Simulating the Evolution of Eavesdropping on Heterospecific Alarm Calls

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Abstract

Acquiring information about predators from heterospecific alarm calls is a commonly observed behaviour across taxa (Magrath et al., 2015a). Previous theory has focused on defining the conditions that favour the use of such information, proposing different principles that explain why some species are observed to flee to heterospecific alarm calls. Recently, quantitative analyses of this phenomenon have suggested that similar vulnerability to predators between species favours eavesdropping. We simulate a population of senders that produce alarm calls and a population of heterospecific receivers that eavesdrop on them. We find that particularly vulnerable receivers are favoured by eavesdropping. Our study replicates previous results that show threat of predation as the main selective force favouring eavesdropping. Moreover, when eavesdropping invades a population, it does so at a fast rate. When the conditions are favourable, eavesdroppers are highly benefited by eavesdropping. We conclude that vulnerable individuals that are benefited by the acquisition of heterospecific information might be exposed to different selective pressures towards sociality than individuals who only rely on conspecifics.

1 Introduction

Communication has largely been studied as the exchange of information from a sender that produces signals to an intended receiver that detects those signals. This exchange of information is beneficial for senders and receivers and both are adapted for it (Stevens, 2013). In reality, communication happens in a network environment, where sender signals can be received by more than one receiver (McGregor, 2005). The use of signal information by unintended receivers is called *eavesdropping*, and we are looking particularly at heterospecific eavesdropping, where receivers eavesdrop on senders of another species.

By eavesdropping, heterospecifics gain access to information about mates (Danchin, 2004), foraging (Goodale et al., 2017) and potentially life-saving information about predators (Magrath et al., 2015a). For example, alarm calls are one kind of signal produced to attract the attention of conspecifics to imminent danger of predation. Heterospecifics that are in danger too may use those signals as *cues* to inform themselves about predation threats.

Heterospecific eavesdropping on alarm calls is in fact widespread across taxa (Magrath et al., 2015), although some species are reported to not eavesdrop in contexts where it is seemingly beneficial. For instance, in herbivore groups of the African savannah, where

impalas (*Aepyceros melampus*) and plain zebras (*Equus quagga*) are both predated by lions (*Panthera leo*), impalas eavesdrop on the alarm calls of zebras, but zebras are not reported to respond to the alarm calls of impalas (Meise et al., 2018, 2020; Palmer & Gross, 2018). Such asymmetries open questions about what enables species to eavesdrop on heterospecifics and why it is the case that some species will eavesdrop on another with shared predators, while the reverse is not observed. To answer these questions we need to understand when the use of information obtained by eavesdropping is selected for, and the constraints which select against it.

Seppänen et al. (2007) considered ecological similarity as a pressure that drives the selection for eavesdropping. This means that for two species sharing predators, eavesdropping will be favoured when predation has similar fitness consequences for both species (i.e., errors are similarly costly and correct detections are similarly beneficial). Other authors have proposed different selective forces for eavesdropping, such as sender reliability, good discrimination by sender, or good reception by receiver (for informal reviews see Goodale et al., 2010; Magrath et al., 2015; Schmidt et al., 2010).

Turner et al. (2021) used signal detection theory to formalise previous theory about the conditions that select for eavesdropping of alarm calls. In their model, they find that selection for eavesdropping is in fact maximised when the ecological conditions of both species are similar, i.e., when both species are predated by the same set of predators, and calling and fleeing decisions have similar fitness consequences.

The purpose of this study is to replicate the analytical predictions of Turner et al. (2021) in a simulation model. We model a population of senders that produce alarm calls, and a population of heterospecific eavesdroppers that detect these calls and can choose to eavesdrop or not. Simulating this process allows us to explore which conditions make eavesdropping adaptive, and which ones constrain it. In addition to providing probabilistic results to complement previous analytic results, we are able to explore the dynamics of selection for eavesdropping. A simulation can show the speed and robustness of selection, and the effect of different combinations of parameters on it. We can not only investigate the effects of the environment on the dynamics of selection, but also what a population that evolves to eavesdrop would look like initially. If we find that eavesdropping becomes favourable to the simulated receiver population under the conditions predicted by Turner et al. (2021), this would provide further support for the idea that ecological similarity drives the selection for eavesdropping on heterospecifics.

In the remainder of the introduction, we explain the basic assumptions of signal detection theory, illustrating them using Turner et al.'s models. First, we explain the model of selection of calling thresholds for a population of senders that faces the problem of predator detection. Secondly, we address Turner et al. 's model for call detection in eavesdropping receivers.

1.1 Signal Detection Model

Turner et al. (2021) used signal detection theory (Herzog et al., 2019) and standard evolutionary invasion analysis (Otto & Day, 2007) to model calling decisions for a population of senders and the selection of eavesdropping for a population of receivers.
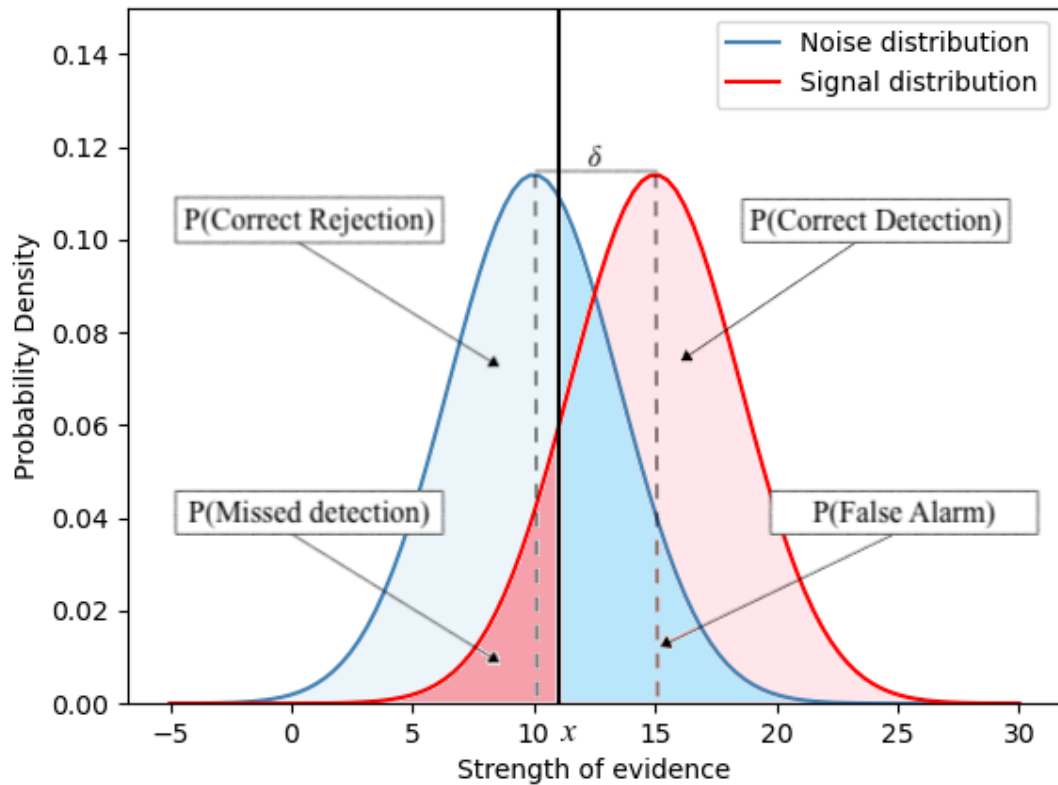
There are two possible states of the environment: predator presence (P_s) and predator absence ($\neg P_s$). For any given state, senders have two possible decisions: fleeing (C_s) or remaining, ($\neg C_s$). As it is assumed that senders call and flee simultaneously, they are modelled as a single decision. Senders have access to environmental cues to assess the state of the world and decide whether to flee or remain. For instance, an individual might observe silhouettes cast on the ground as a cue to determine the presence of predators. In signal detection theory, observed cues which in fact indicate predator presence are called *signals*. Other cues coming from the environment –like silhouettes of other animals– can make the detection of predators more difficult and are called *noise*. Note, in the animal communication literature, a communicative *signal* is an adaptation to elicit behaviour in intended receivers, while cues are incidental pieces of information that might change the behaviour of others but are not selected for it. Here, we use "signal" to refer to information that indicates predator presence and not as a communicative signal.

We assume signals of predator presence have variable strength, where higher values are stronger indications of predator presence. Lower values of the strength of evidence usually correlate with noise. The strength of predator cues and noise are assumed to be random variables described by the standard equal-variance Gaussian model (Wickens, 2002): the signal distribution Q_s and noise distribution Q_n have a variance of $\sigma^2 = 1$, but different centres, such that $Q_s \sim f(0, \sigma^2)$ and $Q_n \sim f(\delta_s, \sigma^2)$. The means are separated a distance δ_s to formalise the assumption that stronger cues correlate with predator presence. However, the two distributions overlap which makes the observed cues ambiguous. Larger values of δ_s make discrimination between signal and noise easier, as the distributions are shifted apart,

and thus it is called the *sensitivity index* of the prey species (see Figure 1). δ_s is a measure of how good the discrimination of cues by senders is (greater values of δ_s indicate better discrimination).

      Assuming that senders have already evolved to produce alarm calls, signal detection theory allows us to examine the decision rule on which the sender calls. The decision rule a sender is assumed to adopt in this case is to set a threshold x. For cues stronger than this threshold, senders accept the presence of a predator and produce an alarm call; for cues weaker, they reject predator presence and remain. Given that the information about the state

Figure 1

Signal detection model

Note. The red curve represents the distribution for the strength of the signal of predator presence. The blue curve represents the strength of noise distribution. Both distributions are separated by a distance δ, the sensitivity index. Senders set a threshold x (black vertical line) as a decision criterion. For detections stronger than x, senders flee and produce correct detections and false alarms. The sender remains for detections lower than x, producing correct rejections and missed detections.

of the environment is uncertain, there are two kinds of correct responses and two kinds of incorrect responses. Correct categorisations are (1) *Correct detection*, calling and fleeing when the predator is present, and (2) *Correct rejection*, safely remaining in the absence of predators. Erroneous categorisations are (1) *False alarms*, fleeing in the absence of predators, and (2) *Missed detections*, remaining in the presence of a predator. Given there is uncertainty, the best a sender can do is to trade one kind of error for another as they shift the threshold along different values of x, with lower values making them more prone to call and flee, or *gullible* –and higher values less prone or *fastidious* (Wiley, 2006, 2015, 2017).

Each decision gains the sender a fitness payoff. Fleeing decisions have a cost of α_s, regardless of it being a correct detection or a false alarm. The cost of a missed detection is γ_s. The benefit of safely remaining is β_s. Payoffs are chosen such that $0 \le 1 - \gamma < 1 - \alpha < \beta \ge 1$. This is because remaining in the presence of a predator has the lowest payoff, followed by fleeing, while safely remaining in the absence of predators has the highest payoff. In a different communicative situation, like signalling for accepting mates, false alarms could be more costly than missed detections, as erroneously accepting an undesirable mate is more costly than missing a desirable one (Wiley, 2013, 2017).

According to Turner et al. (2021), evolution will select for senders with a threshold that tends to the fitness optimum:

$$\widehat{x} = \frac{\delta_s}{2} + \frac{1}{\delta_s} \ln\left(\frac{(\beta_s - (1-\alpha_s))P(\neg P_s)}{(\gamma_s - \alpha_s)P(P_s)}\right) \tag{1}$$

The first term of the equation gives the threshold value at which false alarms and missed detections are equiprobable. The second term is called adaptive bias, and reflects how the conditions of the sender adjust from the equiprobable threshold. When predators are frequent and/or particularly dangerous, the sender optimal threshold $\widehat{x}$ takes on lower values and thus tends towards a more gullible threshold. On the contrary, lower frequencies of predator presence as well as higher costs of fleeing would select for fastidious sender thresholds.

Turner et al. assume a similar detection task for heterospecific individuals that are unintended receivers for the calls of senders. In particular, receivers face the challenge of distinguishing true calls from noise. A population of receivers has their own sensitivity index δ_r (that describes signal reception by receivers), their own detection threshold y, and their own payoffs for fleeing α_r, safely remaining β_r, and facing predation γ_r. Variation in

Table 1

Payoff matrix for fleeing or remaining in the presence or absence of predators

	Predator	No Predator
Flee	$1 - \alpha$	$1 - \alpha$
Remain	$1 - \gamma$	β

detection thresholds is assumed, but the evolvable trait in this model is the probability of eavesdropping u when a call is detected D_r A receiver who detects a call can choose to make use of its information and flee or disregard it and remain. The fitness of an eavesdropping receiver depends on a series of events: (1) a predator of the sender is present or absent (P_s or $\neg P_s$); (2) a predator of the receiver is present or absent (P_r or $\neg P_r$); (3) the sender calls or does not (C_s or $\neg C_s$); (4) the receiver detects a call or does not (D_r or $\neg D_r$); and (5) the receiver eavesdrops, with probability u or not, $(1 - u)$

For eavesdropping to be selected, the fitness gained from eavesdropping should be higher than that of the non-eavesdroppers. Turner, Spike and Magrath found that eavesdropping is selected when:

$$(\gamma_r - \alpha_r)P(D_r, P_r) > (\beta_r - (1 - \alpha_r))P(D_r, \neg D_r) \tag{2}$$

This means that for eavesdropping to be selected the benefit of escaping predation (fleeing to a call detection when a predator of the receiver is present, left term of Inq. 2) is greater than the cost of unnecessarily fleeing (fleeing to a call when a predator of the receiver is absent, right term of Inq. 2). When this condition is met, eavesdropping will invade the population of receivers and become stable, $\hat{u} = 1$ (a list of symbols can be found in Table 1).

Turner et al. found that selection for eavesdropping is maximised when senders and receivers are predated by identical sets of predators, such that $P_s = P_r$ and the fitness consequences of avoiding predation are the same for both species ($\alpha_s = \alpha_r, \beta_s = \beta_r$ and $\gamma_s = \gamma_r$). This is so because the way that senders adjust their calling threshold x to trade-off correct and incorrect detections also favours receivers, as that trade-off has the same fitness consequences for both species. Eavesdropping is also favoured for receivers that are more vulnerable to predation than senders, either because their predators are more likely or deadlier. In contrast, eavesdropping is selected against when receivers do not suffer predation

as much as senders. Turner et al. (2021) predicted that eavesdropping will be selected against when vulnerable senders call too often and produce too many false alarms from the receiver's perspective. This would explain the responses of impalas to the alarm calls of zebras, and why the reverse is not observed (Palmer & Gross, 2018, Meise et al., 2018). Impalas are predated by other species that do not suppose a threat to zebras, so that impala calls produce too many false alarms from the point of view of zebras.

These results support previous theory emphasizing the importance of ecological similarity to select for eavesdropping (Goodale et al., 2010; Seppänen et al., 2007), and fit with previous work that showed how too many false alarms can select against eavesdropping (Magrath et al., 2009; Meise et al., 2018; Palmer & Gross, 2018; Rainey et al., 2004). However, this is only predicted to happen when the sender is more vulnerable and their calls too gullible, producing many false alarms from the point of view of the receiver.

Turner et al. (2021) show that, generally, risk of predation drives the evolution towards gullible thresholds and the selection for eavesdropping. Heterospecifics are most benefited by eavesdropping when relevance is high and when senders suffer similar fitness consequences because of predation.

In the following section, we introduce our use of Turner et al.'s model to simulate the evolution of eavesdropping. We first address the signal detection problem of senders, along with the results of our simulations on how senders evolve towards optimal thresholds. Then, we describe our simulation of receivers who detect sender calls and eavesdrop.

2 Model

We simulate the behaviour of senders who detect predators and heterospecific receivers who eavesdrop on their calls in order to avoid predation, when both species have common predators. We are following Turner et al. (2021) in the use of signal detection theory to determine the animal's decision rule, whether it is for senders who detect the presence of predators or receivers who detect sender calls. From their model, we are assuming standard equal-variance Gaussian distributions for the cue distributions and an abstract payoff matrix. The novelty of this study is in the use of simulations for the evolution of eavesdropping on heterospecific alarm calls.

We first simulate the evolution of sender calling thresholds. If the population converges towards the analytically predicted threshold, our simulation would support Turner et al.'s (2021) results. Moreover, we will be able to check new aspects of the adaptation: (1)

the effects of the initial population on the final result; (2) the rate of evolution (i.e., how many generations are necessary to converge to the optimum, if the population ever converges); and (3) its robustness (i.e., how strong the selection for eavesdropping is).

As an assumption of our model, receivers detect calls of senders who have already evolved to call on an optimal threshold. Thus, we first address the sender model before moving forward to introduce the receiver model. Code for our sender and receiver models can be found in the following link: https://github.com/rgarnelonic/sdt-dissertation

2.1 Evolution of sender calling thresholds

In the first part of this work, we simulate the evolution of a population of senders that face a signal detection problem. The initial population of senders has a size N_s, where each individual sender is defined by a calling threshold x determined in their genomes. Initial sender thresholds are drawn from a standard normal distribution with mean $\mu = -2$ and variability $\sigma^2 = 1$. Initially, each threshold (genome) is equiprobable, $P(x_i) = 1/N_s$. The probability of a predator being present $P(P_s)$, the sensitivity index δ_s and the fitness payoffs α_s, β_s and γ_s are fixed and thus treated as parameters (see the payoff matrix in Table 1).

Fleeing decisions are correct when a cue from the signal distribution Q_s is detected and it is greater than the threshold x of the sender. The probability of a correct detection is calculated using the complement of the cumulative distribution function of the normal distribution (represented by ϕ): $P(C_s|P_s) = 1 - \phi(x - \delta_s)$. The cumulative distribution function gives the probability of a value being smaller than the threshold, i.e., the probability of a *remaining* decision occurring, whereas its complement calculates the probability of values higher than the threshold being encountered, indicating the probability of *fleeing* decisions. For instance, the probability of a correct rejection is the probability of the predator being absent and the strength of the noise being lower than the threshold, and it is calculated with the cumulative distribution function of the noise distribution, $P(\neg C_s|\neg P_s) = \phi(x)$.
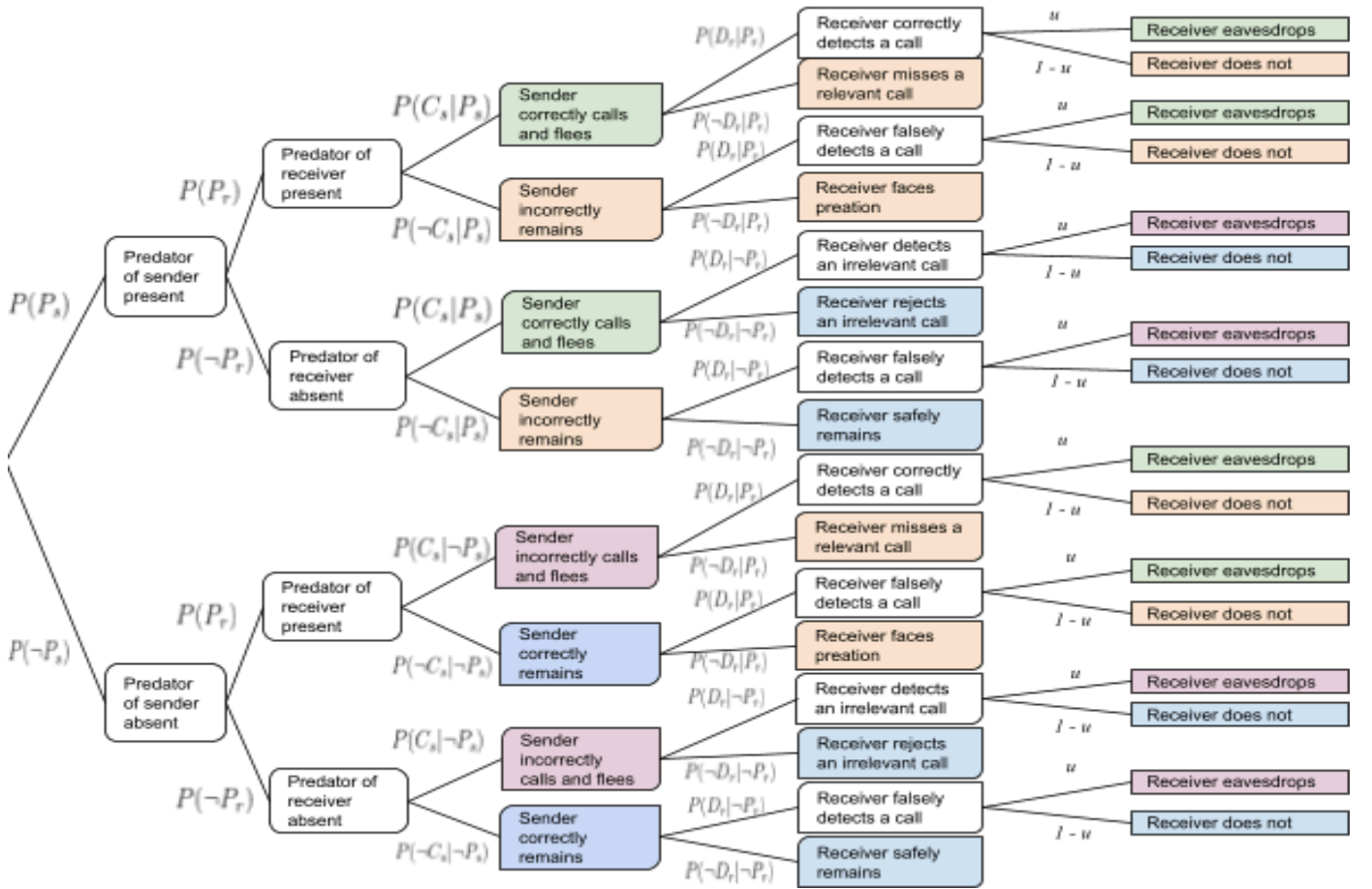
The fitness W_s of an individual is the expected value of each fleeing and remaining decision, in the absence and presence of predators. To calculate it, we first find the probability of each of the four possible outcomes. For instance, the probability of a false alarm is the probability that a predator is absent multiplied by the probability that a call is produced given that the predator is absent $P(C_s|\neg P_s)P(\neg P_s)$ (see Figure 2). Then, we multiply the probability of that outcome by the payoff gained, as shown in Equation 3:

$$W_s = W_s(correct\ detection) + W_s(missed\ detection) \quad (3a)$$
$$+ W_s(correct\ rejection) + W_s(false\ alarm)$$

$$W_s = P(P_s)(P(C_s|P_s)(1 - \alpha_s) + P(\neg C_s|P_s)(1 - \gamma_s)) \quad (3b)$$
$$+ P(\neg P_s)(P(\neg C_s|\neg P_s)\beta_s + P(C_s|\neg P_s)(1 - \alpha_s))$$

Figure 2

Decision tree for senders and receivers.

Note. Each of the coloured squares represents a final fleeing or remaining decision that results in some fitness consequence for the agent. Green squares represent correct detections, orange squares represent missed detections, pink squares represent false alarms and blue squares represent correct rejections. The probability of each outcome is calculated by multiplying the probabilities of each branch that leads to a coloured square.

The fitness of a sender is a function of their threshold $W_s(x)$: senders will produce different fleeing behaviours depending on their individual threshold and thus gain different fitness. Turner et al. (2021) predict that evolution will select for an optimal threshold $\hat{x}$, which

maximises W_s for the sender species (see Eq. 1). During this process, thresholds that yield higher fitness will be selected for and will be more present in subsequent generations, while thresholds that do not produce successful behaviour will tend to disappear from the population. In the present model, mutation is not considered, so the population evolves towards the threshold that is closest to the optimum when the value of $\hat{x}$ is not represented in the initial genomes of the sender population.

Table 2
Index of notation

Symbol	Description
P	Probability of predator present.
R	Relevance index. It is the probability that a predator of the sender is a predator of the receiver.
Cs	Call production by sender.
Dr	Call detection by receiver.
α	Cost of fleeing either when the predator is present or absent, which increases with energy costs of fleeing.
β	Benefits of avoiding predation, which increases with foraging or other social opportunities of safely remaining.
γ	Cost of potentially facing predation, which increases with predation risk.
R	Relevance index. Probability that a predator of the sender is shared with the eavesdropper.
δ	Sensitivity index. It represents the distance between the mean of the signal distribution and the mean of the noise only distribution. δ_s is the sender's discrimination of predators and δ_r is the receiver's reception of calls.
Q	Distribution of observable, environmental cues. Q_s is the signal distribution, where cues correspond to P and Q_n is the noise distribution.
N	Size of the population. It is determined for the initial population and kept constant over time.
x	Sender's detection threshold for strength of evidence of predator presence. $\hat{x}$ is the optimal threshold that maximises sender fitness.
y	Receiver's detection for strength of evidence of a call being produced.
W	Eavesdropping fitness.

| u | Eavesdropping probability. |

Note. Parameters are subscribed with s for the sender, r for the receiver and i for an individual. P(.) denotes the probability of an event or the proportion of a genome, and $\neg$ denotes that the event has not occurred $x,\ y\ \in\ (\infty,\ \infty)$, $\alpha,\ \beta,\ \gamma\ \in\ [0,\ 1]$, $r,\ u\ \in\ [0,\ 1]$ and $\delta\ \in\ [0,\ \infty)$.

We model this evolutionary process by means of the *replicator equation* (Hofbauer & Sigmund, 1998; Skyrms, 2010; Smith, 1982). This equation captures the dynamics of an evolving population where there is variability in behaviour. A behavioural variant is called a *strategy*. In this sense, thresholds represent the different strategies that senders can adopt and, although they are equiprobable in the initial population, their proportions evolve over generations.

The replicator dynamic functions as follows. Let p represent the set of proportions of each threshold in the population, such that $p = p_1,\ p_2,\ p_3, \cdots p_N$. Note that p and not x is the evolvable trait in our simulation, as the set of thresholds in the population is static. The proportion p_i of threshold x_i in the next generation is given by the replicator equation:

$$p'_i = p_i(\frac{W_i}{\bar{W}}) \qquad (4)$$

Where p'_i represents the proportion of strategy i in the next generation, W_i is the fitness of the sender with strategy i and $\bar{W}$ is the average fitness of the population in that generation. Equation 4 captures the idea of an evolution biased towards the most successful strategies (in this case, towards the thresholds yielding higher fitness). In the following generation, thresholds that perform above average will be represented in a larger proportion in order to model how descendants replicate the most successful strategy. At the end of each generation, the proportions of sender thresholds are updated, such that p_i in the next generation is the p'_i of the previous generation. Thresholds close to the fitness optimum will become resident in the population, with other genomes disappearing.
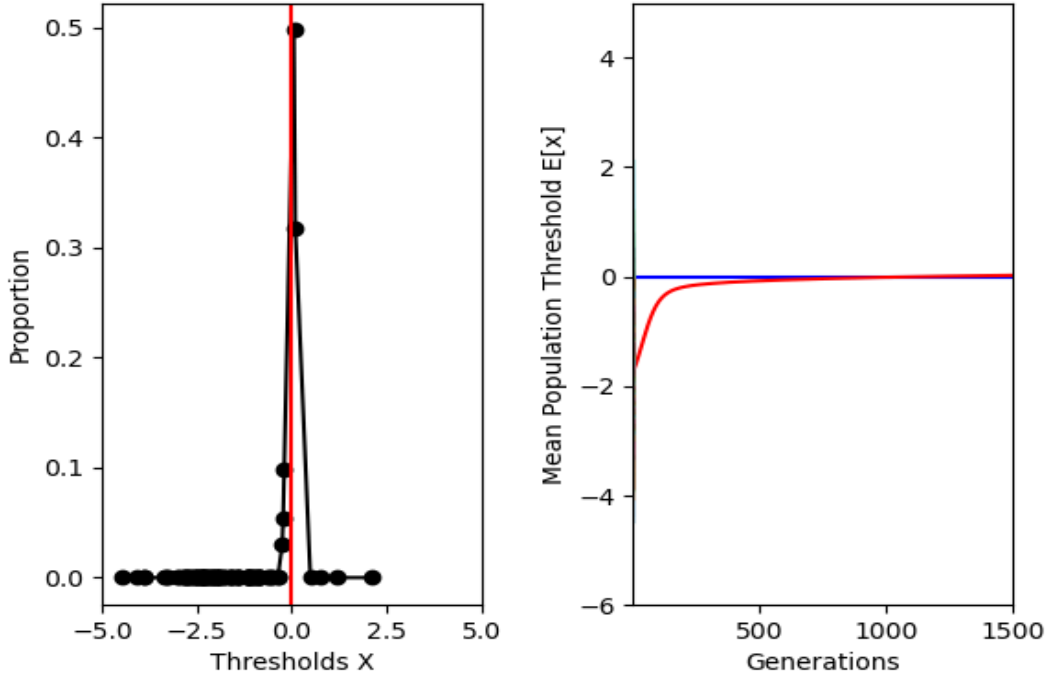
Our simulations confirm the results in Turner et al. (2021). For any combination of parameters tested, senders evolve towards $\widehat{x}$, the analytically predicted threshold (see Figure 3). Depending on the frequency of predator presence $P(P_s)$, the cost of predation γ_s and the cost of fleeing α_s, sender thresholds are adapted to be more fastidious or gullible, as predicted. Generally, the evolution towards the optimal threshold is slow-paced, but robust

once the population tends to the optimum. When the sender population converges towards a threshold value, this threshold invades the population and $p(\widehat{x}) = 1$. However, because mutation is not allowed, for very fastidious optimal thresholds, senders evolve towards the threshold value present in the population which is closest to the optimum. This is just a consequence of the model design, and allowing for random mutation would favour the population of senders to reach $\widehat{x}$.

In order to avoid predation, gullible thresholds are selected when predators are likely dangerous for senders. When predators are extremely likely ($P(P_s) > 0.6$) and deadly

Figure 3

Evolution of sender calling thresholds

Note. Left: proportions of calling threshold present in an evolved sender population, where the vertical red line represents the analytical threshold. Right: evolution drives sender thresholds towards the analytical prediction (blue line) over generations.

($\gamma_s = 0.9$), gullible thresholds are selected as predicted. However, the rate of conversion is extremely slow in comparison to that happening on intermediate values. Moreover, selection does not happen linearly, and there is a first stage in which selection turns towards more fastidious thresholds, until more gullible ones eventually invade the population. A population

that is constantly under threat of predation, where predation is deadly, will always get low fitness payoffs regardless of their strategy, because their environment is dangerous. We argue that convergence is slowed down for high values of $P(P_s)$ when predators are deadly because all the individuals are performing "equally badly", not because of their strategies, but because the environment is equally dangerous for every individual.

When predators are likely, but not particularly dangerous for senders (low values of γ_s), the evolved threshold is placed near $\delta_s/2$, the threshold which makes false alarms and missed detections equally probable. We confirm, then, that it is the likelihood of predation and the danger it poses on senders which select for gullibility in calling thresholds, as selection favours fleeing often over facing deadly predators.

2.2 Selection for eavesdropping

We simulate a population of receivers that detect alarm calls produced by heterospecific senders. Senders are assumed to have evolved to produce calls on a threshold that maximises their fitness. Receivers who eavesdrop are expected to call and flee when they detect a signal stronger than their threshold y. We are interested in whether receivers who flee to sender calls are favoured over receivers who reject detected calls and remain and, if so, under which conditions. Note, Turner et al. (2021) treat y as a fixed parameter, assuming that selection had not yet affected the receiver's thresholds. By contrast, we assume variability in y. Receiver thresholds are randomly drawn from a normal distribution with mean $\mu = -3$ and spread $\sigma^2 = 1$. This distribution includes values centred at a lower mean than that of senders, to model the assumption that receiver thresholds are not evolved to detect sender calls, although still allowing variation in the population.

Receivers detect ambiguous environmental cues that can be indicative of a heterospecific alarm call being produced, or can correspond to noise. The probability of detecting a call or noise is described again using the equal-variance Gaussian model, with call distribution being $Q_s \sim f(\delta_r, \sigma^2)$ and noise distribution $Q_n \sim f(0, \sigma^2)$. Again, Q_s and Q_n are identical except for being shifted apart a distance of δ_r.

Analogous to the sender population, δ_r represents the sensitivity index of receivers. We assume that $\delta_r < \delta_s$ because call signals travel temporally and spatially until they are detected by receivers. The choice for a smaller sensitivity index for receivers translates into a larger overlap between noise and signal distributions, which increases ambiguity, responding

to evidence of distant signals being more difficult to discriminate from noise (Bradbury & Vehrencamp, 2011; Magrath et al., 2015a; Seppänen et al., 2007).

Senders and receivers may be threatened by the same or different predators, as shown in Figure 2. In our model, the probability of a predator present being a predator of the sender *and* of the receiver is measured by the *relevance index*, R. $R = 1$ when $P(P_s) = P(P_r)$, or in other words, it indicates that both species are predated by exactly the same set of predators. When $R \neq 1$, R acts as a measure of how likely a predator of the receiver is present. In this case, errors from the point of view of the sender can be beneficial for receivers, as sender false alarms can correctly inform about the presence of a predator of the receiver (see Figure 2).

We are assuming that receivers do not have access to other signals of predator presence, and can only inform their antipredator behaviour by eavesdropping on sender calls. Senders call with probability $P(C_s) = P(C_s|P_s) + P(C_s|\neg P_s)$, where $P(C_s|P_s) = 1 - \phi(x - \delta_s)$ and $P(C_s|\neg P_s) = 1 - \phi(x)$. Similarly, receivers detect a call and flee with probability $P(D_r) = P(D_r|C_s) + P(D_r|\neg C_s)$, where $P(D_r|C_s) = 1 - \phi(y - \delta_r)$, and $P(D_r|\neg C_s) = 1 - \phi(y)$. Once a call is detected, receivers may flee with probability u or remain, $1 - u$. In other words, u is the probability that receivers eavesdrop.

In this case, we are interested in the evolution of the eavesdropping behaviour of receivers rather than their calling threshold. Thus, receivers in the initial population can be *eavesdroppers* or *non-eavesdroppers*. Both eavesdroppers and non-eavesdroppers detect sender calls, but only eavesdroppers flee to them. The only strategy possible for non-eavesdroppers is to always remain. The eavesdropping behaviour of each individual receiver is initially determined by randomly sampling genomes from a binomial distribution, where the initial probability of an individual being an eavesdropper is $P(u) = 0.5$.

Fitness payoffs for the receiver species are again treated as parameters and may be different from those of senders, depending on the costs of fleeing, the benefits of safely remaining, and how deadly predators are for each species. When sender calls are not detected ($P(\neg D_r)$), receivers do not acquire information about the state of the environment, and both eavesdroppers and non-eavesdroppers remain. In this case, receivers gain a payoff of $1 - \gamma_r$ when a predator of the receiver is present ($P(P_r)$), and β_r when they safely remain in the absence of predators ($P(\neg P_r)$). Only receivers that are eavesdroppers flee when a call is

detected ($P(D_r)$), achieving a payoff of $1 - \alpha_r$ for a detection, either for correct detections or false alarms. Non-eavesdroppers remain regardless of a call being detected, gaining $1 - \gamma_r$ for rejecting a correct detection and β_r when ignoring false alarms. Note that eavesdroppers and non-eavesdroppers only receive different payoffs for their decisions due to calls being detected, as eavesdroppers flee and non-eavesdroppers remain.

The fitness function for senders is relatively simple as it is the combination of the probabilities of two possible states of the environment (predator present or absent) and two decisions (flee or remain). In contrast, the fitness of each individual receiver depends on the combination of the following events: (1) a predator of the sender is present or absent; (2) a predator of the receiver is present or absent; (3) senders produce a call (and simultaneously flee) or they do not, (4) receivers detect a call or do not; and (5) receivers are eavesdroppers and flee to the call or they are non-eavesdroppers and disregard that call. For simplicity, we break down the fitness function of receivers into different fitness functions for decisions after calls are detected $W_r(D_r, y)$ –where eavesdroppers flee and non-eavesdroppers remain– and for decisions when calls are not detected $W_r(\neg D_r, y)$. The total fitness for an individual would be the sum of the two.

When no calls are detected, both strategies –eavesdropping and non-eavesdropping– yield the same fitness payoffs for receivers, because both strategies lead to a decision to remain for $\neg D_r$. As it can be observed in Equation 5a and 5b, incorrect decisions from the point of view of the sender can be beneficial for receivers and vice versa. For instance, a false alarm from the point of view of the sender can result in a correct rejection from the point of view of the receiver, when there is no predation danger, and the false alarm of senders is rejected by receivers.

$$W_r(\neg D_r, y) = W_r(correct\ rejection) + W_r(missed\ detection) \tag{5}$$

$$W_r(correct\ rejection) = \beta_r(P(\neg P_r)(P(P_s)(P(C_s|\neg D_r) + P(\neg C_s|\neg D_r)) \tag{5a}$$
$$+ P(\neg P_s)P(C_s|\neg D_r) + P(\neg C_s|\neg D_r))))$$

$$W_r(missed\ detection) = (1 - \gamma_r)(P(P_r)(P(P_s)(P(C_s|\neg D_r) + P(\neg P_s|\neg D_r)) \tag{5b}$$
$$+ P(\neg P_s)(P(C_s|\neg D_r + P(\neg C_s|\neg D_r))))$$

Call detections (D_r) prompt fleeing behaviour in eavesdroppers, while non-eavesdroppers remain. As a consequence, receivers obtain different fitness payoffs for correct detections and false alarms, depending on whether they eavesdrop and flee, or do not

eavesdrop and remain. The general form of the fitness function for call detection is given by Equation 6, where Equations 6a and 6b specify the fitness gained by eavesdroppers and equations 6c and 6d, that of non-eavesdroppers.

$$W_r(D_r, y) = W_r(correct\ detection) + W_r(false\ alarm) \tag{6}$$

Fitness for eavesdroppers for call detection

$$W_r(correct\ detection) = (1 - \alpha_r)(P(P_r)(P(P_s)(P(C_s|D_r) + P(\neg C_s|D_r)) \tag{6a}$$
$$+ P(\neg P_s)P(C_s|D_r) + P(\neg C_s D_r))))$$

$$W_r(false\ alarm) = (1 - \alpha_r)(P(P_r)(P(P_s)(P(C_s|D_r) + P(\neg C_s|D_r)) \tag{6b}$$
$$+ P(\neg P_s)P(C_s|D_r) + P(\neg C_s|D_r))))$$

Fitness for non eavesdroppers for call detection

$$W_r(correct\ detection) = (1 - \gamma_r)(P(P_r)(P(P_s)(P(C_s|D_r) + P(\neg C_s|D_r)) \tag{6b}$$
$$+ P(\neg P_s)P(C_s|D_r) + P(\neg C_s|D_r))))$$

$$W_r(false\ alarm) = \beta_r(P(\neg P_r)(P(P_s)(P(C_s|D_r) + P(\neg C_s|D_r)) \tag{6d}$$
$$+ P(\neg P_s)P(C_s|D_r) + P(\neg C_s|D_r))))$$

Every generation, the fitness of each individual receiver is calculated. Subsequently, the proportion of eavesdroppers $P(u)$ and non-eavesdroppers $1 - P(u)$ are updated. Again, the proportion of the strategy that produces greater fitness payoffs increases in the following generation, according to the replicator equation, $P'(u) = P(u)\frac{W_u}{\bar{W_r}}$, where W_u is the fitness of the eavesdropping receivers and $\bar{W}_r$ is the mean fitness in the receiver population.

2.3 Simulation

A simulation run consists of two main parts: (1) the initialisation of the population and (2) the evolution of the population. The initial population has a size $N = 100$ and evolution happens over a number of discrete-time units, or *generations, t*. Populations are initialised with genomes that represent calling thresholds for senders or eavesdropping behaviour in receivers.

Each generation, the fitness function is calculated for each individual, as a function of the environmental parameters and individual genomes. The populations evolve in a way where genomes remain unchanged, but proportions of genomes are updated: the most successful genomes (those that give higher fitness) will appear in the next generation in larger proportions, while other genomes will be deleted.

Turner et al. (2021) reported that eavesdropping is selected when call detections by receivers correspond to a considerable danger, which occurs when predators are more frequent and when receivers are particularly vulnerable to them. Thus, we are interested primarily in the effects of R, γ_r and α_r on the selection of eavesdropping. We conduct parameter sweeps where we simulate first a population of senders that evolve to call on $\widehat{x}$, and then a population of receivers that evolve to eavesdrop on those calls. We run simulations where one parameter value is manipulated at a time while the others are kept at a baseline. Due to processing power limitations, we run ten simulations per each parameter value tested. The results of the receiver model are shown in the following section. The results for the sender model are included at the end of 2.1 Evolution of sender calling thresholds.

3 Results

Simulating the selection for heterospecific eavesdropping confirms that greater risk of predation selects for eavesdropping. Risk of predation is represented in our model by the probability of a predator being present, the relevance index and the fitness payoffs, which are a measure of the vulnerability of the species. For every combination of parameter values tested, our simulations confirm that eavesdropping is favoured over non-eavesdropping when the cost of fleeing to escape predators is lower than the cost of unnecessarily fleeing to false alarms. Moreover, we are able to observe the rate of evolution and whether the proportions of types in the initial populations have any effect on the evolution of eavesdropping.

Our results are robust and are not affected by the initial proportions of different genomes in the initial population. In the receiver populations, the initial proportion of eavesdroppers is $P(u) = 0.5$, and the results reported here are obtained assuming this. However, when this initial proportion is manipulated, we do not observe any effects on the results. Even when eavesdroppers are present in the initial population in a proportion as low as $P(u) = 0.1$, eavesdropping will be selected when Inequality 2 is satisfied.

3.1 Threat of Predation to Receivers

Predators affect the selection of eavesdropping in how likely they are to be present and how deadly they are to the prey species. Predators being more likely translates to a population of senders evolved towards gullible thresholds. For receivers, this means that calls are more likely to be present, but these calls represent actual threats for receivers with probability R. How vulnerable receivers are to predators is represented by the cost of predation γ_r and the cost of fleeing α_r.

Our simulations confirm previous results by Turner et al. (2021): selection for eavesdropping linearly increases with the cost of predation γ_r and decreases with the cost of fleeing α_r. This is because the conditions for eavesdropping to be selected (see Inq. 2) are satisfied when fleeing is low-cost and predators are substantially dangerous. Selection for eavesdropping is also positively correlated with R, the likelihood of a predator of the sender being shared with the receiver. This is because when predators are not common for both species, sender calls are less likely to correspond to relevant threats to receivers. The effects caused by the degree of threat of predators tothe selection of eavesdropping is summarised in Table 3.

3.2 Speed of Convergence to Eavesdropping

For every combination of parameters tested, the receiver population converges always to one or the other strategy, such that the proportion of eavesdroppers in the final population is always $P(u) = 1$ or $P(u) = 0$. The rate of evolution is faster than the rate of selection of sender thresholds.

Table 3
Effects of different parameter values in the selection for sender thresholds and eavesdropping behaviour in receivers

	Evolved sender threshold		
Parameter	Parameter value		
	Low	Intermediate	High
$P(P_s)$	Fastidious	Gullible	Gullible

γ_s	Near $\delta_s/2$	Near $\delta_s/2$	Gullible
α_s	Gullible	Gullible	Fastidious
	Selection for eavesdropping		
	Low	Intermediate	High
R	N	E	E
γ_r	N	E	E
α_r	E	E	N

Note. For each parameter value, the others are kept at baseline values which are assumed $\delta_s = 1$, $P(P_s) = 0.5$, $\alpha_s = 0.3$, $\beta_s = 1$, $\gamma_s = .8$ for senders, and $\delta_r = 0.8$, $R = 0.5$ $\alpha_r = 0.2$ and $\gamma_r = 0.9$ for receivers. The reason for these choices is explained in the main text. Gullible thresholds are considered below $\delta_s/2$, the threshold that produces correct and incorrect decisions equiprobably; fastidious thresholds are considered above $\delta_s/2$. For receivers, E means that the final population converges to eavesdropping, while N means that it does not.
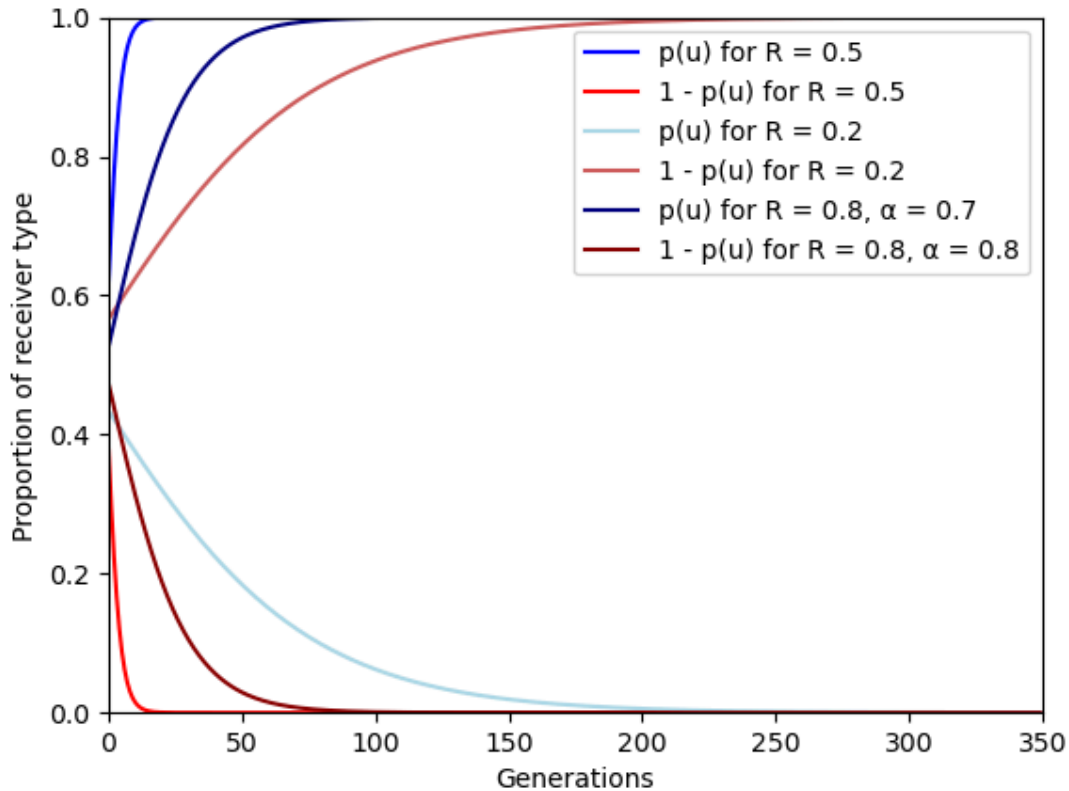
For instance, under intermediate values of $P(P_s)$, and non-extreme values for α_s and γ_s senders need around 500 generations until they converge to the thresholds that perform closest to optimal. In cases where more extreme parameters are chosen, conversion can take up to 1000 generations to happen. For extremely high values of $P(P_s)$, conversion to the optimal thresholds takes $t = 5000$ for intermediate values of payoffs ($\alpha_s = 0.4$, $\gamma_s = 0.8$) and up to $t = 10000$ for more extreme payoffs ($\alpha_s = 0.2$, $\gamma_s = 0.9$). In the case of a receiver population being driven to one of the two strategies, conversion to either of them is remarkably faster, $t < 50$. We explored the possibility of using slow down factors to reduce the speed at which proportions of eavesdroppers and non-eavesdroppers change. In this approach, the new proportions obtained by the replicator equation each generation are subtracted to the proportions at the start of that generation, $p(u) - p'(u)$. The result is a growth rate that is "slowed down" by a factor of 10^{100}. Proportions are updated by summing this slowed down growth rate to $p(u)$. The use of slow down factors had an effect on the speed of convergence to one type or the other, but it still happens fast in relation to the speed of evolution for senders (convergence always happened before $t = 300$).

R and γ_r are positively correlated with selection for eavesdropping. Extremely high values of these parameters prompt the selection for eavesdropping at a fast speed ($t < 20$), whereas extremely low values slow down convergence ($t < 100$). Cheap costs of fleeing α_r

favour a fast-paced selection for eavesdropping, while intermediate values for α_r slow it down ($t < 100$). Extremely high values of α_r select rapidly against eavesdropping when other parameters are kept at the baseline. However, when predators are particularly frequent

Figure 4

Convergence rate of receiver types

and deadly, eavesdropping is still selected at a slowed down rate ($t < 100$), regardless of how costly fleeing is, as shown in Figure 4.

Changes in speed of evolution reflect differences in fitness between the two types: evolution is slower when the difference in fitness is subtle, and happens by slowly changing the type proportions over time. For instance, persistent predators that are particularly deadly to prey will drive a fast-paced selection towards eavesdropping (controlling for low values of α_r), because eavesdroppers would be highly benefited from escaping them, while non-eavesdroppers suffer the costs of predation constantly. This fast paced selection is slowed down if we manipulate fleeing costs to be higher: eavesdropping is still more beneficial, but the difference in fitness between types is not as pronounced (Figure 4).

4 Discussion

We found that the threat predators pose to prey is an important selective pressure that leads to the evolution of eavesdropping on heterospecific alarm calls. As Turner et al. (2021) predicted, eavesdropping is favoured when shared predators are particularly deadly or frequent. Our results support the idea that eavesdropping is selected when the costs of fleeing to avoid predation are higher than the costs of fleeing to false alarms. When heterospecific senders are ecologically similar to receivers, the benefits of eavesdropping are maximised, because their calls trade off the costs of correct detections and false alarms in a way that is maximally beneficial for receivers too, as predation has similar fitness consequences for both species. Simulations allow us to observe that larger differences in fitness between eavesdroppers and non-eavesdroppers in a population favour faster rates of convergence to one of the genome types in the population. Moreover, conversion is always robust and the favoured type always invades the population making the other type disappear.

Our results can be taken as an indication that eavesdropping on heterospecifics may be a more widespread behavior than previously thought. However, these dynamics could also be dependent on our model choice. Signal detection theory best fits situations in which a perception-based decision occurs only once, instead of sequentially. Recent research has pointed out that signal detection theory predictions used in sequential situations can be reversed when the conditions of the signal detection are state-dependent (McNamara & Trimmer, 2019; Trimmer, Ehlman, & Sih, 2017; Trimmer et al., 2017). The basic idea behind a state-dependent signal detection model would be that decisions repeated over time affect the fitness payoffs for each decision. For example, according to our model, a vulnerable species who suffers a great cost of predation will constantly flee to escape predation when the cost of fleeing is cheap. When fleeing behaviour is repeated over time, fleeing should become more and more expensive, as the animal never gains the benefit of staying (i.e., foraging and mating) and hence has to bear repeatedly with the cost of fleeing. For example, McNamara & Trimmer (2019) build a model where payoffs are dependent on the state of the energy reserves of the individual, instead of being fixed over time. When perception-based decisions are sequential, signal detection theory could be adapted to include state-dependent payoffs. Our intuition is that such a state-dependent signal detection model would shed light on how the evolution of heterospecific eavesdropping works, especially for extreme parameter values, where predictions could be reversed.

The present work as well as that of Turner et al. (2021) quantitatively determine the conditions necessary for eavesdropping on heterospecific alarm calls to evolve. As Goodale et al. (2010) point out in a review, the study of interspecific information use and how it affects mixed-species groups is generally qualitative. In recent years, although some of these qualitative hypotheses have been tested (see Magrath et al., 2009; Palmer & Gross, 2018; Tegtman & Magrath, 2020), there is still much to be learned about heterospecific information use and its effects on the formation and maintenance of mixed-species groups. We agree with Goodale et al. (2010) in that quantitative research through modelling and simulation can contribute to making more informed hypotheses to be tested experimentally.

We are ultimately interested in how benefits and costs of information transfer between heterospecifics pose new selective pressures to individuals that are different to those pressures in single-species groups. Harrison & Whitehouse (2011) suggested that birds in mixed-species flocks are exposed to different selective pressures that may result in accelerated rates of evolutionary change. To test this idea, Farine et al. (2012) analyse the social behaviour of mixed-species flocks of tits (*Paridae*) by quantifying dyadic interactions between conspecifics and heterospecifics. They found that bird size serves a proxy for social associations with conspecifics, because larger birds interact more within species. Large birds are dominant within conspecific groups, and have more associates within species than subdominant individuals. However, a social network analysis shows that heterospecific associations happen equally across individuals without any effect on individual size. Farine et al. argue that heterospecific associations might reduce the effects of dominance that larger individuals pose on smaller ones, helping them to still have a central position globally in the mixed-species network. These results support the idea of vulnerable individuals being benefited by eavesdropping, but also open the question of whether different selective pressures are at play for subdominant individuals, which could be benefited by being more social towards heterospecifics.

Increased mutual dependence between individuals of different species is argued to prompt a series of convergent phenotypic traits (Zeder et al., 2006). New evidence emerging from a combination of (paleo-)genomics, anatomy and animal behaviour show convergent anatomical and behavioural phenotypes in different species that have evolved under the pressure of being social towards another species, because both are benefited by interspecific interactions (Theofanopoulou et al., 2017).

Anatomical and behavioural features of these phenotypes have been identified in domesticated populations of different species, such as the silver fox (*Vulpes vulpes*) (Belyaev,

1979; Trut, 1999) or the Bengalese finch (*Lonchura striata domestica*) (Okanoya, 2015), differentiating them from their wild counterparts. Convergent anatomical traits of domesticated species include craneofacial changes, reduction of sexual dimorphism between males and females, more juvenile and docile behaviour as well as more complex vocalizations (see Theofanopoulou et al., 2017).

The remarkable resemblance of these traits with those of anatomically modern humans has led to the proposal of the self-domestication hypothesis: convergent traits observed in domesticated species emerge when prosociality is favoured over aggression in the species environment. Furthermore, Thomas & Kirby (2018) propose that the cognitive traits that emerge as byproducts of (self-)domestication might explain the origins of language in humans, especially the ability to infer communicative intent from interactions with heterospecifics. According to this proposal, cultural transmission, the process shaping the structure of human language, is benefited by the cognitive traits observed in domesticated species.

We suggest that similar evolutionary processes might be at play in eavesdropping species as those of domestication, because of similar pressures favouring prosociality manifesting. Further work should be in the direction of determining conditions and selective forces present in eavesdropping, not only of heterospecific alarm calls, but of other communication settings too. We propose further comparative work across species that associate with heterospecifics and species that habitat single-species groups. If phenotypic differences are found, it may be indicative of different selective pressures at play, which might be caused by differences in selection for prosociality.

5 Conclusion

Overall, eavesdropping seems to be a widespread phenomenon that improves the fitness of vulnerable species, thanks to selective pressures that favour mutualistic relations with other ecologically similar species that act as sources of information. Further research is still needed in order to know how exactly selection works in these environments, as well as what phenotypic changes are prompted. In the case of eavesdropping on heterospecific alarm calls, some crucial factors are not considered in our abstract model: (1) the use of

conspecifics as complementary sources of information; (2) fitness consequences that heterospecific eavesdroppers may have on senders (if any); and (3) more realistic state-dependent payoffs.

Our study demonstrates that eavesdropping on heterospecific alarm calls is beneficial for particularly vulnerable species that share predators with other ecologically similar species. Further research can be done to confirm these results and, zooming out to study interspecific associations more generally, much more may be uncovered about how the flow of information shapes mixed-species groups and whether learning or other cognitive abilities benefit from interactions with heterospecifics.

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