for both the population chorus (c) $\bar{z}$ and (d) population density. Dark blue regions in (a) and dark red regions in (b) denote population collapse. Throughout the auditory sensitivity is assumed to be high, such that $\phi = 1000$.

signaling is favored. From the signaling-dominant region, an increase in r_{min} pushes the system into an alternative stable state regime, where hysteresis in both the evolution of silence versus signaling as well as the resulting population size is observed (figure 3c,d). For signaling populations, increasing the reproductive reward associated with signaling (r_{max}) gradually increases the population size (figure 3b). In contast, increasing the reproductive reward associated with silence (r_{min}) gives rise to a sharp increase in the population size once the alternative stable state regime is traversed (figure 3b,d). The presence of hysteresis alternatively implies that if the population was starting with a high reproductive reward associated with silence, its decline would not result in a population crash until the alternative stable state regime is traversed in the opposite direction. We note that, while signaling and silent regimes can vary in terms of their effects on population size, the alternative steady state regimes tend to associate lower population densities with signaling, and higher population densities with silence. As reproduction continues to increase in either signaling or silent populations, the resultant population growth generates an instability where population fluctuations emerge (figure 4a), followed by a period-doubling cascade and eventually chaos. The onset of chaos serves to crash both signaling and silent populations (dark blue and dark red colors in panels (a) and (b) respectively in figure 3), though populations within alternative stable state regimes can sustain a higher r_{max} than those that are silent.

That signaling can emerge or be abruptly extinguished among populations is a phenomenon that has been observed in natural systems; when signaling incurs additional fitness costs, rapid evolution of silence can result. For example, on the island of Kauai (Hawaii), the presence of parasitoid flies (*Ormia ochracea*) – which target and attack signaling oceanic field crickets (*Teleogryllus oceanicus*) – resulted in the evolution and dominance of a silent flatwing morph within 12-20 generations [43, 44]. This evolutionary transition was notabley abrupt, having been observed during sequential field seasons in Kauai between 1991 and 2003, when the population was observed to go completely silent [43]. However, silent flatwing male morphs also demonstrate increased reproductive output once precopulatory barriers are succeeded [45], such that the relative effects of mortality from parasitoid flies versus the potential reproductive advantages of flatwing morphs are not straightforward. Indeed, our model results would support the notion that the reproductive advantage of the flatwing morph may have been, generally speaking, as important as parasitoid pressure in driving and/or maintaining its eventual dominance. Specifically, our results suggest that a plausible route from signaling to silence is one characterized by the diminution of the reproductive advantage associated with signaling (r_{max}) relative to that associated with silence (r_{min}), where an increase in r_{min} (analagous to the reproductive output of the flatwing morph) clearly transitions the system from a signaling to a silent regime. While the relative importance of parasitoids versus the postcopulatory reproductive advantages of flatwing morphs is not clear [45], and our general model does not include specific genetic mechanisms or potential pleiotropic effects likely at play in the *T. oceanicus* system [45], our framework appears to align qualitatively with the observed evolutionary transition.

The onset of population cycles followed by a period-doubling cascade and ultimately chaos, as reproductive output increases, is a natural result of the logistic relationship assumed for the individual fitness function (equation 3), however its effect on the evolution of signaling versus silence is instructive. With the emergence of cycles, the fitness landscape changes abruptly with sharp inter-generational transitions between high and low population sizes (figure 4a,b). When populations increase to the top of the cycle, phonotactic selectivity is weak, such that signalers cannot be easily distinguished from the population's acoustic background, increasing the relative fitness associated with silence (the silent regime; green point and curve in figure 4a,b, respectively). When populations decrease to the bottom of the cycle, phonotactic selectivity is much stronger because there are fewer individuals to discern, increasing the relative fitness associated with conspicuous signaling (the signaling regime; pink point and curve in figure 4a,b, respectively). This quickly fluctuating fitness landscape means that the strength of selection is very weak, such that the between-generational fitness differences are too

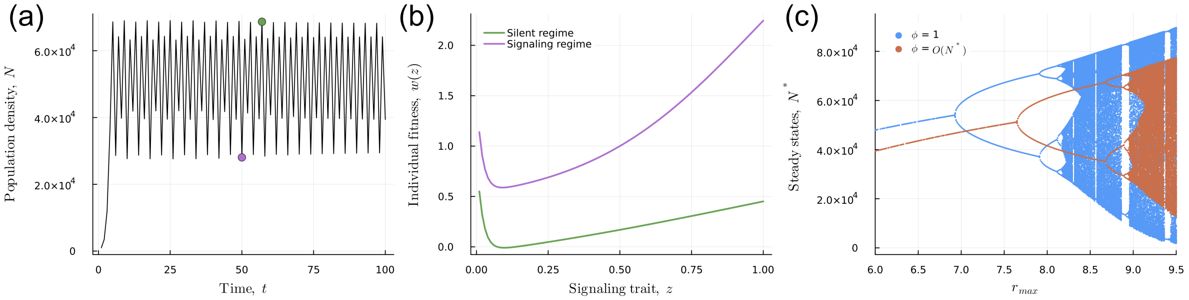

Figure 4. a) Population steady states in the cyclic regime across 100 generations, assuming $r_{\text{max}} = 7$ and $r_{\text{min}} = 2$. b) Individual fitness $w(z|\bar{z})$ as a function of z associated with the population maxima and minima in the cyclic regime as in (a). c) Population steady states N^* as a function of increasing reproductive rewards associated with signaling r_{max}. Population steady states are shown assuming that acoustic sensitivity (ϕ) of signal receivers is low (blue) and on the order of the steady state population size (orange). Increasing the acoustic sensitivity of signal receivers promotes the stability of signaling populations by increasing the value of r_{max} marking the onset of period-doubling cascades and ultimately chaos.

large for selection to produce an evolutionary response. Depending on the relative values of r_{max} and r_{min}, the onset of population cycles can either be associated with a signaling or silent population, where the weak selective forces of the oscillating fitness landscape have little impact on the prevailing trait dynamics. Across the period-doubling cascade, the population devolves into chaos, ultimately resulting in total collapse (figure 4c).

Decreasing the acoustic sensitivity ϕ lowers the signaling advantage, such that signal receivers are less able to distinguish signalers against the backdrop of a signaling population. This means that the fitness advantages that can be realized by signalers when populations are low are reduced. Importantly, we observe that an increased auditory sensitivity results in period-doubling cascades and the onset of chaos occurring at much higher values of r_{max} (figure 4c). As such, increased auditory sensitivity enlarges the stable regime of signaling populations. When signal receivers are unable to discern among signalers even at lower population sizes (low ϕ), silence is nearly always the end-state of selection (except when both r_{min} and r_{max} are very low), a dynamic that emerges from a higher individual fitness peak at silence ($z = 0$; supplementary figure S2). It is this same dynamic that promotes an earlier onset of the period-doubling cascade leading to chaos as r_{max} increases (figure 4c). That increasing auditory sensitivity promotes population stability by delaying the onset of cycles and chaos suggests that the evolution of increasingly sensitive auditory machinery may not only carry with it a reproductive advantage but promote stability of the population as a whole.

That the evolution of silence versus signaling involves an interaction between the rewards of signaling and population size is supported by observations in natural systems. For example, among field crickets (*Gryllus campestris*), signaling dominates when populations are at low densities, whereas silence dominates at high population densities, where mates are sought by alternative means [46]. While this is likely a product of behavioral plasticity (a feature not present in our current approach), it demonstrates how selective feedbacks may direct evolution to alternative outcomes when behaviors are less plastic. It is well-known that changes in population densities impact the fitness of conspicuous signalers, and by extension signal evolution [47, 48], however the mechanistic links between signalers and signal receivers as a function of population size is not well understood. While reproductive incentives to signal are impacted by fluctuations in the biotic and abiotic environment [49, 50, 51, 52, 53, 54, 55], our results support the notion that increased investment in auditory reception may promote stability by reducing the range of growth rates at which population cycles emerge. Of potential importance is the notion that signal receivers with lower auditory sensitivity may be more susceptible to anthropogenic noise [56, 57]. In effect, external acoustic noise such as that produced by anthropogenic sources (e.g. highways or industrial noise), would serve to decrease the native sensitivity of an organism's sending/receiving anatomical equipment, effectively serving to lower ϕ in our framework, which both erodes the parameter space resulting in signaling evolutionary outcomes, and increases the potential for destablizing period-doubling cascades. While the relationship between auditory reception complexity and the stability of acoustic signaling populations has not been explored, we suggest that the potential fragility of species with naturally low acoustic sensitivity – or declining sensitivity due to interference by anthropogenic noise – may be of particular consequence for conservation efforts.

3.2. The costs of signaling

So far, we have focused our analysis on *i*) the reproductive incentive associated with signaling (i.e. the relative values of $r_{\max}$ versus $r_{\min}$), and *ii*) the acoustic sensitivity ϕ, which determines the potential advantage signalers have relative to the size of the population. We have not yet considered the influence of costs associated with signaling, which serves to lower the reproductive yield of individuals as a function of their acoustic trait z. Two common examples of signaling costs frequently considered in natural systems include the mortality incurred by parasitoids that hone on sexual signals to acquire prey [58, 59, 8], as well as the time and energy costs that individuals must invest in signaling at the expense of finding and procuring their own energetic reserves [9, 60, 61], particularly in low-productivity environments. In both cases, we would assume increased mortality risks with increased signaling (as described in equation 2, where $d_{\min}$ is the lower mortality suffered by silent individuals, and $d_{\max}$ is the higher mortality suffered by signaling individuals). For example, cricket mortality is highly environmentally dependent [62, 63], where in arid regions with limited resource availability, small changes in acoustic signal can drastically increase mortality [64, 65]. When resources are more abundant, individuals have greater energetic latitude and may be more likely to to adopt costly signals [66, 67]. Importantly, organisms living in marginal environments may additionally suffer decreased immune function, increasing susceptibility to parasitism [68], and compounding sources of mortality. Given that our

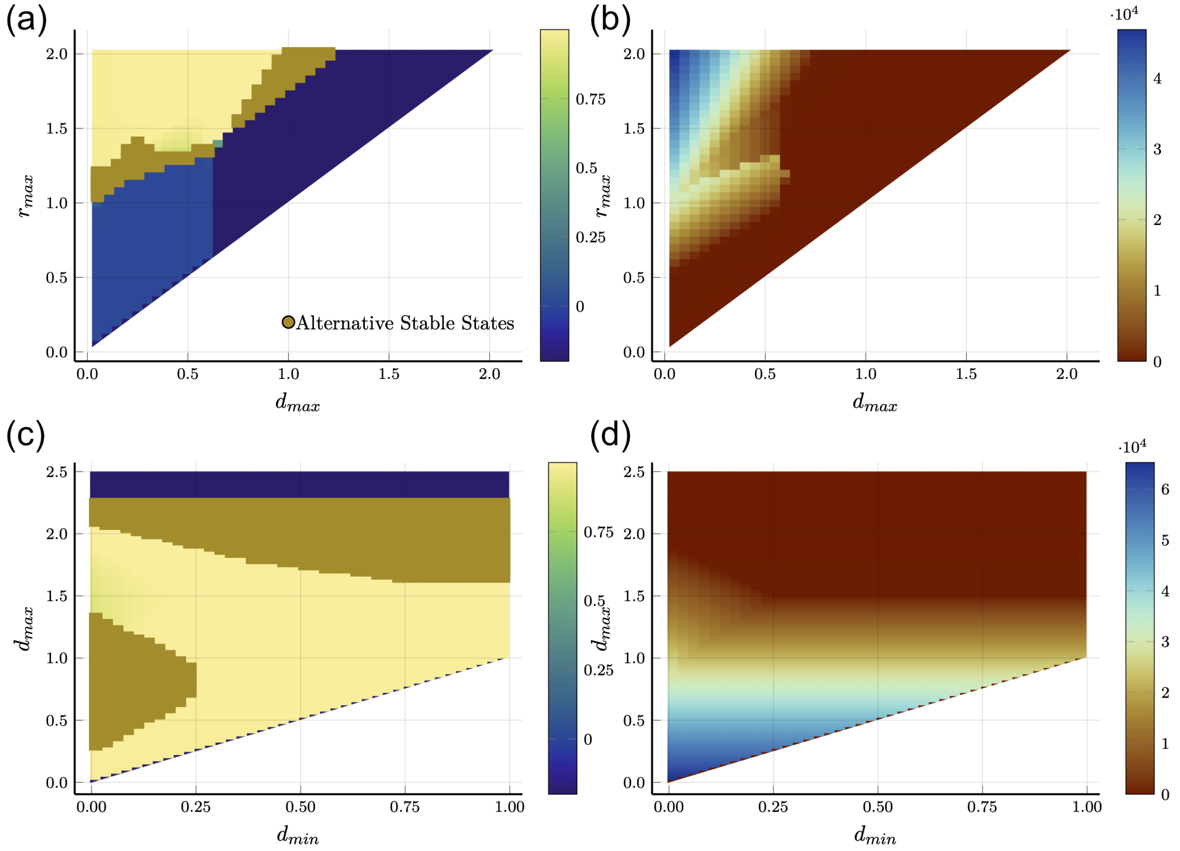

Figure 5. The influence of the mortality associated with signaling ($d_{\max}$) and the reproductive benefits of signaling ($r_{\max}$) on (a) the chorus mean steady state, $\bar{z}^*$ and (b) the population density steady state N^*. The influence of background mortality and mortality associated with signaling on (c) the chorus mean steady state, $\bar{z}^*$ and (d) the population density steady state N^*. Dark blue regions in (a,c) and dark red regions in (b,d) denote population collapse.

framework assumes complete generational turnover from timestep t to $t+1$, mortality is imposed among offspring prior to their reproductive maturity. In that sense, per-individual fitness (equation 3) accounts only for those offspring that survive.

When acoustic sensitivity is higher, and compared to the influence of the reproductive advantage (increasing $r_{\max}$), the impact of increasing signal-related mortality (higher $d_{\max}$) primarily functions to drive the onset of population collapse. In the $r_{\max}$ versus $d_{\max}$ parameter space shown in figure 5a,b, if a signaling population (higher $r_{\max}$) incurs greater mortality costs associated with signaling (higher $d_{\max}$), it first enters an alternative stable state regime followed by population collapse. Here it is important to note that the alternative stable state regime has very low (near extinction) population densities, such that it is effectively moot. Similarly, if a silent population (lower $r_{\max}$) suffers increased mortality associated with signaling (higher $d_{\max}$), population collapse is the eventual outcome without passing through an alternative stable state regime. In the case where the reproductive incentive to signal is very high, and the costs of signaling are very low, population densities peak for signaling populations. Interestingly, we note that for only a small parameter range (intermediate $r_{\max}$ values), an increase in mortality associated with signaling can push the population from a signaling regime to an alternative stable state regime, and then to silence, whilst avoiding population collapse. A similar dynamic occurs if the acoustic sensitivity is very low, except that there is no longer a signaling regime (supplementary figure S2).

We gain additional perspective by comparing the relative effect of the mortality associated with signaling ($d_{\max}$) to that associated with silence, or the background mortality ($d_{\min}$; figure 5c,d). As before, increasing $d_{\max}$ for a signaling populaton serves to push the system into an alternative steady state regime prior to population collapse, however it is one characterized by extremely low population densities. We also observe an alternative stable state regime at intermediate values of $d_{\max}$ and low values of $d_{\min}$ (figure 5c), where population densities remain relatively high, though altogether higher if the population is at the silent stable state (supplementary figure S3). In this case, when the background mortality is very low and the mortality associated with signaling is not so high as to push the population to near-collapse, the fixation of silence or signaling within the population are both feasible evolutionary outcomes.

We have shown that an evolutionary transition from signaling to silence can emerge by either decreasing the reproductive incentives associated with signaling or by increasing the mortality associated with signaling. This transition may either be realized by moving from a parameter space where silence or signaling alone are the singular outcomes, or one where the outcomes are sensitive to initial conditions, and where the transition could be realized by external pressure on the trait distribution. Our general model aligns well with an observed evolutionary transition in signaling behaviors among Hawaiian field crickets facing increased parasitoid depredation [43], alongside potential reproductive benefits associated with the silent flatwing morph [45]. We emphasize that this alignment is purely qualitative in nature, as our model is presented as a general framework that captures only the reproductive and mortality trade-offs associated with silence versus signaling. Reality is clearly more complex. Any direct application of our framework to a single system would require the incorporation of species-specific energetics as well as potentially linking the acoustic trait to multiple functional trade-offs, thereby capturing pleiotropic effects. Yet that the eco-evolutionary dynamics of acoustic signaling are as rich as we observe – even in the minimal model explored here – suggests that such approaches may be instructive, and at the very least showcase how clear trade-offs associated with the gains and costs of signaling can lead to its emergence or loss.

Because acoustic signaling is inherently spatial in terms of the efficacy of both signaling and receiving, an important expansion of our approach may be to introduce a spatial dimension. Where we have here considered a single admixed population, subpopulations inhabiting a geographic mosaic may be important for directly confronting empirical systems, where differences in the auditory background [69], predator pressure [70], and migration between populations [71], contributes to the cumulative selective pressure of the metapopulation. For example, signaling populations that span urban-to-natural gradients may face very different local auditory challenges as individuals compete with anthropogenic sources of noise, including traffic and industrial noise. Among frogs, this has led to the adoption of sexual signals with higher complexity and amplitude [72], potentially impacting both energetic costs and acoustic sensitivity. In such metapopulations, travel between populations that are subject to different selective pressures and evolutionary optima has been shown to lead to 'migrational meltdown' [71], where suboptimal populations can dominate local environments, potentially leading to increased extinction risk [73]. Signaling among conspecifics can in some cases give rise to signal synchronization [74], which can reduce predation risks at the expense of the potential reproductive gains associated with signaling [75]. Understanding how such dynamics operate at the metapopulation level, and across both spatial scales and evolutionarily timescales, may be essential for predicting the selective outcomes of signaling populations in natural environments.

4. Conclusion

The evolution of both signaling and silence is driven by the trade-off between reproductive rewards, energetic costs, and phonotactic selectivity constrained by the acoustic sensitivity of signal receivers. Because the reproductive success of signalers is greater when population densities are low [46], feedback between the size of the population and the strength of selection plays a significant role in determining which evolutionary outcome is realized. In nature, fast-growing populations can be more prone to cyclic oscillations, and perhaps chaos and extinction [76, 77, 78]. The likelihood of these dynamic transitions can be increased by changes in predator interactions, Allee effects, and/or mating success [79, 80]. Moreover, the effects of predation and especially parasitism are expected to not only increase the reproductive costs of signaling, but to have compensatory effects on population size. The results of our framework suggest this may have a large influence on the evolution of signaling. Because the sensitivity of phonotactic selectivity to changes in population size largely determines whether signaling is feasible or not, the introduction of acoustic pollution in disturbed habitats may be expected to influence under what conditions signaling maximizes fitness [81, 82, 83, 84]. In order to gain insight into the evolution of acoustic signaling, we must understand the mechanistic connections that link signalers to signal receivers and the fitness consequences associated with individuals who strive to rise above the noise.

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