

Evolution of signalling through pursuit deterrence in a two-prey model using game theory

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We model the evolution of a pursuit-deterrent signal of 'perception advertisement' for the case in which a predator can travel among many patches, each of which contain two prey. We consider a signal that is difficult for prey to fake, such as approaching the predator, and assume that the signal also alerts other prey in the patch, thereby reducing the overall value of that patch to the predator. We analyse the model using evolutionary game theory and adaptive dynamics on prey and predator fitness-generating functions to determine convergent stable equilibrium solutions for the behaviour of prey and predator. We consider the effects on equilibria of the probability of predator detection, signalling cost, predator travel time and the chance of killing the prey. Depending on the parameter values, we find stable equilibria at pure signalling, nonsignalling and mixed evolutionarily stable strategies (ESSs). For example, prey are more likely to signal when they have a low probability of detecting the predator, and when the predator's missed opportunity costs are higher. We also find that there are two basins of attraction such that the system evolves towards one of them depending on the initial strategy values. This is the first two-prey pursuit-deterrent signalling game we are aware of, providing a novel theoretical basis for the evolution of signalling in group-living prey.

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Adaptive explanations for signalling by prey in the presence of a predator belong to two broad categories. First, a prey may signal other prey about perceived risk in the environment (Shah, Greig, MacLean, & Bonter, 2015; Townsend, Rasmussen, Clutton-Brock, & Manser, 2012). While these signals may inadvertently draw the attention of the predator and thereby increase risk to the signaller, benefits of signalling may arise from the mechanisms of kin selection (Hamilton, 1963) or reciprocal altruism (Trivers, 1971). Second, a prey may signal a predator directly, as described in white-tailed deer, *Odocoileus virginianus* (Caro, Lombardo, Goldizen, & Kelly, 1995), purple swamphen, *Porphyrio porphyrio* (Woodland, Jaafar, & Knight, 1980), guppies, *Poecilia reticulata* (Godin & Davis, 1995), lizards (Leal & Rodriguez-Robles, 1997) and other species across taxa (Caro, 2005). This 'pursuit-deterrent' signalling is hypothesized to inform the predator either that it has been spotted ('perception advertisement'), or that the prey possesses heightened escape abilities ('quality advertisement'), encouraging the predator to abandon attack (Caro, 1995). In principle, both predator and prey

may benefit from this type of signal; the predator avoids wasting time and energy on an unsuccessful attack, while the prey is spared possible death and can continue to forage or engage in other maintenance activities. But the selective advantage of pursuit-deterrent signalling has been challenging to explain since prey intentionally signal the predator. Thus when prey occur in a group, the signaller may, through an attractive signal such as tail flashing or predator inspection (Dugatkin & Godin, 1992; Godin & Davis, 1995), draw the predator's attention away from other prey to itself and delay its own escape (Caro, 1995; Hasson, 1991). Pursuit-deterrent signalling may thereby incur higher costs than prey–prey signalling, which motivates the study of mechanisms other than kin selection and reciprocal altruism that help maintain it. Signals directed to a predator may however also be received by other prey, and therefore we note that these two categories of signals need not be mutually exclusive. Indeed, as we argue below, a pursuit-deterrent signal that is also received by other prey may be especially effective.

Previous theoretical models of pursuit deterrence include the 'watchful babbler' game (Bergstrom & Lachmann, 2001) and its optimal foraging extension (Getty, 2002). These models use evolutionary game theory (Maynard Smith, 1982) to identify conditions required for the existence of evolutionarily stable strategies

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(ESSs) for prey and predator where prey signal and predators receiving the signals do not attack. Several features of these models are noteworthy. First, they focus on conditions that yield a pure ESS in which, depending on system parameters, the prey either always signals or never signals, and the predator receiving the signal never attacks, as opposed to a mixed ESS where prey signal with a probability and the predator receiving the signal attacks with a probability (for cases of hybrid equilibria with probabilistic strategies in the case of dishonest signalling, see [Huttenberger & Zollman, 2010](#); [Zollman, Bergstrom, & Huttenberger, 2013](#)). Existing models also focus on the evolutionary stability in the classical ESS framework of an invasion-resistant equilibrium ([Maynard Smith & Price, 1973](#); [McGill & Brown, 2007](#)), that is to say, these models solve for a strategy or a set of strategies that cannot be invaded when in common use. However, for continuous strategies, it is worth knowing whether the ESS is also convergent stable ([Apaloo, Brown, & Vincent, 2009](#); [McGill & Brown, 2007](#)). Finally, these models consider one prey–one predator systems that cannot deal with the realistic possibility that when there is a group of prey, the individual who signals to the predator draws a disproportionate amount of the predator's attention, and as a result increases its risk relative to other prey in the group.

To address some of the restrictions of previous pursuit deterrence models and extend their applicability, we model a two prey–one predator signalling game using adaptive dynamics. By modelling two prey we allow the possibility that interactions between prey may indirectly influence the evolution of signalling by affecting the predator's behaviour. Similar to [Getty \(2002\)](#), we allow the predator to respond in an optimal manner to prey behaviour by modelling its missed opportunity costs. This cost comprises the predator's expected loss of energy intake from not spending time searching for and hunting in patches other than the focal patch. If the missed opportunity cost is higher than the expected value of hunting in the focal patch, then a predator will leave the patch in search of a better one. A pursuit-deterrent signal may alert all prey in the patch and the predator may lower its expected value of the patch. If a signal reduces the value of a patch below the missed opportunity cost, a predator will depart the patch, leading to successful pursuit deterrence. A number of factors influence the predator's missed opportunity cost; it should increase, for example, with the density of prey patches in the environment as well as the predator's expected success within those patches. Thus, a pursuit-deterrent signal does not have to reduce the expected value of the focal patch to zero, but just enough to encourage the predator to seek higher returns elsewhere. This is an example of the predator pass-along effect ([Lima, 2002](#)), and including missed opportunity cost in this way allows us to apply the pass-along effect to the problem of pursuit-deterrent signalling. We model the evolution of signalling under this 'patch value reduction' mechanism for two prey as described in the following section.

Our model extends existing pursuit deterrence models by considering convergent stable ESSs ([Eshel, 1983](#); [McGill & Brown, 2007](#)). Convergent stability addresses not just a rare mutant's ability to invade the resident strategy, but also the ability of a small perturbation in the equilibrium resident strategy to evolve towards that equilibrium ([Abrams, Matsuda, & Harada, 1993](#); [McGill & Brown, 2007](#)). We solve for the Nash equilibrium strategies of prey and predator such that if all individuals played their Nash strategies, no one individual could increase their fitness by switching to an alternative strategy. Such an equilibrium may be considered stable if it is also able to resist invasion by mutant strategies ([Maynard Smith & Price, 1973](#); [Vincent & Brown, 2005](#)). We find the convergent stability of equilibria using adaptive dynamics ([Dieckmann & Law, 1996](#); [Metz, Geritz, Meszena, Jacobs, & van Heerwaarden, 1995](#)), a method that tracks the resident strategy

as it evolves in a continuous strategy space in response to the (changing) gradient of the frequency-dependent fitness landscape.

We use our model to predict how the evolution of pursuit-deterrent signalling in group-living prey depends on parameters such as signalling cost, predator detection probability and predator missed opportunity cost on the ESS. We show that, depending on parameter values, the equilibrium may be nonsignalling, a mixed ESS in which the prey signal with a probability and the predator attacks post-signal with a probability, or a pure strategy in which the prey always signal and the predator never attacks post-signal. Finally, we discuss possible applications and extensions.

THE PURSUIT DETERRENCE SIGNALLING GAME

We consider a single predator that travels among multiple patches, each of which contains two prey. Upon entering a patch, the predator may be undetected by either prey, or it may be detected by one or both prey. A prey that detects the predator becomes harder to catch. It may also signal this fact to the predator (perceptual advertisement). Additionally, the other prey in the patch will also note the signal and likewise become harder to catch. We assume this signal is 'unfakeable' in the sense that a prey cannot produce it without having detected a predator ([Broom & Ruxton, 2012](#)). An example of an unfakeable signal is predator inspection. Unfakeable signals eliminate the possibility of dishonest signalling by the prey for this scenario.

A predator that receives no signal may be undetected, or detected by prey that do not signal. Such a predator that receives no signal should always attack because its expected return from attacking nonsignalling prey is always higher than its missed opportunity cost. If the predator receives a signal, it reduces its estimate of the value of the patch, because both prey are alert and harder to catch. If the value of this patch is now less than the expected value of searching for other patches containing possibly unwary prey (i.e. predator's missed opportunity cost), the predator departs the patch in search of better hunting opportunities elsewhere. If patch value is higher than missed opportunity cost, the predator attacks, preferentially pursuing the signaller. If both prey detect the predator, they each signal with their strategy-specific probability, and again, the predator may call off or continue the pursuit. If the predator continues pursuit after both prey signal, then both prey have an equal chance of being attacked. Possible sequences of this interaction between predator and prey are presented in [Fig. 1](#).

We define prey strategy s , as the probability of signalling after detecting a predator, and predator strategy a , as the probability of attacking after receiving a signal. We let p represent the probability that a prey detects the predator (refer [Fig. 1](#)). We let k_0 represent the probability that an undetected predator kills a prey during an attack and k_1 represent the predator's probability of killing a prey that detects it but does not signal. In the latter case, we assume that the prey escapes to a refuge instead of remaining vulnerable in the open, thus reducing its chance of being caught. Because an undetected predator is likely to have a higher chance of killing prey, we assume $k_0 > k_1$. A prey that signals pays a cost Φ , which represents the increase in probability of being targeted for attack from drawing the attention of the predator. Thus, if Φ is zero, the signaller and nonsignaller have an equal chance of being targeted. But if Φ is greater than zero, the signaller is more likely to be targeted in the event of an attack. Note that the value of Φ is limited to values from 0.0 to 0.5 in order to limit overall probability of attack to be less than or equal to 1, and that this cost is paid only if there is an attack. If both prey signal, this cost is divided equally between them. Costs for the predator include time spent within a patch (pursuit time, t_{pursuit}) and time spent between patches searching for prey (travel

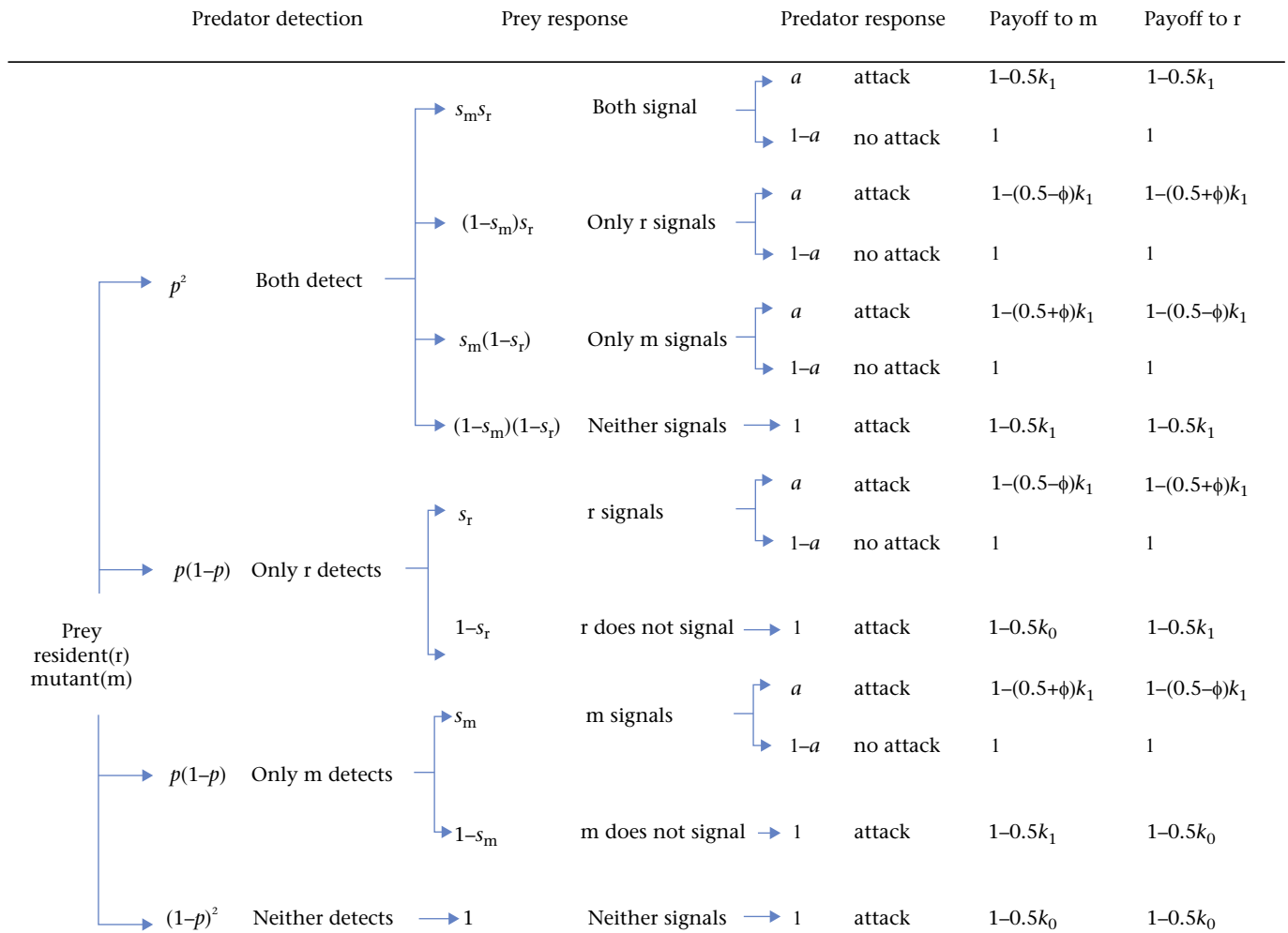


Figure 1. Extended form of the two-prey signalling game. A prey may detect the predator with probability p . If it detects a predator, the prey may choose to signal with probability s (s_r for resident and s_m for mutant). If a signal is given, the signalling prey pays a cost ϕ that is paid only when there is an attack. Upon receiving a signal, the predator attacks with probability a . If there is no signal, we assume that the predator will attack with a probability 1. The highest chance of a successful attack, k_0 , occurs when the prey has not detected the predator. If the predator is detected, its chance of a successful attack drops to k_1 . Parameters apply to both prey, and payoffs from each possible interaction are provided; however, prey fitness refers to the fitness of the mutant with respect to the resident strategy.

time, t_{travel}). The list of mathematical symbols used is given in Table 1.

For the inner game (sensu Vincent & Brown, 2005) between prey, we consider a resident (common) strategy s_r , used by almost all prey in the population, and a rare mutant strategy s_m , used by a small proportion of individuals. We assume that the value of the mutant strategy (i.e. signalling probability) is near to that of the resident, i.e. the mutant strategy represents a small deviation from

the resident. If the gradient of the fitness surface has a nonzero slope, then we assume that the mutant in the upslope direction will invade and replace the resident strategy. An equilibrium occurs where the gradient of the fitness surface is zero. We verify the stability of the equilibrium (i.e. that it is an attractor) by observing the rest point of the trajectories, and we verify the negativity of the real part of the eigenvalues from the linearized dynamics at the equilibrium.

Table 1
Definition of mathematical symbols used in the model

Symbol	Definition
p	Probability of prey detecting predator
s_r, s_m	Probability of resident and mutant prey signalling upon detecting predator
a	Probability of predator attacking after receiving signal
k_0	Probability of undetected predator killing prey; no signal
k_1	Probability of predator killing prey that has detected it
ϕ	Signalling cost of drawing predator's attention (values from 0.0 to 0.5)
t_{travel}	Average time spent by predator travelling between patches
t_{pursuit}	Time spent by predator in focal patch if the predator attacks
F	Prey fitness function
G	Predator fitness function
c_1, c_2	Rate constants of the adaptive dynamic process for prey and predator

We define prey fitness F as the overall probability of surviving an encounter with a predator. This probability is the sum of the weighted survival probabilities from each possible interaction. Given below is the mutant fitness as played against the resident prey strategy.

$F =$	$p^2 [(1-s_m)(1-s_r)(1-(0.5)k_1) + s_r(1-s_m)[1-a(0.5-\Phi)k_1] + s_m(1-s_r)[1-a(0.5+\Phi)k_1] + s_m s_r [1-(0.5)ak_1]] + p(1-p)[s_r(1-a(0.5-\Phi)k_1) + (1-s_r)[1-(0.5)k_0]] + (1-p)p[s_m(1-a(0.5+\Phi)k_1) + (1-s_m)[1-(0.5)k_1]] + (1-p)^2[1-(0.5)k_0]$	Both prey see predator, with neither, one or both signalling Only resident sees predator Only mutant sees predator Neither prey see predator
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We do not include terms for competition or relatedness between prey. Furthermore, we assume that both prey are identical in all aspects except signalling probability and that they affect each other's fitness through the predator's behaviour.

The fitness of the predator G , is its expected rate of prey capture, which is the probability that it kills a prey in a patch divided by the expected time required to travel to and exploit the patch.

The probability of killing a prey in a patch is.

$\text{Pr(kill)} =$	$p^2[(1-s)^2k_1 + 2s(1-s)ak_1 + s^2ak_1] + 2p(1-p)[sak_1 + (1-s)(0.5)(k_0 + k_1)] + (1-p)^2k_0$	Both prey see predator; neither, one or both signal Only one prey sees predator Neither prey see predator
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The average time to exploit a patch is the sum of the travel time between patches and the pursuit time spent in a patch averaged over each of the possible interactions listed above. Let t_{travel} be the average travel time between patches and t_{pursuit} be the average pursuit time of a prey if the predator attacks. The average time to exploit a patch then becomes,

$$E(\text{time}) = t_{\text{travel}} + t_{\text{pursuit}} \left[p^2 [(1-s)^2 + sa(2-s)] + 2p(1-p)[sa + (1-s)] + (1-p)^2 \right]$$

Now, predator fitness G can be written as the expected rate of prey capture given by,

$$G = \frac{\text{Pr(kill)}}{E(\text{time})}$$

Behavioural Adaptive Dynamics

We find the convergent stable equilibrium of this signalling game using behavioural adaptive dynamics (Mitchell & Angilletta, 2009; Nowak & Sigmund, 2004). To define our adaptive dynamics equations, we denote the resident prey and predator strategies by s_r and a_r respectively, and the corresponding mutant strategies by s_m and a_m .

We define change in the resident prey strategy s_r as the partial derivative of prey fitness with respect to the probability of signalling, evaluated at the resident strategies of the prey and predator, multiplied by a rate constant, c_1 .

$$\frac{ds_r}{dt} = c_1 \frac{\partial F}{\partial s} \bigg|_{a=a_r, s=s_r} \quad (1a)$$

Similarly, change in the predator's resident strategy, multiplied by rate constant c_2 is,

$$\frac{da_r}{dt} = c_2 \frac{\partial G}{\partial a} \bigg|_{a=a_r, s=s_r} \quad (1b)$$

Equations (1a) and (1b) describe a dynamic system of the ordinary differential equations. For each case, we examined the

dynamic system converged on an attractor, which we consider an equilibrium of the system. We numerically solved for the equilibria and associated eigenvalues, as well as representative trajectories of the adaptive dynamics, using the numpy and scipy packages on

Python (Python Software Foundation, <https://www.python.org/>). The program is available through a repository (https://bitbucket.org/divya_ramesh/patchvalue/src/default/).

RESULTS

We focus on the effects of four system parameters on the predator–prey ESS – predator detection, signalling cost, prob-

ability of killing and travel time. Depending on parameter values we find nonsignalling ESSs, mixed ESSs and pure signalling ESSs. We illustrate how the equilibrium in the space of s and a varies with each parameter. Note that because the dynamics are constrained within the unit square in our model, the effective equilibrium of the trajectory will lie within the square.

Predator Detection

In our model, prey signal to the predator only after the predator is detected. This means that the signal provides information about the prey's awareness of the predator that the latter might then use to update its attack probability. The occurrence of the signal, however, depends on the probability p that prey detect a predator. Our analysis shows that the predator–prey signalling ESS changes with p . Specifically, at values of p between 0 and 0.2 (Fig. 2), a pure signalling equilibrium occurs where prey always signal and the predator never attacks after a signal (Fig. 3a). An intermediate value of p between 0.2 and 0.4 (Fig. 2) produces a mixed ESS at which prey signal with a probability and the predator attacks post-signal with a probability (Fig. 3b). Values of p greater than 0.4 result in a nonsignalling equilibrium where prey never signal and thus the predator always attacks post-signal (Fig. 3c). Overall, as p increases, the equilibrium shifts with a decrease in s and an increase in a .

Signalling Cost

Signalling cost in our model is the additional risk a signaller pays by becoming the predator's focal target. Higher cost implies greater risk or an increased chance that the signaller becomes the predator's target. Signalling cost may therefore affect the probability of signalling (prey behaviour), and consequently predator behaviour. We find mixed ESSs at all values of signalling cost, where prey signal with a probability and the predator attacks post-signal with a probability (Fig. 4). Although the equilibrium value of a decreases as cost increases, the equilibrium value of s does not vary with signalling cost (Fig. 4).

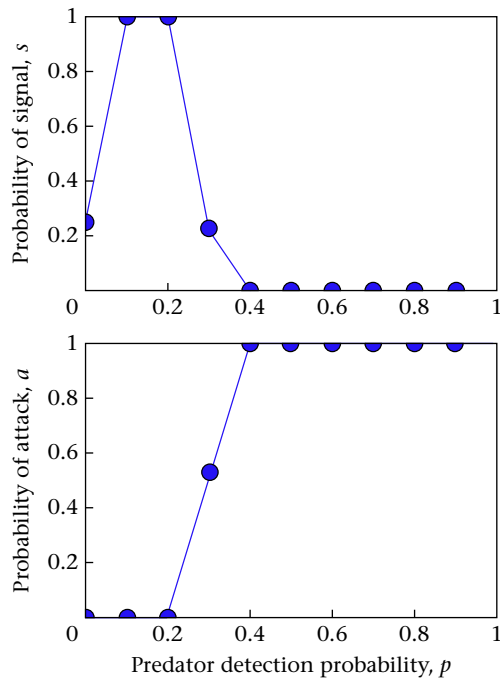


Figure 2. Change in prey behaviour (probability of signalling s , top) and predator behaviour (probability of post-signal attacking a , bottom), with increase in predator detection p . Probability of killing unaware prey $k_0 = 0.4$, probability of killing non-signalling aware prey $k_1 = 0.1$, signalling cost $\Phi = 0.4$, predator travel time $t_{\text{travel}} = 2.0$, pursuit time $t_{\text{pursuit}} = 1.0$.

Probability of Killing

In our model, k_0 is the chance that the predator kills unaware prey, and while we assume that this is higher than the chance of killing prey that have detected the predator (k_1), the magnitude of difference between k_0 and k_1 is important. When k_0 is marginally higher than k_1 , i.e. if the difference between k_0 and k_1 is less than 0.2, the model predicts a nonsignalling equilibrium (Fig. 5). When k_0 is moderately larger than k_1 , i.e. if the difference between k_0 and k_1 is between 0.2 and 0.4, we find a mixed ESS where prey signal with a probability and the predator attacks post-signal with a probability (Fig. 5). If the difference between k_0 and k_1 is greater than 0.4, we find a pure signalling equilibrium where the prey always signal and the predator never attacks post-signal (Fig. 5). In general, as the difference between k_0 and k_1 increases, the equilibrium shifts as s increases and a decreases.

Travel Time

We define travel time as the time spent by the predator moving between patches of prey. Longer travel times reduce the predator's missed opportunity cost, and so may increase the probability of attack after a signal is given. Consistent with this expectation, we find a signalling equilibrium for short travel times less than 1.5, where prey always signal and the predator never attacks post-signal (Fig. 6). Intermediate values of travel time between 1.5 and 2.5 result in a mixed ESS (Fig. 6), while longer travel times result in a nonsignalling equilibrium (Fig. 6). Overall, as travel time increases, we find a shift in the equilibrium with decreasing s and increasing a .

Dynamics and Basins of Attraction

We find pure signalling, mixed signalling and nonsignalling equilibria for different initial values of signalling probability s and attack probability a under a given set of parameter values. That is to say, the same set of parameter values results in two attracting equilibria, each with their own basin of attraction. An example is shown in Fig. 7 with two possible attractors; a nonsignalling equilibrium and a mixed ESS. One range of initial s and a values converges on the nonsignalling equilibrium while other initial s and a values converge on the mixed ESS.

DISCUSSION

Our model of a signalling game between predator and prey shows that stable signalling can evolve under the novel mechanism of 'patch value reduction'. While the signal in our model is directed to the predator, it has the potential to also alert other prey in the patch and this may drastically decrease the predator's chance of successfully catching any prey, signallers and nonsignallers, in the given patch. If the signal decreases the expected value of the patch such that it is lower than the predator's missed opportunity costs, then the predator will leave the focal patch, resulting in successful pursuit deterrence. While previous models have considered a reduction in value of just the signaller (Getty, 2002), we consider the value of the entire patch, i.e. both prey in the patch where a signal has occurred drops considerably as a result of the signal. A signalling prey clearly benefits if the signal deters attack. But if the signal does not deter attack, then the signaller pays a cost of increasing its chance of becoming the predator's target. We discuss our results of how the ESS varies with parameters by considering the influence of those parameters on the benefits and costs to the

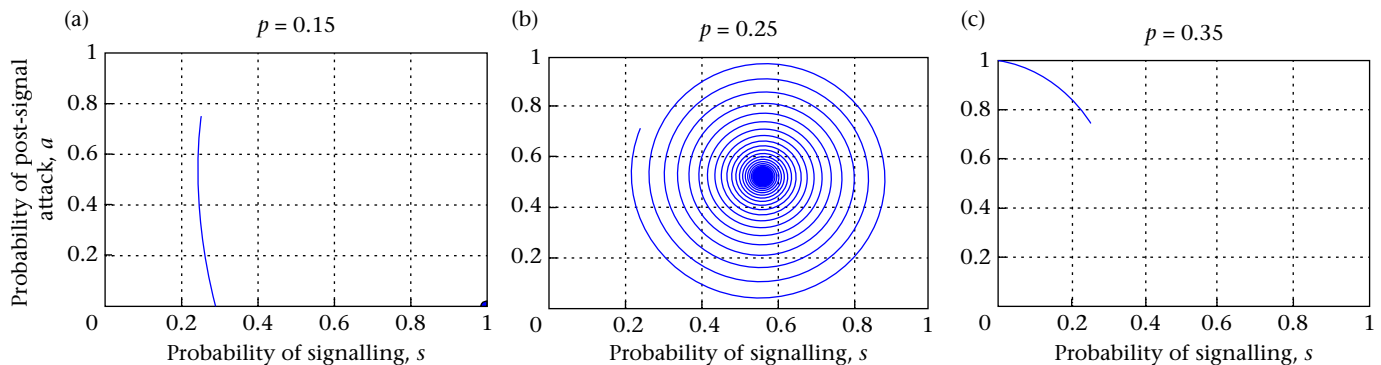


Figure 3. Low predator detection probability p results in pure signalling equilibrium with $s = 1$ and $a = 0$ (a). As p increases, we find mixed ESSs (b) where prey signal with a probability of 0.57 and predators attack with a probability of 0.517. For higher values of p we find a nonsignalling equilibrium where $s = 0$ and $a = 1$ (c). Initial values of s and a are 0.25 and 0.75, respectively, probability of killing unaware prey $k_0 = 0.4$, probability of killing non-signalling aware prey $k_1 = 0.1$, signalling cost $\Phi = 0.4$, predator travel time $t_{\text{travel}} = 2.0$, pursuit time $t_{\text{pursuit}} = 1.0$.

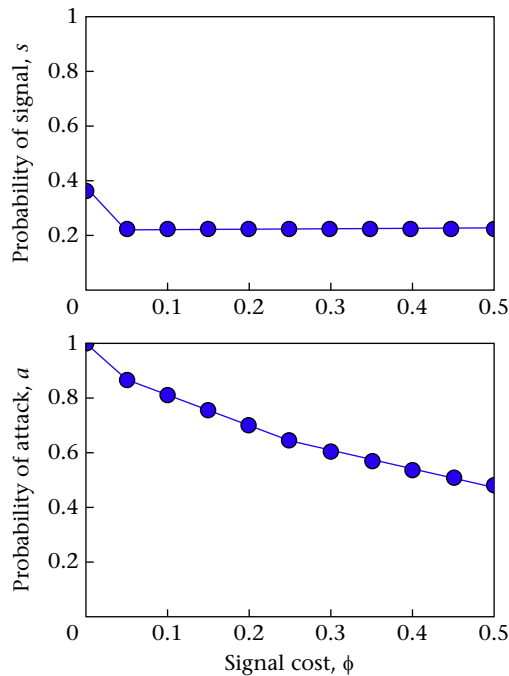


Figure 4. Change in prey behaviour (probability of signalling s , top) and predator behaviour (probability of post-signal attacking a , bottom), with increase in signalling cost Φ . Note that when $\Phi = 0$ and $a = 1$, there is no selection on s . Probability of killing unaware prey $k_0 = 0.4$, probability of killing nonsignalling aware prey $k_1 = 0.1$, predator detection probability = 0.4, predator travel time $t_{\text{travel}} = 2.0$, pursuit time $t_{\text{pursuit}} = 1.0$.

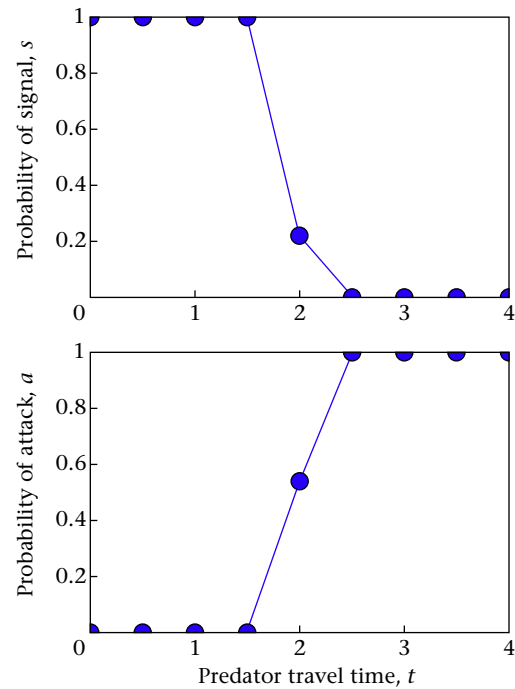


Figure 6. Change in prey behaviour (probability of signalling s , top) and predator behaviour (probability of post-signal attacking a , bottom), with increase in predator travel time t_{travel} . Probability of killing unaware prey $k_0 = 0.4$, probability of killing nonsignalling aware prey $k_1 = 0.1$, predator detection probability = 0.25, signalling cost $\Phi = 0.4$, predator pursuit time $t_{\text{pursuit}} = 1.0$.

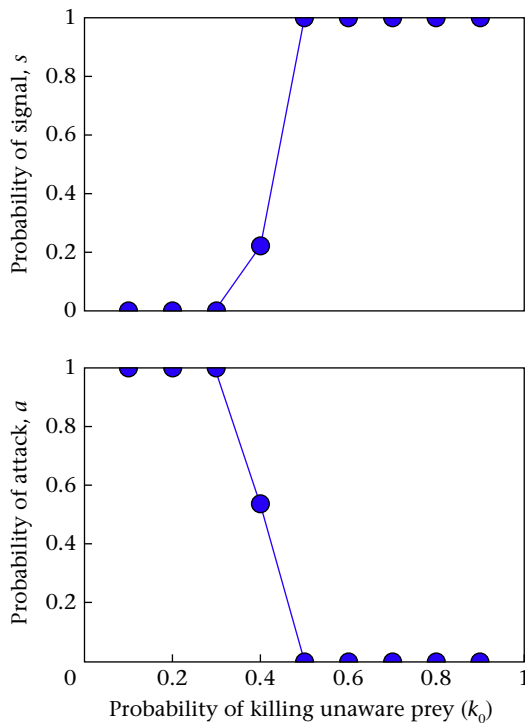


Figure 5. Change in prey behaviour (probability of signalling s , top) and predator behaviour (probability of post-signal attacking a , bottom), with increasing probability of killing unaware prey k_0 . Probability of killing aware prey $k_1 = 0.1$, predator detection probability = 0.25, signalling cost $\Phi = 0.4$, predator travel time $t_{\text{travel}} = 2.0$, pursuit time $t_{\text{pursuit}} = 1.0$.

prey and predator of their respective decisions. We find either pure or mixed ESSs depending on the values of signalling cost, the probability of predator detection, the probability the predator kills a prey and the predator's travel time cost.

Signalling cost in our model is the additional risk of being targeted by the focal detected predator after producing a signal. We find that, at a mixed ESS, an increase in signalling cost decreases the predator's probability of attacking post-signal (Fig. 4) but has no effect on the probability that prey signal. At first glance it may seem odd that signalling cost could influence the behaviour of the predator but not the prey; however, we can understand this intriguing result by considering the necessary conditions for a

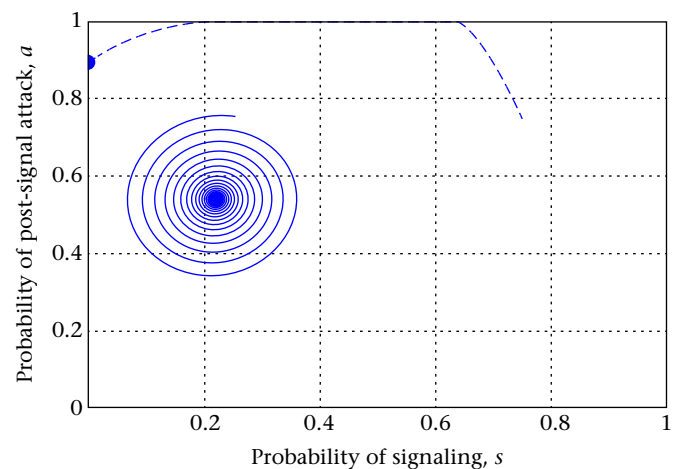


Figure 7. Two attractors (filled circle), a mixed ESS (dashed line) and a nonsignalling equilibrium (solid line) showing two basins of attraction based on different initial values of s and a .

mixed ESS. At the mixed ESS, two conditions must be true. First, the payoff to the prey from signalling and not signalling must be equal. Note that signalling cost is only included when there is a signal. So in this case, the payoffs for signalling with increasing costs are adjusted by a decrease in a in order to equal the payoff when there is no signal. This can be ascertained when we look at the second condition, the mixed ESS for the predator. At this equilibrium, the predator's expected value from the focal patch must equal its missed opportunity costs. The expected value from the patch is reduced after a signal. At this stage, an increase in a would decrease the predator's missed opportunity cost and enable the predator to stay in the patch. Given that the expected value from the patch is low, a decrease in a would increase the missed opportunity cost and encourage the predator to leave the focal patch. So, as prey suffer higher signalling costs, the predator reduces its attack probability a , while the prey maintain a constant signalling probability s .

Although signalling cost does not change prey behaviour s , other parameters do. For example, when values of predator detection probability p are greater than 0.4, signalling does not evolve (Fig. 2). Note that for the predator, the value of the signal is information, but when p is high, the predator already expects that it has likely been detected even in the absence of a signal. Thus, at high p , a signalling prey is less likely to change the predator's behaviour by deterring an attack while still paying the signalling cost of increased chance of being the target of the attack. Therefore, in this case, prey may choose not to signal after detecting the predator, consequently leading to higher attack probability a and the evolution of a non-signalling equilibrium. Meanwhile, when prey have a low chance of detecting the predator, prey are more likely to signal when they do detect the predator, and we find a concurrent reduction in predator attack probability (values of p less than 0.2, Fig. 2). This results in the evolution of a signalling equilibrium. Overall, these results indicate that there is benefit to detecting the predator before an attack, and that subsequent signalling depends on the probability of detecting the predator.

In the preceding sections we assumed that signalling prey incurred a cost Φ in that, if the predator did attack post-signal, it would bias its attack to the signaller. But in some cases the predator may interpret certain signals, such as stotting (Fitzgibbon & Fanshawe, 1988) as an indicator of the prey's ability to escape; in these cases the predator may bias its attack to the nonsignaller. We examined this possibility by changing the sign of Φ , thus converting the cost of signalling to a benefit. Assigning a benefit to signalling produces two notable changes in the results. First, we found no mixed ESS; this is due to the fact all equilibria we examined had at least one eigenvalue with positive real part, and the equilibria tended to shift out of the unit square in the strategy space. Second, assigning a benefit to signalling produced a new type of pure ESS not observed when signallers incurred a cost. At this pure ESS the prey always signals, and the predator always attacks, biasing its attack to the nonsignaller. To directly compare cases with positive and negative Φ we consider the parameters used in Fig. 3, but with a change in sign of the parameter Φ . When the probability of detecting the predator is small ($p = 0.15$), the ESS is the same whether the signal represents a cost or a benefit; in both cases the prey that detects the predator signals and the predator does not attack. However, the ESS differs between the two cases at both intermediate and high probability of predator detection ($p = 0.25$, $p = 0.35$, respectively). When signalling incurs a cost, there is either a mixed ESS or a pure ESS where prey never signal and the predator always attacks. But when signalling carries a benefit, the ESS is a pure strategy where the prey always signal and the predator always attacks. At high predator detection regardless of the sign of Φ , the predator always attacks; the only difference for the prey between

these cases with positive and negative Φ is who the predator preferentially attacks, the nonsignaller or the signaller.

Previous models of predator deterrence have considered the role of missed opportunity cost, however, they have not examined the influence of other components of the predator's fitness on the ESS. In addition to missed opportunity cost, the current model includes the predator's probability of killing prey; k_0 for prey that have not detected the predator, and k_1 for prey that detect the predator. The predator's probability of killing prey is a key component of the predation risk perceived by prey (Lima & Dill, 1990). While predator detection probability p provides information to the prey about presence of the predator, probability of being killed adds value to that information by providing some measure of threat associated with the presence of the predator. We assume that the predator has a higher probability of killing prey that have not detected it (k_0) than those that have (k_1). The model predicts a nonsignalling equilibrium for low values of k_0 (Fig. 5). If k_0 is only marginally higher than k_1 , i.e. if the chance of killing unaware prey is close to the chance of killing prey that are aware of the predator, then the information that a signal provides to the predator has little value and is unlikely to result in the predator abandoning an attack. In this case, there may not be a net benefit in detecting the predator and subsequent signalling. If the difference between k_0 and k_1 is large, then the signal carries useful information to the predator and the prey may be more likely to signal. A large value of k_0 means that unaware prey have a high probability of being killed and thus, there is a clear disadvantage in not detecting the predator. Meanwhile, for prey that detect the predator but do not signal, the probability of being killed is the lower k_1 . If prey detect the predator and choose to signal, a signalling cost increases its probability of being killed but this is still lower than k_0 . In this case, prey that detect the predator may be more likely to signal and inform the predator that it has been detected. The signal may lead to successful pursuit deterrence if the predator's missed opportunity cost is higher than the expected value of the patch.

The time spent by the predator travelling between patches in search of prey can be thought of as directly proportional to distance between patches. An increase in travel time decreases the predator's missed opportunity cost and thus increases the likelihood that the predator attacks, even if it has received a signal from the prey. And, because the predator will tend to attack the signaller, an increase in the predator's travel time decreases the chance of a prey signalling. The current model predicts a signalling equilibrium for short travel times (Fig. 6). If patches are close together and travel time between patches is short, a signal may reduce the predator's expected value from a patch relative to its missed opportunity cost. In this case, the predator benefits from leaving the focal patch in search of better hunting opportunities in other patches, and pursuit deterrence is successful. If distance between patches is large, i.e. travel time is long, then the predator's missed opportunity cost may be lower than the expected value of the patch even after a signal, such that the predator continues to attack post-signal, leading to a nonsignalling equilibrium (Fig. 6). A parallel can be drawn to the marginal value theorem (Charnov, 1974), where increasing distance between patches decreases missed opportunity cost, thereby encouraging the forager to accept a lower marginal rate of return from a patch.

Nature of Equilibria

A mixed ESS was not described in the predator deterrence model of Bergstrom and Lachmann (2001), and while the possibility was mentioned by Getty (2002), he did not specify the conditions for stability. And indeed, asymmetric games, such as those between a prey and predator, can make the stability of mixed equilibria problematic (Selten, 1980); but some predator–prey

interactions may result in a mixed ESS (e.g. Mitchell & Angilletta, 2009). For example, an equilibrium will not be dynamically stable if the equations for the dynamics of each state variable (i.e. probability of a behaviour) do not contain the state variable itself – in this case the isoclines of each variable in the dynamic system are parallel to the axis of the variable; this means that a perturbation from the equilibrium will result in a neutral limit cycle, not a trajectory that decays to an attracting equilibrium. In our pursuit deterrence game, the stability of the mixed ESS appears to flow from the fact that there is more than one prey individual involved in each interaction with the predator. This means the equation for the dynamic of the probability of signalling does include the state variable (the resident strategy); the behaviour of the resident strategy influences the fitness of any mutant strategy because the individual using the mutant strategy does so in the presence of an individual using the resident strategy. Thus the isocline for the probability of signalling is not parallel to the axis of signalling probability but rather has a negative slope, and it is the negativity of the slope that results in an attracting equilibrium. For a broad set of signalling games involving the possibility of deceptive signals, the existence of hybrid equilibria has been noted (Huttegger & Zollman, 2010; Zollman et al., 2013). In a hybrid equilibrium, a signaller of low quality may ‘lie’ some proportion of the time. For example, a low-quality prey that would be unable to escape attack may signal with some probability less than one that it is highly capable of escaping attack. This type of hybrid equilibrium has similarities to our mixed ESS, but as we noted above, we are focusing on unfakeable signals where such deception is difficult or impossible.

We find convergent stable equilibria forming basins of attraction with different initial s and a values for a fixed set of parameter values (Fig. 7). This indicates that the type of equilibrium the system evolves towards, whether signalling evolves or not, depends on the initial predator and prey behaviours. When initial values of signalling probability s are closer to zero, a nonsignalling equilibrium occurs and signalling does not evolve (Fig. 7). This result indicates that a signal must already exist in the population. How does such a signal arise in the first place? We propose that these signals could appear initially through the mechanisms of kinship (Axelrod & Hamilton, 1981; Hamilton, 1963) or reciprocal altruism (Trivers, 1971). Our model then examines if it is possible for a different mechanism to invade at this stage and become stable, and we find that pursuit-deterrent signalling can indeed evolve through this process. Studies have shown that signals may serve multiple functions, perhaps evolving first under a specific context that is later co-opted to others. For example, the turquoise-browed motmot, *Eumomota superciliosa*, performs a tail-wag display as a pursuit-deterrent signal but also during the breeding season near its nests in the absence of predators (Murphy, 2007). The latter might represent an original function of the signal that is currently beneficial in a pursuit-deterrent context. We consider these alternative mechanisms to support the initial viability of the signal, whereupon we show that the signal can assume a pursuit deterrence function, maintained through the ‘patch value reduction’ mechanism.

Potential Applications of Model Predictions

Empirical evidence for pursuit deterrence is a mixed bag of potential signals and uncertainty regarding predator response (Ruxton, Sherratt, & Speed, 2004). Because predators are difficult to observe in nature, there is little opportunity to see whether they are in fact deterred by a signal. Theoretical models can help make testable predictions to aid in the understanding of pursuit deterrence. The current model may apply to a number of natural systems. Several species produce signals that are used by other individuals of the same or different species to gather information about risk in the

environment. For instance, mobbing behaviour is known to occur in single-species bird flocks such as babblers (Ridley, Raihani, & Bell, 2010) and in mixed-species flocks such as chickadees–titmice–nuthatches (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Nolen & Lucas, 2009). This behaviour typically involves a few individuals calling loudly after detecting a predator followed by other individuals moving into the area and continuing to call, in an apparent attempt to encourage the predator to leave (Bradbury & Vehrencamp, 1998; Goodale et al., 2010). Temporary groups are formed in this way, where the signal is directed to the predator and all individuals are likely to signal and share the signalling cost. Mobbing behaviour by unrelated individuals implies kin selection would not be applicable; however, our patch value reduction mechanism and reciprocal altruism may work here.

Predator inspection is another behaviour our model could explain. Godin and Davis (1995) found that guppy individuals that inspected a cichlid predator were less likely to be attacked than noninspecting guppies. This suggests that signalling (inspection, in this case) has a cost of approaching the predator and a benefit of reducing the likelihood of an attack. The patch value reduction mechanism may be relevant here since these experiments used unrelated individuals and also suggest that cooperation may not be necessary for signalling to be evolutionarily stable (Godin & Davis, 1995). Our model may also help understand sentinel behaviour as described in Florida scrub-jays, *Aphelocoma coerulescens*, (McGowan & Woolfenden, 1989), suricates, *Suricata suricatta* (Manser, 1999), and other species, although this behaviour is more likely to occur in stable, family groups (Lima & Dill, 1990). Zahavi (2008) suggested that sentinel behaviour in babblers may be a result of altruism interpreted through the handicap principle rather than kin selection or reciprocal altruism, indicating that other pathways to signal evolution may exist. Despite the role of kin selection in maintaining this behaviour in related groups, our model adds another possible mechanism for the evolution of signalling in such systems. It is important to note that each example above likely possesses features that make it uniquely complex and we do not incorporate all of these features in our model in an attempt to broaden its general applicability.

The predictions from this model may be tested with experiments that manipulate certain components of predation risk. For instance, in the experimental set-up similar to that used by Godin and Davis (1995), one could add chemical cues of the predatory cichlid with information about its diet to the tank with prey guppies. Guppies in water with higher concentrations of predator cues would experience a greater level of predation risk. According to the model predictions, one should see increased rates of predator inspection by guppies in water with stronger cues, where inspection is a pursuit-deterrent behaviour. Distance between prey patches can be controlled in simple experimental designs to test these predictions. For instance, in the guppy–cichlid system mentioned previously, one could isolate groups of guppies in separate sections (‘patches’) within a larger tank, such that guppies would be allowed to move within a patch but not between patches. The patches could be created at different distances from each other, while allowing a cichlid predator to travel in the larger space between patches. If the cichlid travels between patches that are farther apart, then the model predicts that the cichlid is more likely to stay despite predator inspection by guppies. If patches are closer together, then we would expect the cichlid to leave a patch after predator inspection and move to other patches.

Model Extensions

This signalling game is one of several possible analyses to understand the evolution of pursuit-deterrent signalling. Although our model is the first to consider multiple prey, it is limited in the

extent of the interaction between those prey and how this might impact signal evolution. For instance, in the event that both prey detect the predator and choose to signal, we assume that they signal at the exact same time. Alternatively, signalling probability can be made dependent on whether a signal has already occurred. If a signal occurs and results in the additional risk of being targeted, as in our model, one would expect that other prey would be less likely to produce additional signals and may instead choose to be alert or perhaps run to refuge. It is possible then that cheaters arise in such a game, with prey other than the signaller consistently choosing not to produce additional signals and share the cost. This situation may also lead to a type of 'waiting game' between prey in which the prey that signals pays a cost, but if neither prey signals, then both prey pay an average cost. Dishonest signalling may also arise if prey 'always' signal, i.e. prey signal without detecting the predator. For the model presented here we focused on signals that are not 'fakeable' in the sense that the prey cannot produce the signal unless it has detected a predator (e.g. predator inspection). But some types of signals can be produced even if a predator has not been detected. Indeed, modelling signal honesty has been integral to previous work and will make a valuable extension of the current model. Additionally, in the absence of a signal, we assume the predator always attacks. This is a reasonable assumption for our model because the expected benefit to the predator of attacking in the absence of a signal is always greater than the missed opportunity cost. However, there may be circumstances where the predator may stay undetected (no signal) and still choose not to attack. This may occur if the predator can determine that prey in some patches would be inherently easier to catch, perhaps due to proximity or lack of cover. Such a possibility could be introduced into the model in two ways: (1) let attack probability be less than 1 if there is no signal or (2) let k_0 be variable and drawn from a distribution instead of a constant value as in the current model. These are but a few extensions that can enhance our understanding of pursuit-deterrent signalling. Our model is designed to be simple and yet include key components of a basic signalling interaction between predator and prey. Despite its limitations, the model generates novel predictions about pursuit-deterrent signalling. Further such work can lead to a better understanding of current theory on signalling behaviour.

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