

# Soundspace partitioning to increase communication efficiency in bird communities

Reiji Suzuki · Charles E. Taylor · Martin L. Cody

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**Abstract** Birds do not always vocalize at random, but may rather divide up soundspace in such a manner that they avoid overlap with the songs of other bird species. In effect, a high degree of communication efficiency can be achieved by many simultaneously active vocalists that finely integrate songs with minimal overlap. We describe this phenomenon from several recordings at our principal study location, near Volcano, California. The most-studied models for conceptualizing and studying such de-synchronized systems come from scheduling algorithms in computer science, where internet protocols involve packets of information that are broadcast widely; any collisions between them will corrupt the colliding packets so that they need to be resent. We have simulated some of these methods that might be appropriate for the soundspace of bird communities. Some features of these de-synchronized depend on specifics of the algorithms used.

**Keywords** Simulated evolution · DESYNC · Soundspace · Resource partitioning · Bird song

## 1 Introduction

Our laboratory is concerned with developing acoustic sensor arrays so that they will be useful for observing and analyzing bird diversity and behavior. In these studies we observed that birds do not always vocalize at random, but may rather divide up soundspace in such a manner that they avoid overlap with the songs of other bird species.

For example, at our primary field site, in a mixed conifer-oak forest near Volcano, CA, we typically encounter 30+ species of birds during a short observation period. Not all of these species sing, but many do, and those that sing appear to avoid collisions that would occur from singing at the same time. Table 1 shows the amount of time during which we observed 0, 1 or 2+ birds singing at the same time during a recording of approximately 3 min on the morning of 22 June 2010. The species singing at this time were: Spotted Towhee (*Pipilo maculatus*); Pacific-slope Flycatcher (*Empidonax difficilis*); Orange-crowned Warbler (*Vermivora celata*); Nashville Warbler (*V. ruficapilla*); Black-throated Gray Warbler (*Dendroica nigrescens*); Hutton's Vireo (*Vireo huttoni*); Red-breasted Nuthatch (*Sitta canadensis*); and Common Bushtit (*Psaltirparus minimus*). From the proportion of the total time each species sang, we can calculate the number of seconds we expect to be vacant (empty), monopolized by a single species, or occupied by the songs of 2+ species, given the species sing independently of each other. What we observed was that less time was vacant or occupied by 2+ species, and more time was monopolized, than expected by chance ( $\chi^2 = 14.1$ ,  $df = 2$ ,  $p < 0.001$ ).

We believe this avoidance of collisions in soundspace to be typical, if not universal. Others have observed such partitioning, in a variety of locations and species, including Wrentits (*Chamaea fasciata*) and Bewick's Wrens

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R. Suzuki (✉)  
Graduate School of Information Science, Nagoya University,  
Furo-cho, Chikusa-ku, Nagoya 464-8601, Japan  
e-mail: reiji@nagoya-u.jp

R. Suzuki · C. E. Taylor · M. L. Cody  
Department of Ecology and Evolutionary Biology,  
University of California,  
Los Angeles, Los Angeles, CA 90095, USA

**Table 1** The observation and expectation of singing behaviors in the recording in a mixed conifer-oak forest near Volcano, CA

Time	Vacant (0)	Mono (1)	2+	Total
Expectation	102.4	64.8	18.8	186.0
Observation	92.4	85.8	7.9	186.0

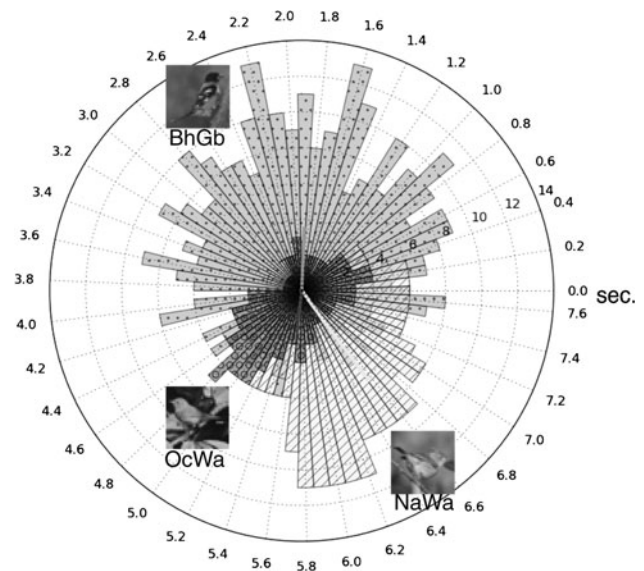
(*Thryomanes bewickii*) [1], Least Flycatchers (*Empidonax minimus*), and Red-eyed Vireos (*Vireo olivaceus*) [2], and a set of four species—Wood Thrush (*Hylocichla mustelina*), Eastern Wood Peewee (*Contopus virens*), Great Crested Flycatcher (*Myiarchus crinitus*), and Ovenbird (*Seiurus aurocapillus*) [3].

In the study reported below we first describe a way to visualize soundspace partitioning in a way that may prove to be generally useful, propose some general procedures that the birds might use to avoid collisions, then report on some evolutionary computer simulations that illustrate how these procedures might accomplish what we have observed. Attention is drawn to particulars that might permit experimental determination of just which procedures the birds employ in nature.

## 2 Materials and methods

Observations plotted in polar coordinates, as used in circular statistics, can help visualization of soundspace partitioning. Birds typically sing repeated sequences of phrases, with only a short time between phrases. The entire sequence of phrases constitutes a song [4]. There is then a break of a few seconds, and then a new song begins. Examples of some such songs for the species present are available at the web sites for xeno-canto (<http://www.xeno-canto.org/>) or Macaulay library (<http://macaulaylibrary.org/>).

Figure 1 shows polar representations of recordings made at our study site during the mornings of 19 April 2010 (recording 10–21). In this figure, the “driver” species was Black-headed Grosbeak (*Pheucticus melanocephalus*), BhGb, in bars with dots. Other species singing in the interstices are Orange-crowned Warblers, OcWa, in bars with open circles and Nashville Warblers, NaWa, in bars with hatched lines. The mean vector of the distribution of singing events for each species is indicated by a bar. Time elapsed since the beginning of the period is indicated around the outside, and number of instances for each time interval by the inner circles. These recordings were made as described in [5], and are posted at our web site, <http://taylor0.biology.ucla.edu/al/bioacoustics/>. In this recording Black-headed Grosbeaks were dominant. The average time between starting songs was approximately 7.7 s. This was taken as the period of the cycle, as represented around the

**Fig. 1** Circular diagram of de-synchronized singing

circumference of the diagram. Time is represented as an angle, taken to be 0 at the beginning of the recording, then progressing to 360° at the end of each period, and then repeated.

At each 0.1 s in the recording, we checked whether a species was singing or not, accumulated the number of instances of singing, and represented this number as the radius length in the diagram. This was done separately for each species, then plotted. The average time between song starts usually gave the best representations, but some trial and error adjustments often helped clarity, and is, of course, necessary if there is no dominant species.

There are many procedures that the birds might use to partition soundspace. The most-studied models for conceptualizing and studying such de-synchronized systems come from scheduling algorithms in computer science, where internet protocols govern packets of information that are broadcast widely, and any collisions between them will corrupt the colliding packets so that they need to be resent.

For this study we have simulated three procedures under the assumption that all individuals begin to sing with the shared period  $T$  if their songs do not overlap with other songs.

- (a) “simple trial and error” If there is no overlap with the songs of others, then that individual will sing again exactly one time period later. But if the song of that individual overlaps at all with the song of another, then that focal individual will change slightly the time it starts its next song with a genetically determined probability  $p$  interpreted as its behavioral plasticity. Specifically, it begins to sing the next song with the interval of  $T + dt(-DT, DT)$ , where  $dt(x, y)$  is a random value generated from the uniform distribution

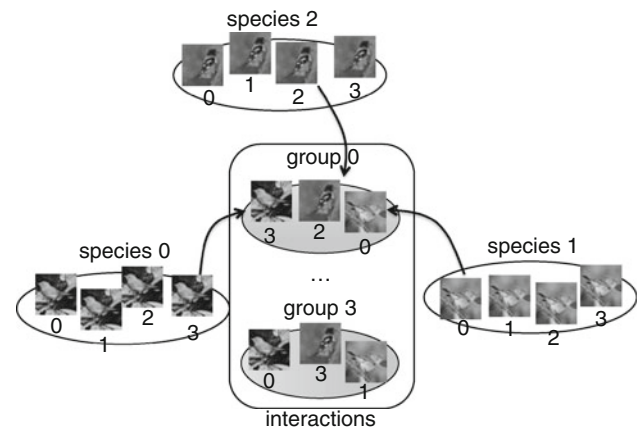
on  $[x, y]$ . DT is a parameter that determines the maximum amount of random change in the interval. Otherwise, it will sing again exactly one time period ( $T$ ) later.

- (b) non persistent CSMA, or “back off” At its time to sing, the focal individual checks whether any other individuals are singing or not. If no one is singing, it begins to, and then decides to sing the next song one time period later. Otherwise (if other birds are singing), it delays its time to sing for the random time  $dt(0, DB)$  with a probability  $p$ . DB is a parameter that determines the maximum amount of delay.
- (c) DESYNC-based TDMA (Time division multiple access) or just DESYNCH The basic idea of the DESYNC algorithm [6] is that each agent modifies its own timing to fire so that it will occur midway between the preceding and the next firing events. We modified this slightly for birds.

In our simulations each individual modifies its own timing to sing the next song with a probability  $p$  so that the timing gets closer to the relative distance ratio among the mid time point of the preceding ( $m_p$ ), the focal  $m_f$  and the next song  $m_n$  becomes  $(m_f - m_p):(m_n - m_f) = (SL_p + SL_f):(SL_f + SL_n)$  in the future songs.  $SL_f$ ,  $SL_n$  and  $SL_p$  are the length of the focal, next and preceding songs, respectively. The next timing to sing ( $t_n$ ) is set in between this desired timing ( $t_d$ ) and the scheduled timing with the period  $T$  ( $t_s$ ) using an interpolation coefficient DD ( $|t_d - t_n|:|t_n - t_s| = 1 - DD:DD$ ). Otherwise, it will sing again exactly one time period ( $T$ ) later. This method can be shown to achieve full utilization of the available bandwidth, yet no global clock is required and the algorithm automatically adjusts to any number of participants. These acoustic interactions are conducted until the time reaches  $R \times T$ .  $R$  is a parameter that corresponds to the approximate number of singing behaviors for each individual through acoustic interactions.

For our simulations the population structure and evolutionary process were as follows: We assume  $S$  different species and the population of each species is composed of  $N$  individuals as shown in Fig. 2. In this example there are three species, with 4 individuals each. The whole population is randomly divided into the  $N$  groups of  $S$  individuals so that each individual participates in one group and each group includes exactly one individual for each species. The acoustic interaction is conducted among the members of each group independently to determine the fitness contribution of each individual. The fitness of each individual is taken to be the total duration during which the focal individual can sing solo (without interference).

We modeled the evolution of the plasticity parameter  $p$ . Each individual has its own genetically determined



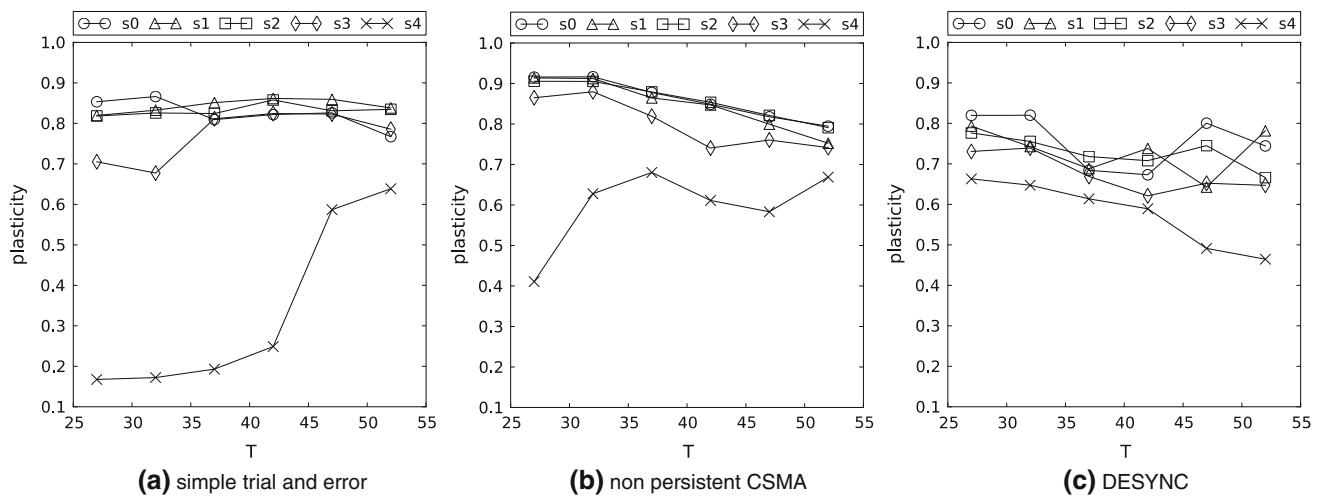
**Fig. 2** Population and interaction model for evolution

$p$  that determines its behavior in acoustic interactions. The population of each species is evolved independently according to the genetic algorithm based on selection and mutations. The selection of offspring in the next generation is based on a “roulette wheel selection” according to fitness. For each gene of offspring, a mutation occurs with a small probability  $p_m$ , which adds a small random  $dt(-DM, DM)$  to the current value.

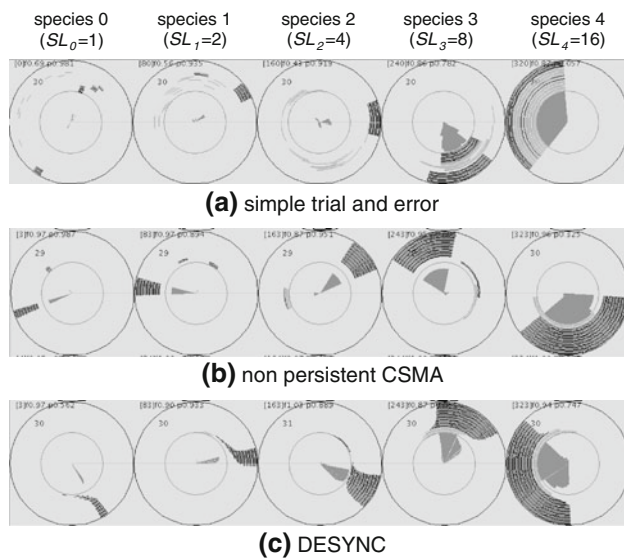
### 3 Results and discussion

For each procedure we conducted experiments with various settings of  $T$  for 500 generations using  $N = 80$ ,  $S = 5$ ,  $R = 30$ ,  $DT = 7.0$ ,  $DB = 13.0$ ,  $DD = 0.5$ ,  $DM = 0.1$  and  $p_m = 0.01$ . We assumed the species-specific length of song of the  $i$ th species  $SL_i = \{1, 2, 4, 8 \text{ and } 16\}$ . The initial population was generated with initial values of  $p$  sampled from the uniform distribution over  $[0, 1]$ . We focused on the effects of  $T$  on evolution because it determines the degree of congestion in the acoustic space. Figure 3 shows the average  $p$  in the last generation with the three different temporal avoidance mechanisms. We see that the evolutionary process of plasticity is strongly dependent on the basic temporal avoidance mechanisms and the setting of  $T$ .

In the case of (a) “simple trial and error”, the plasticity of all species was high when  $T$  was large enough. This means that species will generally evolve to avoid temporal overlap of songs in less crowded acoustic spaces. As  $T$  decreased, the plasticity of the species with the longest song tended to be small while those of the other species remained high. In other words, the species with the longest song typically evolves to become dominant—what we term the “driver species.” The driver species does not change the timing of its song to avoid overlap very much, but keeps its original periodicity, while species with shorter songs adapt to fit into the remaining time segments.



**Fig. 3** The average  $p$  in the last generation with the three different temporal avoidance mechanisms. Each value is the average over 15 trials



**Fig. 4** Examples of interactions with different temporal avoidance procedures when  $T = 42$ . The five circular diagrams correspond to a group for acoustic interactions. Each diagram represents the singing behavior of an individual. The distribution of its singing events is represented in the inner area in the same way as represented in Fig. 1. The arcs in the outer area show the distribution of songs over the circular timeline where each succeeding period  $T$  is arranged from inner- to the outer-most position. Grey or black arcs are the songs with or without overlaps, respectively

Figure 4 shows examples of interactions among evolved species in three groups with the different temporal avoidance mechanisms when  $T = 42$ . In this case, we see that the shorter songs randomly fluctuated several times, but they finally fit into the rest of the space left by the driver species with the longest song. This phenomenon can be explained by focusing on the benefit and cost of the adopted temporal avoidance behaviors. In this case, the

benefit is to be able to resolve existing overlaps in the future interactions. However, this avoidance can fail and yield another overlap with other songs because of the randomness of the trial and error procedures. Because the effect of this cost is approximately proportional to song length, the species with the longest song is least likely to make timing adjustments and, instead, the species with short songs will make the behavioral adjustments to fit into the soundspace with minimal overlaps.

In the case of (b) “non persistent CSMA”, we see that the plasticity of shorter songs converged to higher values as  $T$  decreased, while that of the longest song evolved to relatively smaller values although this tendency was not so dramatic as in the previous case. We see from Fig. 4b that the individuals successfully converged to the state with no overlaps by actively delaying their timing to sing in a counterclockwise fashion. The main reason for the evolution of the smaller plasticity of the longest song is not due to the same reason that was observed in case (a). In case (b), the benefit of temporal avoidance is to be able to avoid the overlap with other songs being currently delivered. This benefit is essential for the species with shorter songs because their songs are often completely masked by other longer songs if they do not actively avoid overlap, and vice versa. However, delayed song delivery means that individuals risk losing chances to sing within a limited, finite time span. Thus, the species with the longest song will evolve low plasticity to reduce the cost of avoidance behavior and maximize song delivery opportunities.

In the case of (c) “DESYNC”, we see that the plasticity of all species evolved to be high in all conditions of  $T$  although  $p$  of the longest song was slightly smaller than that of others. This is due to the fact that the  $p$  of the longest song evolved to low plasticity in a small number of trials at higher  $T$ , implying that somewhat reduced  $p$  could



be adaptive in those cases. Figure 4c shows that all individuals actively adjusted their timing to sing in both clockwise and counterclockwise manners, and as a result, the population quickly converged to the state with no overlaps. This implies that our modified DESYNC algorithm is adaptive and has almost no cost for adjustment processes. Thus, we did not observe significant effects of the differences in the length of songs on the evolution of the behavioral plasticity of individuals.

Although discussion of similarities between the simulations of a few rules and a very few recordings would contribute only speculation, we could observe some degree of soundspace partitioning in both Figs. 1 and 4. We hope to pursue the relationship among them by collecting more field and simulation data.

## 4 Conclusions

We discussed soundspace partitioning to increase communication efficiency in bird communities. We described this phenomenon from several recordings, using a way to visualize soundspace partitioning based on a circular diagram. We also proposed some general procedures that the birds might use to avoid collisions, then reported on some evolutionary computer simulations that illustrate how the procedures might accomplish what we have observed. The dynamics of soundspace partitioning that emerge as behavioral plasticity evolves to minimize interspecific song

overlap are illuminated with our simulation procedures, which can be used to elucidate the communication protocols employed by birds in complex, real-world situations.

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