

Separating acoustic signal into underlying behaviors with self-exciting point process models

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ABSTRACT

In animal communication, signals can arise endogenously or in response to cues, such as signals by conspecifics. When one signal serves dual functions, such as in birds that use the same song for mate attraction and territorial defense, the underlying reason for a vocalization cannot be determined without direct observations, and even then, may be hard to discern. We present an inhomogeneous, self-exciting point process model to estimate the underlying reasons for why an individual initiates a signal. In our application of these models, endogenous signals are assumed to arise at a constant rate, but each signal can also instigate (“self-excite”) additional signals by conspecific individuals. When applied to bullfrog (*Rana catesbeiana*) calls and ovenbird (*Seiurus aurocapilla*) songs, our model performs as well as a homogeneous point process model typically used to describe count data, while providing additional detail on the underlying motivations for signals. Although we apply the models to acoustic signals, our model can be applied to any self-exciting process and can be extended to include spatio-temporal dynamics in signals.

1. Introduction

The evolution of reliable signals in animal communication is governed by fitness benefits accrued by signalers and receivers (Smith and Harper, 2003; Searcy and Nowicki 2005; Wells and Schwartz 2007). For example, the role of acoustic signals in resource acquisition and defense has long been assumed, with early ecologists taking it for granted that bird song and other signals are used in mate attraction and territory defense (e.g. Howard 1920, Tinbergen 1939, Nice 1941), as since confirmed by decades of research. Countersinging, chorusing, and other aggressive vocal responses are used by songbirds (Smith 1959; Heck-enlively 1967; Wasserman 1977; Yasukawa 1981), anurans (Wells 1977; Gerhardt 1992), orthopterans (Schatral et al., 1984), and primates (Cowlshaw 1992), among others, in territory establishment and defense. Acoustic signals are also associated with mate attraction (Left-wich and Ritchison, 2000; Morris et al., 2002; Wells and Schwartz 2007; Proppe and Ritchison 2008; Lohr et al., 2013), mate guarding (Diniz et al., 2018), and pair bond maintenance (Whittingham et al., 1997;

Ham et al., 2017). Species also use acoustic signals for other functions such as predator deterrence (e.g. Pereyra and Morton 2010) or as a warning to alert other individuals of predator presence (e.g. Halkin 1997; Park et al., 2004).

Broadly speaking, acoustic signals can be grouped into three classes based on the cause and subject of the signal: 1) those that arise endogenously, such as widely broadcast bird songs to attract a mate or advertisement calls in anurans, 2) those that arise in response to a signal by a different individual, such as countersinging or chorusing to defend territorial boundaries, and 3) those that arise due to a stimulus external to both the signaler and receiver, such as presence of a predator (Smith and Harper, 1995). We will focus on the first two classes since they involve only intraspecific interactions (Searcy and Nowicki, 2005) and they rely on self-reporting instead of information external to the signaler and receiver, making them relatively predictable based on the evolutionary history of the system that led to these signals being reliable (Smith and Harper, 1995). For example, one can predict how frequently a male songbird should sing to attract a mate or to defend territorial

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boundaries based on costs and benefits of the signal, but it is harder to predict the occurrence of alarm calls without knowing whether or not there is a cue (i.e. a nearby predator). When the underlying reasons for an acoustic signal are known, it is possible to model and predict not only the pattern of signals (e.g. Dawson and Efford, 2009), but also the patterns of behavior associated with the signals (e.g. Byers 2007; Upham-Mills et al., 2020).

For species with multi-signal repertoires where signal types are associated with specific behaviors, ascertaining the underlying reason for a signal can be done by linking signals to observed behaviors. For example, observations of songbirds have been used to determine which song types or elements (e.g. buzzes, trills) are linked to territoriality and which to mate attraction (Trillo and Vehrencamp 2005; Proppe and Ritchison 2008; Lohr et al., 2013). Similarly, some anurans alter the frequency with which they combine call types (e.g. whines, chucks) to attract females when perceived predation risk is high (Bosch et al., 2000). When a signal type is used for multiple behaviors, however, the reason for any given signal requires direct observation of the individual at the time it occurs (Leftwich and Ritchison, 2000). To make behavioral inferences for species with such signals, or for which the functional role is unknown, researchers either need detailed field observations, which may be impossible to obtain and are often subject to detection bias and observation error, or a modeling framework that partitions the underlying behavioral processes and estimates their parameters separately.

To break behavioral patterns into their component parts, researchers can use a class of self-exciting point process models (Hawkes, 1971), a specific case of an inhomogeneous point process in situations where the history of the process predicts future events. These methods have been used in a wide variety of settings, such as to understand the occurrence of earthquakes (e.g. Türkyilmaz et al., 2013; Fox et al., 2016), infectious disease transmission and outbreaks (e.g. Meyer et al., 2012; Kim et al., 2019; Schoenberg et al., 2019), or the behavior of financial market traders (e.g. Hewlett, 2006; Bowsher, 2007; Chavez-Demoulin and McGill, 2012; Bacry et al., 2015). Here, we present a self-exciting point process model that can be used to estimate whether a given signal arises unprompted or in response to a conspecific signal. We illustrate the model using case studies of intraspecific signals in frogs and songbirds and demonstrate how the models can be used to test hypotheses about underlying reasons for signals.

2. Materials and methods

2.1. Model

Self-exciting point process models (Hawkes, 1971) are used to model counting events that arise from an inconsistent rate that varies with the history of events. Models in this class assume some intrinsic background rate of event occurrence, and that when an event occurs, it incites (or “self-excites”) additional occurrences of that event. For example, an earthquake triggers aftershocks that are spatially and temporally linked (Vere-Jones, 1970), and buyer behavior in stock markets is influenced by other buyers’ decisions (Hewlett, 2006). Depending on the nature of the process generating the events, however, over time the self-exciting nature of the process declines and additional event occurrences cease until a new instance of the event (Hawkes, 1971).

Classical self-exciting point process models (Hawkes, 1971) and their extensions treat time as a continuous process and estimate the instantaneous rate of events. In many systems, it is more feasible to treat time as discrete and to only consider the influence of events in previous time bins. For example, although biological processes operate in continuous time, data measurements and analysis are often done in discrete time due to logistical constraints in recording observations (Kass et al., 2011). In such cases, the true distribution of the data is assumed to arise from a continuous process, but the observed data are not; thus, researchers often create time bins that are sufficiently small to only capture either 0 or 1 signals and model the observed data using a discrete-time logistic

approximation. These types of extensions of the general class of self-exciting point process models make fitting the models more feasible for a broad range of biological processes with different observational challenges that make continuous time recordings difficult or impossible.

In our model (Fig. 1), we treat time as discrete with sufficiently small time bins to only include either 0 or 1 observed signals. Due to observation error and limitations of data measurement (see below for recording details), we assume the true distribution of signals arises from a Poisson process and more than one simultaneous signal can occur in a time bin but cannot be distinguished. Thus, the occurrence of one or more signals at time t arises from a Poisson process with a variable rate (λ_t) (Eq. 1) that describes the overall rate of signals in the system. This rate (λ_t) in turn depends on an intrinsic background rate of the signal process (μ) and a conditional intensity at time t (γ_t) based on the history of signals prior to t (Eq. 2). The background rate (μ) is assumed to be constant and is modeled with uninformative priors (Eqs. 4–8). In situations where data could inform μ , additional parameters and covariates could be used to estimate it. The conditional intensity (γ_t) is modeled as a function of individual motivation to respond to a signal, the self-excitement parameter (α), based on memory of the history of signals (η_t), which decays at an exponential rate based on the memory kernel (β) (Eq. 3). We specified an exponential rate of decay based on models of animal ‘forgetting’ that assume exponential decay in memory and response to signals (Speed 2000), however, alternative specifications of the memory kernel could be used. The self-excitement parameter (α) and memory kernel (β) are drawn from uninformative gamma distributions that have been truncated at arbitrary maxima that represent biologically implausible scenarios (Eqs. 9 and 10). The history of the process (η_t) is a

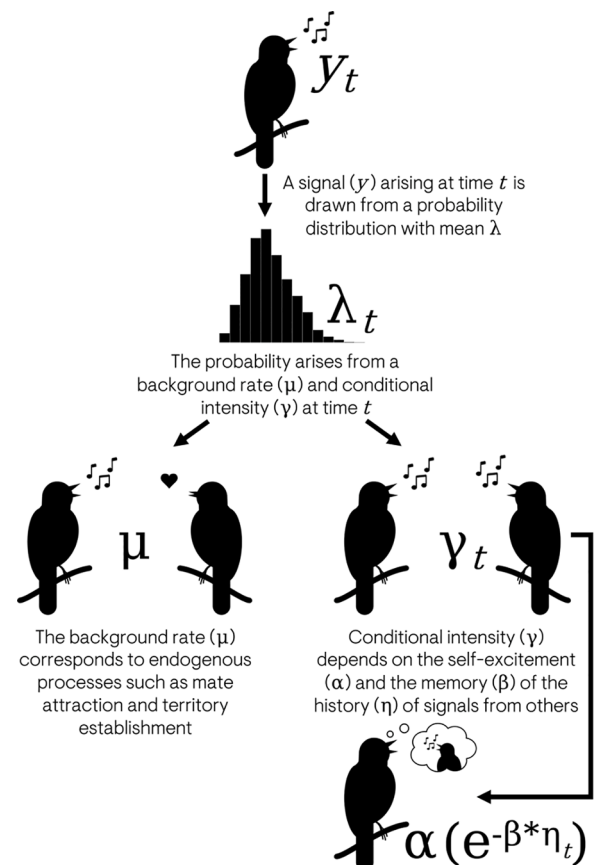


Fig. 1. Conceptual diagram illustrating our model, in which a signal arising at a given time arises from a background rate of singing (e.g. to attract a mate or establish a territory) and a conditional intensity (e.g. countersinging behavior) based on self-excitement of the process which decays over time as the memory of the history of signals diminishes.

vector of time differences between the current time t and event occurrences in previous time steps leading up to time t (i.e. $\eta_t = t - t_i:t$). We restrict the history based on the memory (m) of the process, where m is a constant that is determined based on biological assumptions of the system. Thus, t_i is indexed starting from $i = t - m$ for all times $t > m$; times $t < m$ are indexed starting from $i = 1$. By setting a limit on the maximum memory (m) of the process, this restricts the window of previous events that can influence signals at the current time step t . Signals from all previous time bins could be modeled, but the inclusion of this cutoff reduces computational intensity by fixing the influence of signals outside the memory to zero rather than estimating many infinitesimally small values.

$$y_t \sim \text{Pois}(\lambda_t) \quad (1)$$

$$\lambda_t = \mu + \gamma_t \quad (2)$$

$$\gamma_t = \sum_{i: t_i - m < t_i < t} \left[\alpha * \left(e^{-\beta \eta_{t_i:t}} \right) \right] \quad (3)$$

$$\mu \sim \text{Gamma}(k, \theta) \quad (4)$$

$$k = x^2 / \sigma^2 \quad (5)$$

$$\theta = x / \sigma^2 \quad (6)$$

$$x \sim \text{Unif}(0, 100) \quad (7)$$

$$\sigma \sim \text{Unif}(0, 100) \quad (8)$$

$$\alpha \sim \text{Gamma}(0.0001, 0.0001)[0.0001, 1] \quad (9)$$

$$\beta \sim \text{Gamma}(0.0001, 0.0001)[0.0001, 5] \quad (10)$$

The underlying processes governing when events occur, μ and γ_t , correspond to the first two classes of behavior described earlier – a background level of signals such as those used to attract a mate, and responsive signals such as countersinging. The background rate (μ) arises endogenously with no influence of previous signals from conspecifics. It could, however, be modeled based on environmental factors that influence mate attraction in systems where these factors are hypothesized or known. The conditional intensity (γ_t) depends on the history of the process, representing signals by conspecifics that increase the probability that an individual responds with a new signal that does not arise endogenously. By separating these processes, self-exciting point process models (Hawkes, 1971) let us make predictions about factors that affect behavioral processes and understand why signals occur when they do, and for what reasons. This ability sets them apart from homogenous point process models, which are commonly used to describe count data such as songs (e.g. Byers, 2007; Upham-Mills et al., 2020), that do not distinguish the underlying reasons for a signal.

2.2. Applications of the model to empirical case studies

To illustrate use of our model, we applied it to two acoustic signal datasets. The first dataset consists of times when American bullfrogs (*Rana catesbeiana*) initiated calls in a single pond in eastern Connecticut, USA, during the 2006 and 2007 breeding seasons. Calls were collected with an autonomous, continually recording unit placed nightly in a new, randomly selected, position around the 135 m perimeter of the study pond, and each call was automatically detected with the Song Scope® bioacoustics software (version 2.4; Ingranat 2007, 2009) (see Herrick et al., 2018 for detailed data collection methods). For the second dataset, we sampled singing behavior of male ovenbirds (*Seiurus aurocapilla*) using autonomous recording units in 15 Connecticut forest fragments ranging in size from 19 to 1014 ha during the 2017 and 2019 breeding seasons. Within each forest fragment, observers made 3–7 recordings

(mean = 5.81, sd = 1.04) at different points within the fragment, each separated from every other point by several hundred meters. Due to habitat heterogeneity within forest fragments, not all points included ovenbirds and these recordings were not included in this study. The recordings are repeated samples of the same forest fragment on the same day but include different individual birds. Each recording began with a human voice interruption that reset the process, ensuring that the first signal recorded was endogenous and not influenced by previous signals. Recordings lasted eight minutes, thus, variation in rates of signals over the course of the day were not a concern within each recording. The start time of every ovenbird song from each recording was manually transcribed and measured to the nearest 0.5 second to produce a discrete time series of songs in time bins of 0.5 s. If two songs were initiated simultaneously, we could not detect this in the recording, and thus each time bin consisted of either a 0 or 1 indicating if a signal was initiated. We measured all signals captured by the recording device, however, there may be edge effects (Zhuang et al., 2004) introduced by individuals that were vocalizing outside the range of the recording device and that influenced signals by individuals which we did detect. We analyzed data from each forest fragment separately because each site is physically separated from the others by sufficient distance to represent independent groups of ovenbirds during the breeding season.

2.3. Model performance and applications

To test model performance, we compared predictive ability of the self-exciting point process models to that of homogenous point process models. For each time series, we fit both models in a hierarchical framework with uninformative priors, in R 3.5.1 (R Core Team, 2018) using R2jags 0.6.1 (Su and Yajima, 2015) and simulated time series with the estimated parameters (see Appendix A for code). We ran three MCMC chains and assessed convergence using the potential scale reduction factor ($\hat{R}$) with a cutoff of <1.1 (Gelman and Rubin 1992; Brooks and Gelman 1998). As a benchmark to compare performance of our model and the homogenous model, we assessed correspondence between the simulated time series from each model and the observed time series. We calculated the mean and 90% credible intervals for the difference in total number of estimated vocalizations in the simulated time series from each model compared to the observed vocalizations.

The unique features of our model can be used to test hypotheses about the underlying causes of signals. For example, large forest patches represent high quality habitat for forest interior songbirds such as ovenbirds, resulting in higher densities (Porneluzi et al., 1993) and thus greater motivation for territorial males to respond to the songs of neighbors (Leftwich and Ritchison, 2000). To demonstrate this potential application of the model, we fit generalized linear models with a gamma response distribution and identity link to the background rate of singing (μ), which must always be positive and is assumed to be nonzero, in response to time in the breeding season (x) for both large forests and small forests (Eqs. 11 and 12) with uninformative priors (Eqs. 13–15). Note that although the background rate of singing (μ) is shared between these models and the model described earlier, the parameters (α , β , k) and covariate (x) are distinct and symbols are only recycled for consistency with conventions.

$$\mu \sim \text{Gamma}(k, k / e^p) \quad (11)$$

$$p = \alpha + \beta * x \quad (12)$$

$$\alpha \sim \text{N}(0, 0.0001) \quad (13)$$

$$\beta \sim \text{N}(0, 0.0001) \quad (14)$$

$$k \sim \text{Unif}(0, 500) \quad (15)$$

3. Results

There were no differences in the total number of vocalizations predicted by our model and homogenous models for either bullfrogs or ovenbirds (Fig. 2a–d). Both models over and under-predicted total vocalizations at similar rates (Fig. 2e), with slight underestimates on average. Mean differences in the number of bullfrog calls predicted and observed was -1.05 calls ($se = 0.11$) for our model and -0.83 calls ($se = 0.18$) for homogenous models. For ovenbird songs, averaged across all sites, the mean difference was -0.66 songs ($se = 0.02$) for our model and -0.58 songs ($se = 0.03$) for the homogenous models.

Our models show that the mean proportion of the overall signaling rate explained by conditional intensity (i.e. countersinging in response to conspecifics) was 0.55 ($se = 6.59e-04$) for bullfrog calls, and ranged from 0.02 to 0.59 for ovenbird songs depending on site, with an overall average across all sites of 0.33 ($se = 3.95e-04$). This proportion is based on the relative weight at each time step t of the background rate of singing and the conditional intensity based on the history of signals leading up to time t . Our analyses suggest a decline in the background rate (μ) of singing in larger forest fragments over the course of the breeding season (Fig. 3), with an estimated slope of -0.04 μ /ha (90% CI -0.05 , -0.03). The background rate (μ) remains constant in smaller fragments throughout the breeding season, however, with an estimated slope of -0.01 μ /ha and a credible interval that overlaps zero (90% CI -0.03 , 0.02) indicating no directional effect of time in the breeding season within smaller forest fragments.

4. Discussion

The primary strength of our model is its ability to partition the processes generating acoustic signals into those that arise endogenously, measured as the background rate, and those that arise in response to

conspecific signals, measured as the conditional intensity. This partitioning enables researchers to make predictions about environmental factors that affect these separate classes of signals, which can help identify tradeoffs that govern when animals expend energy to emit different types of signals. In our bird song case study, for example, we were able to determine how the extent to which songs are used for territory establishment and mate attraction (i.e. the background rate of singing) change over the course of the breeding season in high quality (large forests) and low quality (small forests) breeding habitat. Parameter outputs of the model could also be used to determine when bird singing shifts from one purpose to another over time, or if males in habitats with low resource availability allocate more time to countersinging than males in areas with high resource availability. Our models can distinguish between unprompted singing and responses to conspecific signals (e.g. territory defense), which provides substantial improvements over simple homogenous point process models in our ability to make behavioral inferences from acoustic signal datasets. That our model performed similarly to the homogenous point process model suggests that there is no performance cost associated with these gains in interpretation.

Determining the proper form of the memory kernel is critical for model interpretation. Self-exciting point process models are sensitive to misspecification, which can result in biased estimates of the magnitude and timescale of influence of self-excitement on the process (Reinhart and Greenhouse, 2018). Thus, it is important to consider the biology of the system when specifying the memory kernel. We implemented an exponential memory kernel because animal ‘forgetting’ is assumed to decay exponentially based on experimental studies (Speed, 2000), however, this may not be a good assumption for many questions. For example, responses that arise from linked network interactions, such as the spread of infectious disease within a wild population (Meyer and Held, 2014) or long-lasting neuron memory (Kauer and Malenka, 2007),

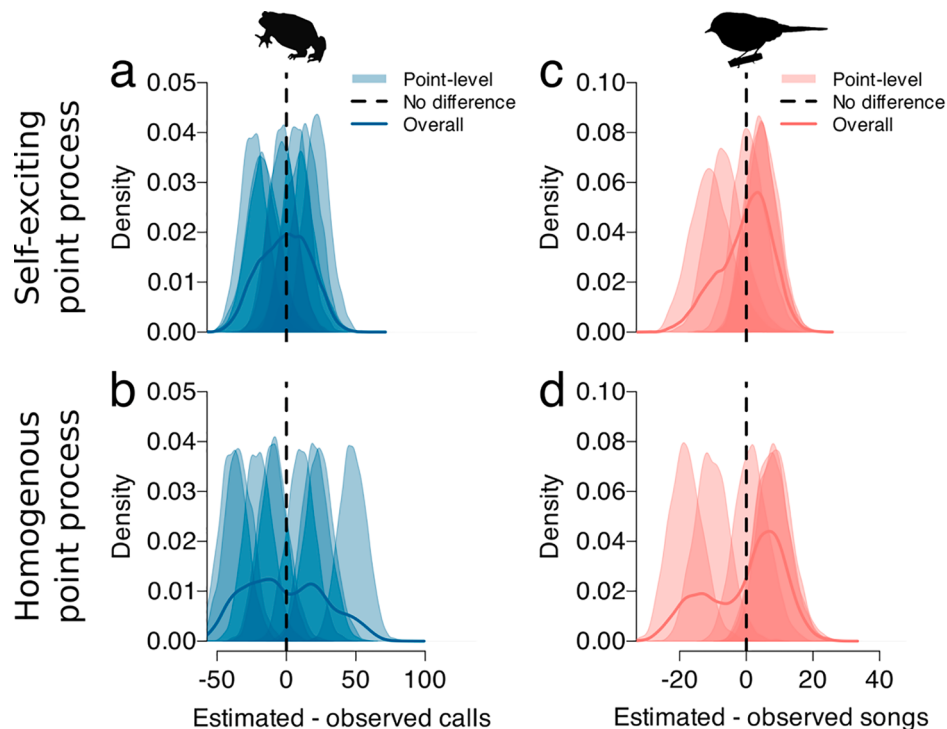


Fig. 2. Differences between the number of estimated and observed bullfrog calls (teal) and ovenbird songs (coral) using our model (a,c) and a homogenous model (b, d). The dashed line represents perfect prediction, and negative values indicate underprediction of the number of vocalizations. For both the bullfrog site and a representative ovenbird site, differences between observed and estimated vocalizations are shown for each repeated sample with a sample-level density of posterior predictions (colored shading); overall density of posterior predictions across all samples from a site is indicated by the heavy colored line. Differences in estimates between our model and homogenous models (e) are shown for each recording, with each line representing a single site; positive numbers indicate that predictions from our model were closer to observations than those from homogenous models.

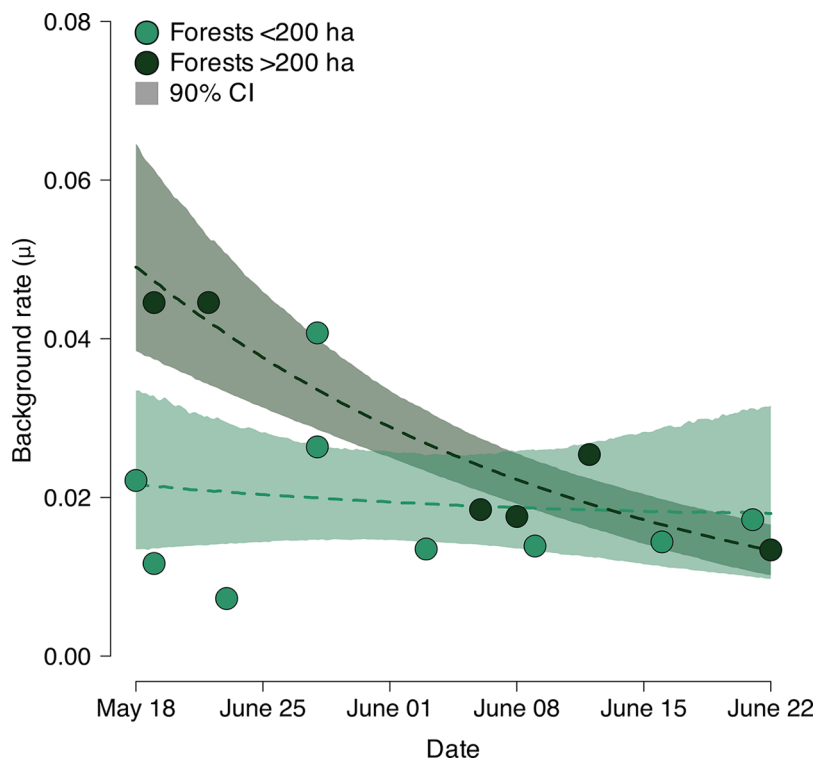


Fig. 3. Background rate of ovenbird singing, corresponding to mate attraction and territory establishment, in relation to date in the breeding season and forest size class. In large forests (>200 ha), the background rate declines over the breeding season (dark green) whereas it remains relatively constant in small forests (light green). Dashed lines show the effect of date on the background rate of singing, for each forest size class respectively, from a generalized linear model with a gamma identity link. The shaded areas are the 90% credible intervals for these effects.

may be better modeled with a power-law decay function. Similarly, spread of signals within a socially complex system (e.g. non-human primates) may be better modeled with a power-law decay function due to the strong ties between individuals (Sueur et al., 2011). Researchers adapting the model should consider alternative specifications of the memory kernel appropriate to their system, including those which include a spatial component.

In our case study, we extended the model to test hypotheses about the effects of forest size and time in the breeding season on the rate of background singing; many extensions are possible depending on what additional information researchers have about the system and what hypotheses are being tested. Because our model can be fit in a hierarchical structure and all components are modular, it can be adapted to a wide range of behaviors, hypotheses about what influences those behaviors, and systems with vastly different characteristics. For example, where pairing status is known and mate attraction can be ruled out for signals produced by paired males (i.e., no extra-pair mate attraction), one could incorporate this information into the background singing rate (μ) to more precisely estimate the probability that any given song is a response to a conspecific signal. Similarly, some environmental factors can be allowed to influence only the background rate of singing or only the conditional intensity, depending on the biology of the system being modeled. We did not test any hypotheses with the bullfrog call data, however, this second case study demonstrates that the models are flexible and can be applied to systems with orders of magnitude more acoustic signals per time period than our bird case study.

The models could also be extended to incorporate information about the spatial structure of signals. Our model assumes that all individuals within the area being sampled are equally likely to respond to all others, however, this is unlikely to be an accurate assumption (Simpson, 1985). For example, individuals may have higher motivation to respond to close neighbors than to distant neighbors, or to strangers rather than to known neighbors (Galeotti and Pavan, 1993). In our case study, we were unable to identify the spatial history of signals because all recordings were done from a single point and we were thus unable to account for edge effects introduced by individuals signaling from outside the range

of the recording unit. When the spatial arrangement of individual songs is known, however, the spatial history of signals could be incorporated into the models (Reinhart, 2018). In many animal systems, the location of each signal could be determined through arrays of recording units (Mennill et al., 2012), or if individuals are highly territorial and territory boundaries are mapped through other means such as visual surveys. In these cases where the spatial history of signals is known, alternative specifications of the memory kernel that include both a time decay and a spatial decay can be used to predict not only when and why a signal would occur, but also where in the landscape.

Our model is only one of many inhomogeneous point process models that could be used to analyze behavioral signal patterns. The value of our modeling approach is in the simplicity of the framework that relies only on the signals themselves to make behavioral inferences, though contextual data can improve inferences based on the models and be used to test hypotheses about the underlying processes generating the signals. This simple framework can easily incorporate additional information about a system to improve inferences about the underlying reasons for signals. Although we have only applied the models to acoustic data, they could be applied to any class of animal communication that is initiated both endogenously and in response to others. For example, the models could be applied to displays in lekking species (e.g., Gibson and Bradbury, 1985) or to any type of coordinated visual display (e.g., Buck and Buck, 1968). Because self-exciting point process models provide a means for separating signal patterns into different behavioral components, they provide an opportunity to study behavioral trade-offs and factors influencing when and why animals signal and countersignal.

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Data accessibility

All data, code to fit the models, and test model fit are archived at <https://doi.org/10.5281/zenodo.6377992> (Grames et al., 2022).

CRediT authorship contribution statement

Eliza M. Grames: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Visualization, Funding acquisition. **Piper L. Stepule:** Methodology, Investigation, Data curation, Writing – review & editing. **Susan Z. Herrick:** Resources, Data curation, Writing – review & editing. **Benjamin T. Ranelli:** Conceptualization, Writing – review & editing. **Chris S. Elphick:** Conceptualization, Resources, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2022.109965](https://doi.org/10.1016/j.ecolmodel.2022.109965).

References

- Bacry E., Mastromatteo I., Muzy J.-F. 2015. Hawkes processes in finance. *Market Microstruct Liquidity*. 1: 1550005.
- Bosch, J., Rand, A.S., Ryan, M.J. 2000. Signal variation and call preferences for whine frequency in the tungara frog, *Physalaemus pustulosus*. *Behav. Ecol. Sociobiol* 49, 62–66.
- Bowsher, C.G., 2007. Modelling security market events in continuous time: intensity based, multivariate point process models. *J. Econ* 141, 876–912.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph Stat* 7, 434–455.
- Buck, J., Buck, E., 1968. Mechanism of rhythmic synchronous flashing of fireflies: fireflies of Southeast Asia may use anticipatory time-measuring in synchronizing their flashing. *Science* 159, 1319–1327.
- Byers, B.E., 2007. Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behav. Ecol* 18, 130–136.
- Chavez-Demoulin, V., McGill, J., 2012. High-frequency financial data modeling using Hawkes processes. *J. Bank Financ* 36, 3415–3426.
- Cowlishaw, G., 1992. Song function in gibbons. *Behaviour* 121, 131–153.
- Dawson, D.K., Efford, M.G., 2009. Bird population density estimated from acoustic signals. *J. Appl. Ecol* 46, 1201–1209.
- Diniz, P., da Silva, E.F., Webster, M.S., Macedo, R.H., 2018. Duetting behavior in a Neotropical ovenbird: sexual and seasonal variation and adaptive signaling functions. *J. Avian Biol* 49 jav-01637.
- Fox, E.W., Schoenberg, F.P., Gordon, J.S., 2016. Spatially inhomogeneous background rate estimators and uncertainty quantification for nonparametric Hawkes point process models of earthquake occurrences. *Ann. Appl. Stat* 10, 1725–1756.
- Galeotti, P., Pavan, G., 1993. Differential responses of territorial tawny owls (*Strix aluco*) to the hooting of neighbors and strangers. *Ibis* 135, 300–304.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci* 7, 457–472.
- Gerhardt, H.C., 1992. Multiple messages in acoustic signals. *Semin Neurosci* 4, 391–400.
- Gibson, R.M., Bradbury, J.W., 1985. Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. *Behav. Ecol. Sociobiol* 18, 117–123.
- Grames, E.M., Stepule, P.L., Herrick, S.Z., Ranelli, B.T., Elphick, C.S., 2022. *elizagrames/self-exciting-signals: v1.0 (v1.0)* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.6377992>.
- Halkin, S.L., 1997. Nest-vicinity song exchanges may coordinate biparental care of northern cardinals. *Anim. Behav.* 54, 189–198.
- Ham, S., Lappan, S., Hedwig, D., Choe, J.C., 2017. Female songs of the nonduetting Javan gibbons (*Hylobates moloch*) function for territorial defense. *Int. J. Primatol* 38, 533–552.
- Hawkes, A.G., 1971. Spectra of some self-exciting and mutually exciting point processes. *Biometrika* 58, 83–90.
- Hecklenively, D.B., 1967. Role of song in territoriality of black-throated sparrows. *Condor* 69, 429–430.
- Herrick, S.Z., Wells, K.D., Farkas, T.E., Schultz, E.T., 2018. Noisy neighbors: acoustic interference and vocal interactions between two syntopic species of ranid frogs, *Rana clamitans* and *Rana catesbeiana*. *J. Herpetol* 52, 176–184.
- Hewlett P. 2006. Clustering of order arrivals, price impact and trade path optimisation. Workshop on Financial Modeling with Jump processes, Ecole Polytechnique: 6–8.
- Howard, H.E., 1920. *Territory in Bird Life*. J. Murray, London, UK.
- Ingrat I. 2007. Automatic detection of cerulean warblers using autonomous recording units and song scope bioacoustics software. Wildlife Acoustics Inc. www.wildlifeacoustics.com.
- Ingrat I. 2009. Automatically identifying animal species from their vocalizations. Wildlife Acoustics Inc. www.wildlifeacoustics.com.
- Kass, R.E., Kelly, R.C., Loh, W.L., 2011. Assessment of synchrony in multiple neural spike trains using loglinear point process models. *Ann. Appl. Stat* 5, 1262–1292.
- Kauer, J.A., Malenka, R.C., 2007. Synaptic plasticity and addiction. *Nat Rev Neurosci* 8 (11), 844–858.
- Kim, M., Paini, D., Jurdak, R., 2019. Modeling stochastic processes in disease spread across a heterogeneous social system. *PNAS* 116, 401–406.
- Leftwich, C., Ritchison, G., 2000. Singing behavior of male Henslow's sparrows (*Ammodramus henslowii*). *Bird Behav* 18, 1–7.
- Lohr, B., Wakamiya, S.M., Ashby, S., 2013. The function of song types and song components in grasshopper sparrows (*Ammodramus savannarum*). *Behaviour* 150, 1085–1106.
- Meyer, S., Held, L., 2014. Power-law models for infectious disease spread. *Ann. Appl. Stat* 8, 1612–1639.
- Porneluzi, P.J., Bednarz, C., Goodrich, L.J., Zawarda, N., Hoover, J., 1993. Reproductive performance of territorial ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conserv. Biol.* 7, 618–622.
- Simpson, B.S., 1985. Effects of location in territory and distance from neighbours on the use of song repertoires by carolina wrens. *Anim. Behav.* 33, 793–804.
- Smith, M.J., Harper, D.G., 1995. Animal signals: models and terminology. *J. Theor. Biol.* 177, 305–311.
- Mennill, D.J., Battiston, M., Wilson, D.R., Foote, J.R., Doucet, S.M., 2012. Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods Ecol. Evol.* 3, 704–712.
- Meyer, S., Elias, J., Höhle, M., 2012. A space-time conditional intensity model for invasive meningococcal disease occurrence. *Biometrics* 68, 607–616.
- Morris, G.K., DeLuca, P.A., Norton, M., Mason, A.C., 2002. Calling-song function in male hagglids (Orthoptera: hagglidae, Cyphoderris). *Can. J. Zool* 80, 271–285.
- Nice, M.M., 1941. The role of territory in bird life. *Am. Mid. Nat* 26, 441–487.
- Park, S.-R., Cheong, S., Chung, H., 2004. Behavioral function of the anomalous song in the bush warbler, *Cettia diphona*. *Korean J. Biol. Sci* 8, 89–95.
- Pereyra, M.E., Morton, M.L., 2010. Flight songs of dusky flycatchers: a response to bird-hunting raptors? *J. Field Ornith* 81, 42–48.
- Propp, D.S., Ritchison, G., 2008. Use and possible functions of the primary and sustained songs of male grasshopper sparrows. *Am. Mid. Nat* 160, 1–7.
- R Core Team, 2018. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Version 3.5.1.
- Reinhart, A., 2018. A review of self-exciting spatio-temporal point processes and their applications. *Stat. Sci* 33, 299–318.
- Reinhart, A., Greenhouse, J.B., 2018. Self-exciting point processes with spatial covariates: modelling the dynamics of crime. *J. Roy. Stat. Soc. C* 67, 1305–1329.
- Schatral, A., Latimer, W., Broughton, B., 1984. Spatial dispersion and agonistic contacts of male bush crickets in the biotope. *Z. Tierpsychol* 65, 201–214.
- Schoenberg, F.P., Hoffman, M., Harrigan, R.J., 2019. A recursive point process model for infectious diseases. *Ann. Inst. Stat. Math* 71, 1271–1287.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton, NJ.
- Smith, R.L., 1959. The songs of the grasshopper sparrow. *Wilson Bull* 71, 141–152.
- Smith, J.M., Harper, D., 2003. *Animal Signals*. Oxford University Press.
- Speed, M.P., 2000. Warning signals, receiver psychology and predator memory. *Anim. Behav* 60, 269–278.
- Su Y.-S., Yajima M. 2015. R2jags: using R to run JAGS.
- Sueur, C., Jacobs, A., Amblard, F., Petit, O., King, A.J., 2011. How can social network analysis improve the study of primate behavior? *Am. J. Primatol* 73, 703–719.
- Tinbergen, N., 1939. *The Behavior of the Snow Bunting in Spring*. Press of LS Foster, New York, NY.
- Trillo, P., Vehrencamp, S., 2005. Song types and their structural features are associated with specific contexts in the banded wren. *Anim. Behav* 70, 921–935.
- Türkyilmaz, K., van Lieshout, M.N.M., Stein, A., 2013. Comparing the Hawkes and trigger process models for aftershock sequences following the 2005 Kashmir earthquake. *Math. Geosci* 45, 149–164.
- Upham-Mills, E.J., Reimer, J.R., Haché, S., Lele, S.R., Bayne, E.M., 2020. Can singing rate be used to predict male breeding status of forest songbirds? A comparison of three calibration models. *Ecosphere* 11, e03005.

- Vere-Jones, D., 1970. Stochastic models for earthquake occurrence. J. R. Stat. Soc 32, 1–45.
- Wasserman, F., 1977. Intraspecific acoustical interference in the white-throated sparrow (*Zonotrichia albicollis*). Anim. Behav 25, 949–952.
- Wells, K.D., 1977. The social behaviour of anuran amphibians. Anim. Behav 25, 666–693.
- Wells, K.D., Schwartz, J.J., 2007. The Behavioral Ecology of Anuran Communication. Hearing and Sound Communication in Amphibians. Springer, New York, NY.
- Whittingham, L.A., Kirkconnell, A., Ratcliffe, L.M., 1997. The context and function of duet and solo songs in the red-shouldered blackbird. Wilson Bull 109, 279–289.
- Yasukawa, K., 1981. Song and territory defense in the red-winged blackbird. Auk 98, 185–187.
- Zhuang, J., Ogata, Y., Vere-Jones, D., 2004. Analyzing earthquake clustering features by using stochastic reconstruction. J. Geophys. Res 109, 65.