Soft song: help thine enemy!

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Abstract

Background: Soft song is a low amplitude call observed in many bird species which reliably predicts the probability of imminent attack. The reliability of soft song is a topic of debate in the current literature as it is not clear that how can such a low-cost signal be a reliable signal of intent.

Results: Here I show that the function of soft song is to help the estimation of distance between opponents. However, such help only benefits those individuals who are willing to attack. As a result, soft song is an honest cue of proximity and in turn it is an honest cue of aggressive intent.

Conclusions: Soft song is embedded in the species-specific threat display. It is not possible to understand the function and context of soft song without understanding how threat displays work.

Keywords: soft song, proximity, threat displays, ranging signals, aggressive communication

1. Introduction

Soft songs are low-amplitude calls observed in a number of species, mostly in aggressive context [1]. Empirical studies shown that out of a number of song types associated with aggressive context, i.e. song type switching, song matching, soft-song [2] only soft song predicts the probability of attack. Soft song is a reliable predictor of attack in many species including song sparrows (*Melospiza melodia*) [3-5], in swamp sparrows (*Melospiza georgiana*) [6], in brownish-flanked bush warbler (*Cettia fortipes*) [7] and in black-throated blue warblers (*Dendroica caerulescens*) [8]. Soft call, a low amplitude call, which appears to be the equivalent of soft song is a reliable signal of aggression in corncrakes (*Crex crex*) [9, 10].

Despite being in the centre of attention the function of soft song is not clear. There is a long list of ideas proposed in the literature. The main ones are as follows: (i) the vulnerability handicap hypothesis [11, 12], (ii) the receiver retaliation cost hypothesis [4, 5, 13], (iii) the competing cost hypothesis [6, 14], (iv) the eavesdropping reduction hypothesis [1], and (v) the readiness hypothesis [15].

Two questions dominate the discussion on the function of soft song: (i) why is it that soft song (i.e. a low amplitude song) is a good predictor of aggressive intent and not song type matching or song switching? [2, 4] (ii) How can an apparently low production cost signal be a reliable signal of intent -as opposed to the prediction of the handicap principle [5, 15, 16]? As Anderson and her colleagues [16] write: „It is not clear what if any cost acts to maintain the reliability of soft song as a signal of aggressive intent in song sparrows” (p. 1273). Akcay at al. [17] ask the same question: “So how can a signal that is apparently not costly to produce be a reliable aggressive signal?” (p. 380)

In recent years “receiver retaliation” gained ground as an explanation for the second question. According to this idea the honesty of such low-cost signal is maintained by the response of receivers (i.e. receiver retaliation cost) [4, 5, 13]. This idea is not novel however, as it was modelled as early as 1985 by Enquist [18]. In fact, Enquist model [18] shows that there is no need for “retaliation”; simple frequency dependent interactions can maintain the honesty of cost-free signals in the context of aggressive communication under some conditions. One crucial condition is that potential cheaters should not be able to flee the conflict even if they want to do so. ‘Proximity risk’ was proposed as a potential proximate mechanism behind this condition [19]. The idea of the proximity risk model is that potential cheaters cannot get away with bluffing when they are close enough to the opponent and this is the distance within which threat displays are expected to be honest [19].

Számadó’s [19] model assumes that contestants are able to judge the distance perfectly. However, this is rarely the case in nature: errors of estimation are expected to happen. Such errors in turn might decrease the fitness of the individual if it picks the wrong strategy as a function of the distance. This applies to the opponent as well, in fact errors of the opponent might decrease the fitness of the ego. Here I propose that it could be the interest of the ego to help the opponent to estimate the distance correctly; in order to avoid costly mistakes of the opponent. I call such signals as ‘ranging signals’ since the function of these signals is to help with the estimation of range between opponents. Here I propose that soft-song is such a ranging signal. I investigate why and under what conditions would such help benefit the signaller and thus under what conditions are ranging signals evolutionarily stable.

2. The model

Enquist's [18] model is a game of aggressive communication where two individual competes for an indivisible resource. The game has three stages: (i) at the first stage Nature picks the state of the contestants, which can be weak (W) or strong (S); (ii) at the second stage the contestants can chose between two cost-free signals A or B; finally (iii) at stage three the contestants can either flee (F), attack (A) or wait for the opponent to flee and attack only if the opponent stays to fight (cond.A). Figure 1 depicts the structure of the game (after Számadó, 2017). Let V denote the value of the resource. The cost of fighting depends on the strength of the ego and that of the opponent; accordingly, there are four cost parameters: C_{WW}, C_{WS}, C_{SW} and C_{SS}. The following relation is assumed to hold between these parameters: $C_{WS} > C_{WW}$, $C_{SS} > C_{SW}$. On top of the cost of fighting there are other potential costs as well: (i) attacking a fleeing opponent (F_A), (ii) pausing when the opponent attacks (F_p), and finally there is a cost to flee (F_f). Table 1 sums up the pay-offs of the game.

While in Enquist's [18] game an attack was always successful, Számadó [19] investigated a scenario where the chance of a successful attack depends on the distance between the participants. This is especially relevant when one of the participants wants to flee and the other wants to attack. Let x denote the distance between the opponents and $f(x)$ denote the probability of successful attack a function of distance. The function $f(x)$ is assumed to be monotonically decreasing function of x, i.e. the further is the opponent the smaller is the chance to strike it successfully. Számadó [19] assumed that individuals know the distance separating the opponents (x^*). Here I assume that they estimate this distance (x_e) and this estimation has an error $\varphi(0, \sigma)$ normally distributed, where σ denotes the standard deviation.

Enquist [18] defined the honest global strategy denoted S_A as follows (p. 1155):

„ If strong, show A; if the opponent also shows A attack and if the opponent shows B, repeat A and attack only if it does not withdraw immediately. If weak show B and give up if the opponent shows A and attack if the opponent shows B."

Enquist [18] investigated the evolutionary stability of this strategy S against a cheater type in which weak individuals show A instead of B. The corresponding global strategy (S_B) can be written up as follows [20] (p. 222):

„Display always A in the first round, regardless of strength; then in the second round if strong attack unconditionally if opponent shows A or wait until opponent flees if it has shown B; if weak withdraw if opponent signals A or wait until opponent flees if it has shown B."

Here we assume that the strategy of an individual is defined as playing the honest (S_A) with probability 1-$p(x)$ and playing S_B with probability $p(x)$ as a function distance (x).

3. Results

Here, I investigate the evolutionary stability of ranging signals using the proximity risk model proposed by Számadó [19]. There is a region in the proximity risk model where a mixed strategy (S_M) is an evolutionarily stable strategy (ESS). This mixed ESS is supported by cheater and honest pure strategies, where the probability of playing these strategies are p and 1-p respectively. The equilibrium ratio of mixing is given by the following equation [19]:

$$p^* = \frac{q\left(\frac{1}{2}V + C_{WW}\right) - (1-q)f(x)C_{WS}}{2qC_{WW}} \quad (1)$$

Starting from this equation one can calculate the threshold distance between honest signalling and mixed cheating (x_{HSD}) where p^*=0, as well as the threshold between mixed cheating and no signalling (x_{DSD}, see [19]) where p^*=1:

$$x_{HSD} = f^{-1}\left(\frac{q\left(\frac{1}{2}V + C_{WW}\right)}{(1-q)C_{WS}}\right); \qquad (2)$$

$$x_{DSD} = f^{-1}\left(\frac{q\left(\frac{1}{2}V - C_{WW}\right)}{(1-q)C_{WS}}\right). \qquad (3)$$

Figure 2 depicts an example. The blue line shows the threshold below which honesty is the ESS whereas the red line shows the threshold above which there is no honest communication. The mixed strategy S_M is an ESS between these thresholds. Figure 3 shows the equilibrium proportion of cheaters (p^*) in this region.

Let's assume that estimating the distance without any help is prone to errors. Let's further assume a population where individuals give a ranging signal (*Rs*) to help the opponent to estimate distance *x*. At the equilibrium both opponent will use this signal; both of them will estimate the distance correctly, thus they both will play p^*. Can this equilibrium be invaded by a mutant strategy that does not use *Rs*? The use of *Rs* to be ESS the following condition must hold [21]:

$$\mathrm{E}(R_s, R_s) > E(N_s, R_s) \qquad (3)$$

if $\mathrm{E}(R_s, R_s) = \mathrm{E}(N_s, R_s)$ then

$$\mathrm{E}(R_s, N_s) > E(N_s, N_s) \qquad (4)$$

Since opponents of individuals using *Rs* can estimate distance correctly, whereas opponents of individuals not giving *Rs* cannot do so, hence Eq.3 implies:

$$\mathrm{E}(\mathrm{p}^*, \mathrm{p}^*) > E(\mathrm{p}^*, \mathrm{p}). \qquad (5)$$

The fitness of an individual playing p* against individuals playing the honest strategy (S_A) is as follows:

$$E(p*,0) = p*V + (1-p*)(1/2V - Cww). \quad (6)$$

The fitness of an individual playing p* against individuals playing the cheater strategy (SB) is as follows:

$$E(p*,1) = p*(1/2V) + (1-p*)0. \quad (7)$$

Then the equilibrium condition (Eq. 5) can be expressed with these terms as follows:

$$(1-p*)E(p*,0) + p*E(p*,1) > (1-p)E(p*,0) + pE(p*,1). \quad (8)$$

After rearrangement it is:

$$(p-p*)E(p,0) - (p-p*)E(p,1) > 0. \quad (9)$$

There are two obvious cases: either $p>p*$ or $p<p*$. In the first case the following inequality has to hold:

$$E(p*,0) > E(p*,1) \quad (10)$$

In the second case the following inequality has to hold:

$$E(p*,0) < E(p*,1). \quad (11)$$

Let's define ΔE as a fitness difference between playing honest and dishonest opponent, while the ego plays $p*$:

$$\Delta E = E(p*,0) - E(p*,1) \quad (12)$$

Let's further define Δp as follows:

$$\Delta p = p^* - p. \quad (13)$$

Finally, let's define $\Delta E(p^*)$ as a difference in fitness when playing against an opponent playing the equilibrium probability of mixing and an opponent playing an out-of-equilibrium mixing:

$$\Delta E(p^*) = \mathrm{E}(p^*, p^*) - \mathrm{E}(p^*, p). \qquad (14)$$

Figure 4 shows an example for the error of estimating the difference between opponents (x_e). ΔE can be calculated for a given parameter combination; Figure 5.a shows an example. Eq. 9 shows that ΔE takes effect only if $p \neq p^*$.; Fig 5.b shows the change in the frequency of cheaters (Δp) as a result of this error of estimation. Finally, Figure 5.c shows $\Delta E(p^*)$. There are two regions where playing p^* has higher fitness than a mutant (i.e. regions where p^* is an ESS): (i) the first region is at low value of resource and large distance; (ii) whereas the second region is at high value of resource and low distance. Assuming that territorial disputes represent high value of resource and individuals are aware of the fact that they are fighting for a territory, it is clear that the use of ranging displays (*Rs*) is an honest cue of proximity in this region. In other words, individuals receiving a ranging display from the opponent contesting a resource of high value can be certain that the opponent is close enough to strike with a high success rate. Figure 6 and 7 shows examples for Δp and the corresponding $\Delta E(p^*)$ values for different σ.

So far it was assumed that ranging signals are cost-free. However, introducing a small cost (c_R) makes the first region (low value of resource, high distance) disappear. Figure 8 shows an example. Thus, ranging signals are honest cues of proximity regardless of the value of resource under such scenario. Figure 8.a also shows that the use of *Rs* might not be an ESS when *Rs* is costly if the error of estimating the distance is small.

4. Discussion

I have shown that the use of ranging signals is evolutionarily stable when there is an error of estimating the distance between the two opponents. When ranging signals are cost-

free the use of them is an honest cue of aggressive intentions in the (i) low cost, high distance and in the (ii) high cost, low distance regions (Fig. 7). Assuming that animals are aware of the value of resource they are competing for then the use of ranging signal is an honest cue of low distance in case of high value of contested resource. A small production cost of ranging signals eliminates the first region; thus, the use of ranging signal is an honest cue of low distance under this scenario (Fig. 8). The intuitive interpretation of this result is that uncertainty benefits cheaters, only honest individuals are expected to reduce it. Accordingly, if I see my opponent *to help me* to reduce the uncertainty regarding the estimation of distance between the two of us then it is honest cue of my opponent's (aggressive) intentions.

How can we explain the opening questions? (i) Why is it that soft song is a good predictor of aggressive intent? (ii) How can an apparently low production cost signal be a reliable signal of intent? Soft song is a good predictor of aggressive intent because it is only the interest of honest individuals to reduce uncertainty. A low production cost signal can be a reliable signal of intent because it is an honest cue of proximity, and it is the proximity to the opponent that makes threats credible [19].

Recent empirical results support the conclusion of the model: it was found that the structure of soft song is adopted to short range communication [22]; the authors concluded that "both the acoustic structure and low amplitude of this song mode are adapted to reduce transmission range" [22] (p. 119). They interpreted this result in term of the eavesdropping hypothesis, however this result is equally consistent with the recent proposal.

How does the current proposal relate to the other ideas? Almost all of the previous theories capture some relevant insight about threat displays: the importance of proximity [11], prevention of misdirected threats (i.e. prevention of eavesdropping) [1], preparing the animal to fight (readiness) [15]. These are not mutually exclusive proposals but features of threat displays that follow from the function and design of threat displays [19, 23, 24].

The ‘threat’ vs. ‘dominance’ display distinction was originally proposed by Walther [23]. Walther argues that dominance displays (e.g. broadside displays) advertise ownership, they may not require immediate response from the receivers and they do not imply immediate threat to others. It follows that dominance displays are highly detectable, one-to-many type broadcast signals. On the other hand, threat displays (e.g. medium horn presentation) convey the intention to attack, aimed at a specific receiver and they require immediate response. The functional differences between threat vs. dominance displays imply differences in design. Dominance displays (territorial bird song, scent marking) are designed to reach as many receivers as possible. Prevention of eavesdropping makes no sense in dominance displays. On the other hand, signallers are interested to narrow down threats to the target individual to avoid unnecessary conflict with others. As a consequence, most threat displays have some “pointing” element (pointing or staring), which functions to pinpoint the targeted individual. Threat displays also involve a show of weaponry in ready to fight form, thus they are related to the first steps of species specific fighting technique [23]. All in all, prevention of eavesdropping makes perfect sense in threat displays as well as readiness to fight and proximity to opponents.

While soft song is not a threat display itself *sensu* Walther [23] as it is not related to the fighting technique of the species, yet soft song is embedded into threat displays for logical reasons. It makes only sense for the ego to help the opponent in the estimation of distance if the ego expects the opponent to withdraw (otherwise the ego just should attack). Convincing the opponent to withdraw is the function of threat displays: displaying weaponry, the readiness to attack (by closing in on the opponent) and helping the opponent to correctly estimate the distance should function synergistically. It follows, that it is not possible to understand the context of soft song without understanding how threat displays work.

All in all, the current proposition predicts that soft song is an honest cue of proximity and it is embedded in the threat displays of the species. It is proximity to the opponent that maintains the honesty of this low amplitude, low cost signal [19]. It follows that understanding of the context and function of this signal is not possible without the understanding of the structure and function of threat displays [19, 23].

Ethics approval and Consent to Participate

Not applicable.

Consent for publication

Not applicable.

Availability of Data and Materials

Not applicable.

Competing Interest

The author declares that he has no competing interests.

Founding

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Author contribution

S.S. conceived the idea, analysed the model and wrote the paper.

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Figure Legends

Figure 1. Schematic description of Enquist's game [18] (modified after [25]). Stage zero: Nature picks the state of the contestants; this stage is hidden from other players. Stage one: each contestant picks a signal, A or B. Stage two: each contestant picks a behaviour as a response to the signal: Flee, Conditional Attack or Attack.

Figure 2. Honest, mixed cheating and dishonest regions in spatially explicit game of aggressive communication. Blue line (x_{HSD}): threshold between honest (S_A) and mixed cheating (S_M); red line (x_{DSD}): threshold between mixed cheating (S_M) and dishonest region (only S_B).

Figure 3. Frequency of cheaters (p) as a function of distance (x) and the value of the resource (V).

Figure 4. The probability of successful attack as a function of distance (x) without and with error of estimation (σ).

Figure 5. (a) The difference in fitness when playing against an honest opponent vs. playing against a cheater (ΔE). (b) The change in the probability of cheating (Δp) as a result of the error of estimating the difference as a function of distance (x) and the value of the resource (V). (c) The difference in fitness ($\Delta E(p^*)$) when using a ranging signal (*Rs*) vs. not using (*Ns*) in a population of individuals using *Rs*.

Figure 6. The change in the probability of cheating as a result of the error of estimating the difference as a function of distance (x) and the value of the resource (V) as a function of different errors of estimation: (a) σ=5, (b) σ=15, and (c) σ=25.

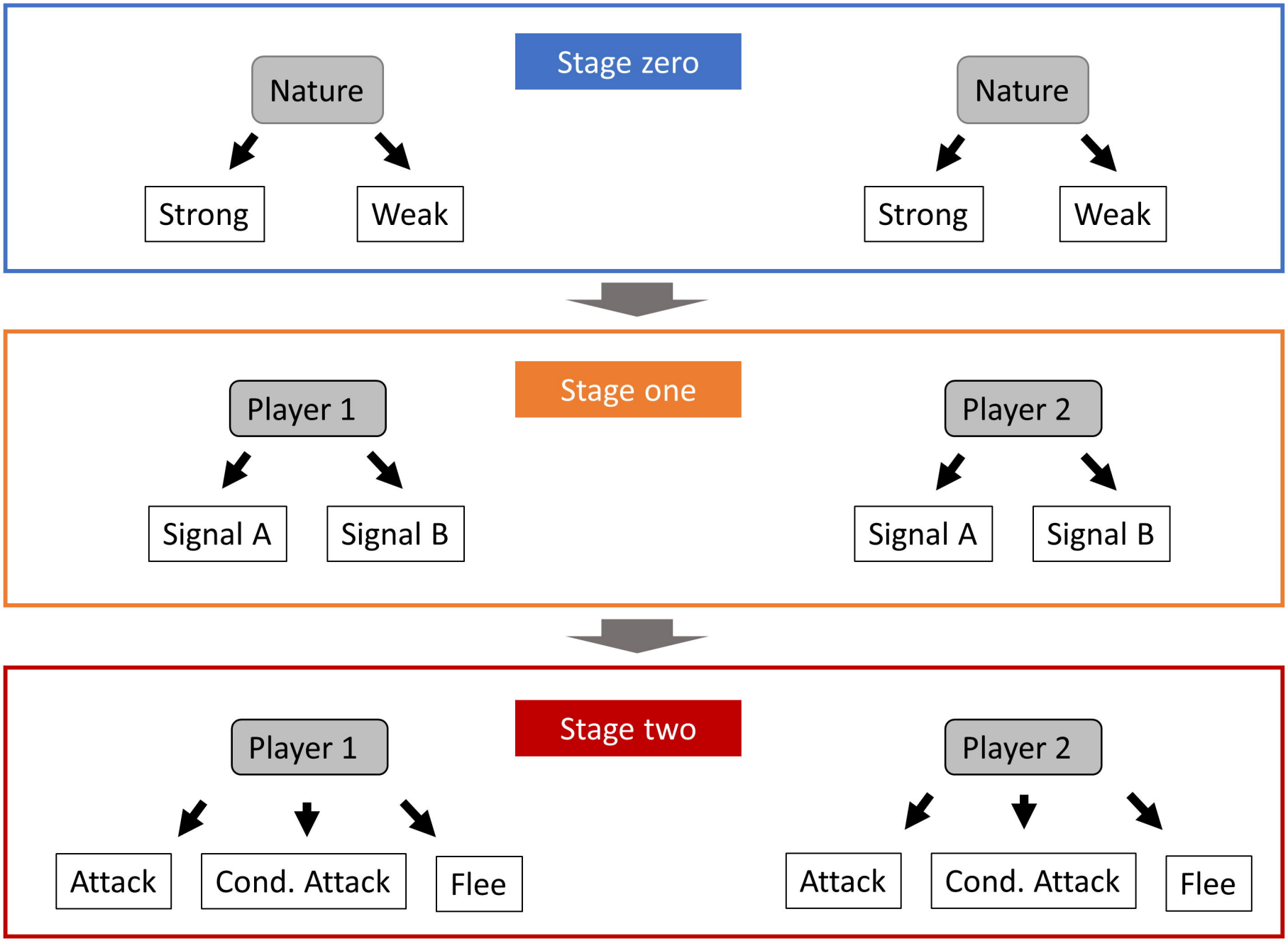
Figure 7. The difference in fitness ($\Delta E(p^*)$) when using a ranging signal (*Rs*) vs. not using (*Ns*) in a population of individuals using *Rs* as a function of different errors of estimation: (a) σ=5, (b) σ=15, and (c) σ=25.

Figure 8. The difference in fitness ($\Delta E(p^*)$) when using a ranging signal (*Rs*) vs. not using (*Ns*) in a population of individuals using a costly (c_R) *Rs* as a function of different errors of estimation: (a) σ=5, (b) σ=15, and (c) σ=25.

Table 1. Payoffs matrix (modified after [20]).

Ego Strength		Opponent Strength: Strong – Attack	Strong – Cond. attack	Strong – Flee	Weak – Attack	Weak – Cond. attack	Weak – Flee
Strong	Attack	$0.5V\text{-}C_{SS}$	$0.5V\text{-}C_{SS}$	$V\text{-}F_A$	$V\text{-}C_{SW}$	$V\text{-}C_{SW}$	$V\text{-}F_A$
	Cond. attack	$0.5V\text{-}C_{SS}\text{-}F_P$	$0.5V\text{-}C_{SS}$	V	$V\text{-}C_{SW}\text{-}F_P$	$V\text{-}C_{SW}$	V
	Flee	$-C_{SS}$	0	$0.5V$	$-C_{SW}$	0	$0.5V$
Weak	Attack	$-C_{WS}$	$-C_{WS}$	$V\text{-}F_A$	$0.5V\text{-}C_{WW}$	$0.5V\text{-}C_{WW}$	$V\text{-}F_A$
	Cond. attack	$-C_{WS}\text{-}F_P$	$-C_{WS}$	V	$0.5V\text{-}C_{WW}\text{-}F_P$	$0.5V\text{-}C_{WW}$	V
	Flee	$-C_{WS}$	0	$0.5V$	$-C_{WW}$	0	$0.5V$

V: amount of the contested resource; C_{SS}, C_{WW}: expected cost of fight between equal opponents; C_{SW}: cost payed by strong individual to beat weak one; C_{WS}: cost payed by weak individual when beaten by strong one; F_f: cost of fleeing; F_A: cost of attacking fleeing opponent; F_P: cost of waiting if the opponent attacks unconditionally.


Stage zero
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Strong
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Nature
Strong
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Stage one
Player 1
Signal A
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Player 2
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Stage two
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Attack
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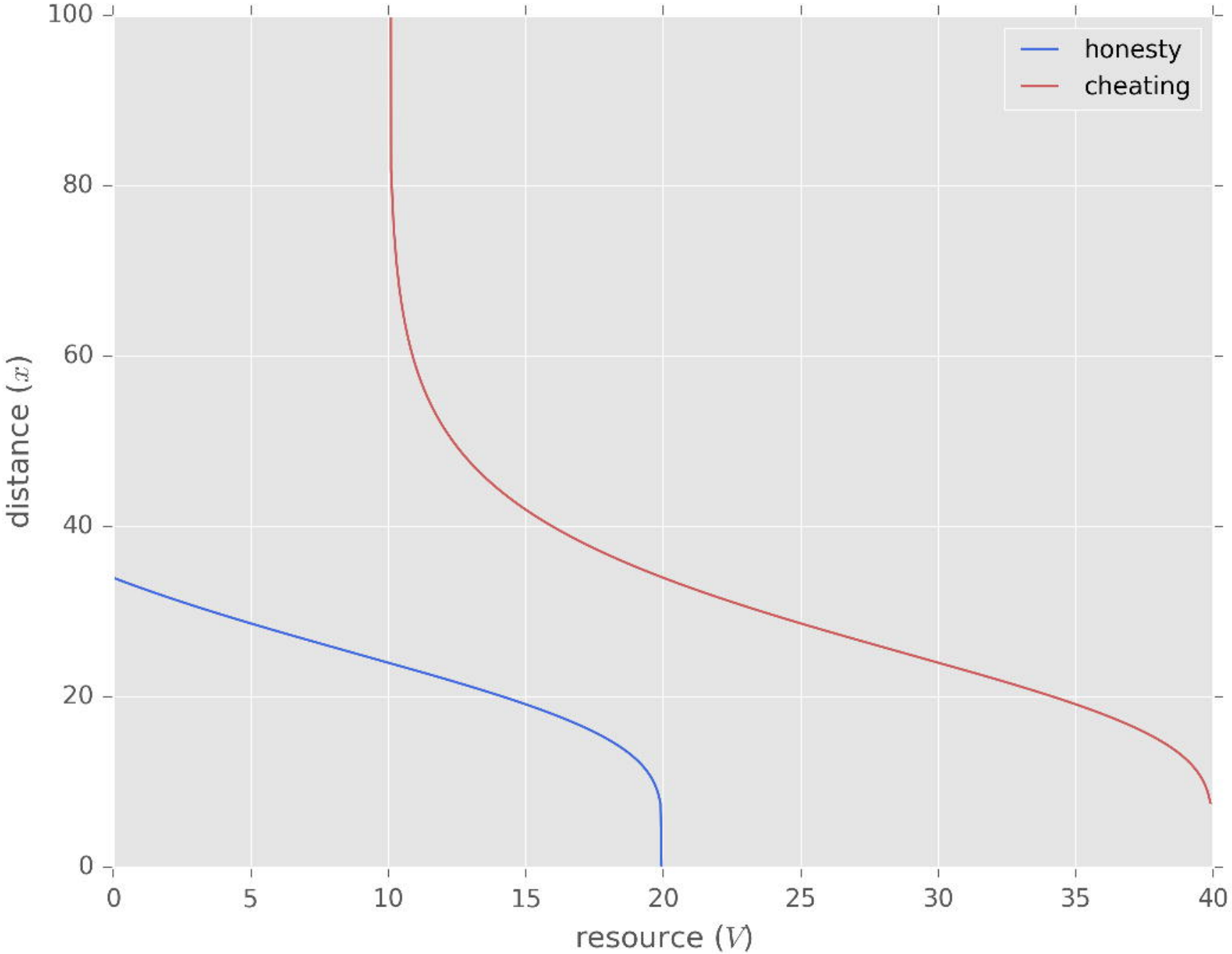
Flee
Player 2
Attack
Cond. Attack
Flee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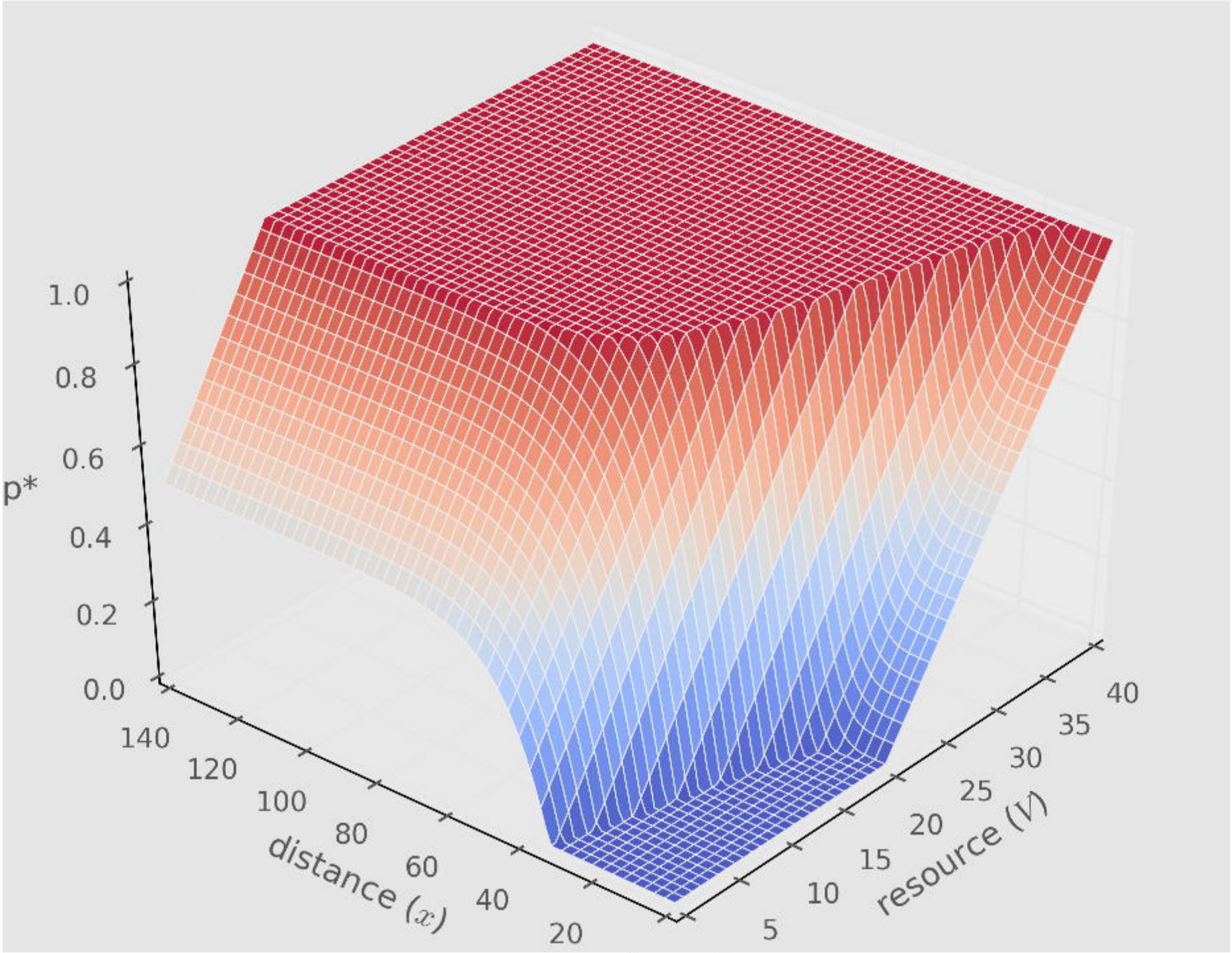
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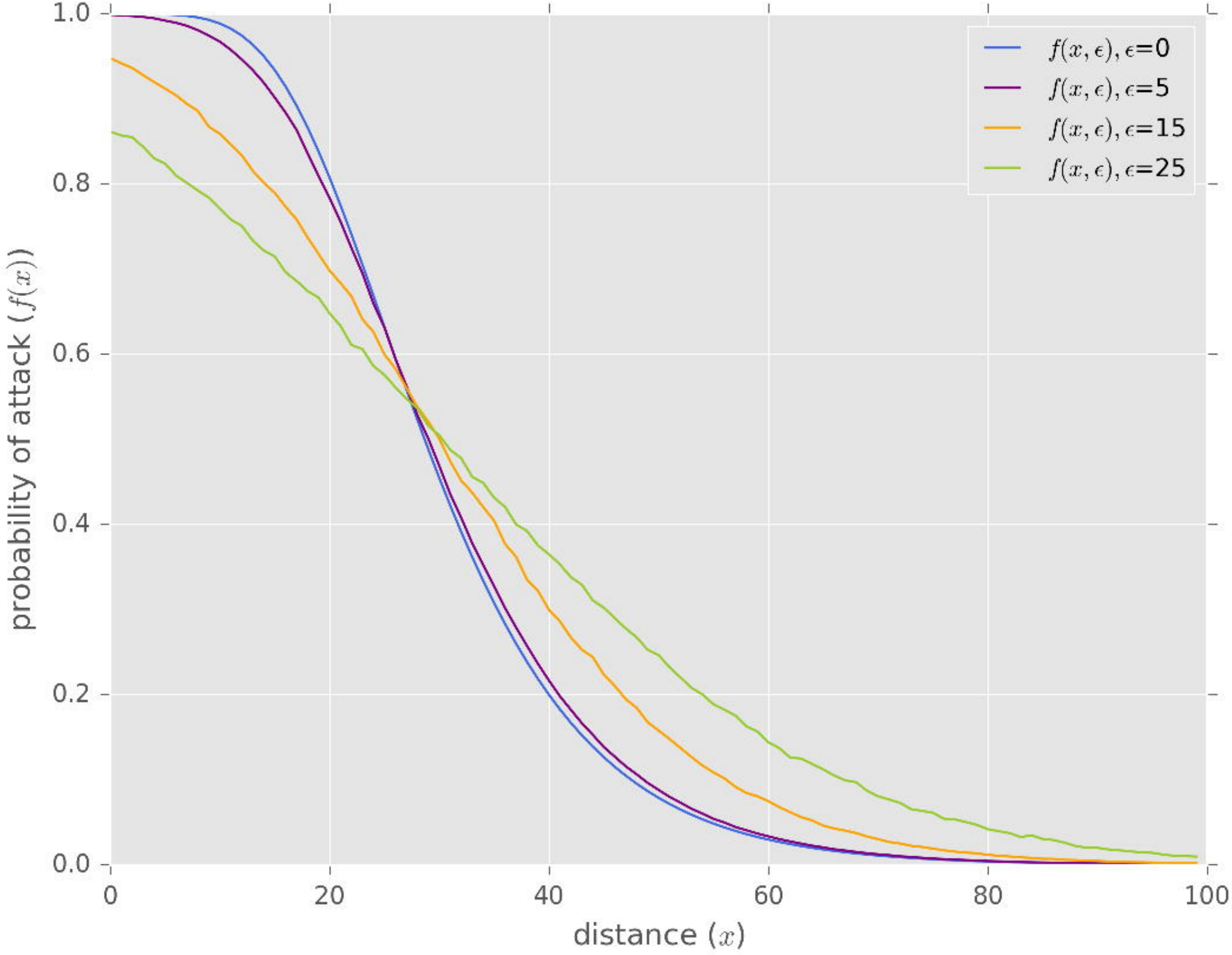
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probability of attack ($f(x)$)
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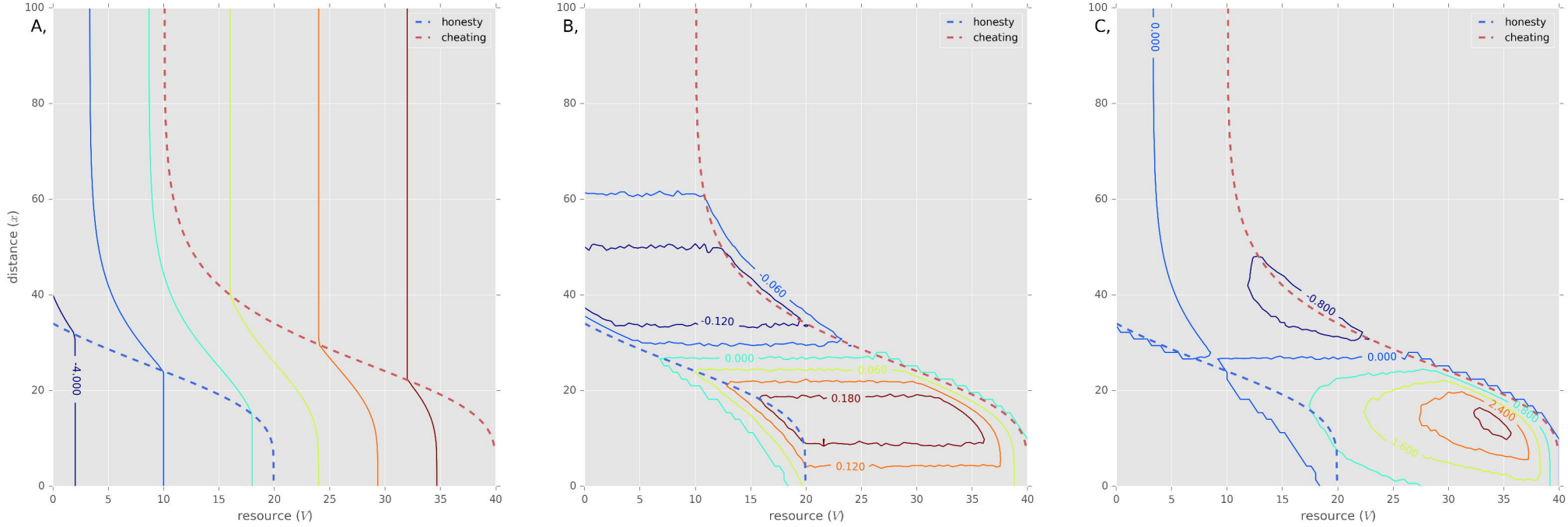
$f(x, \epsilon), \epsilon$=5
$f(x, \epsilon), \epsilon$=15
$f(x, \epsilon), \epsilon$=25


A,
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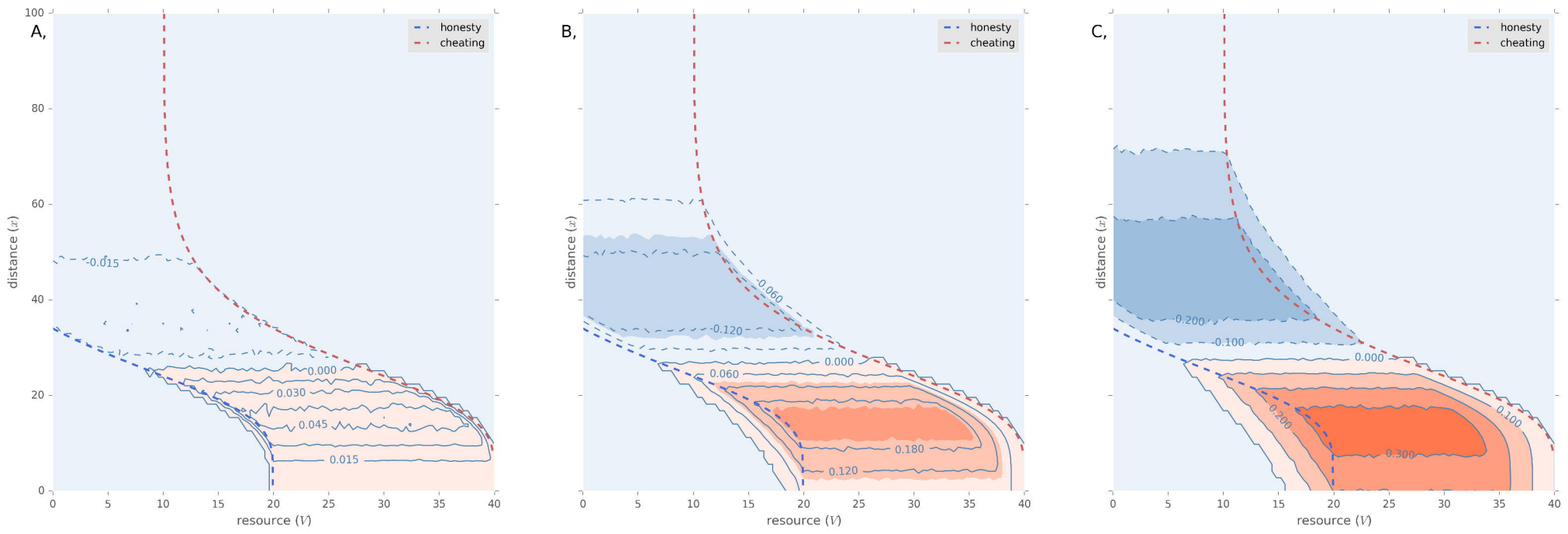
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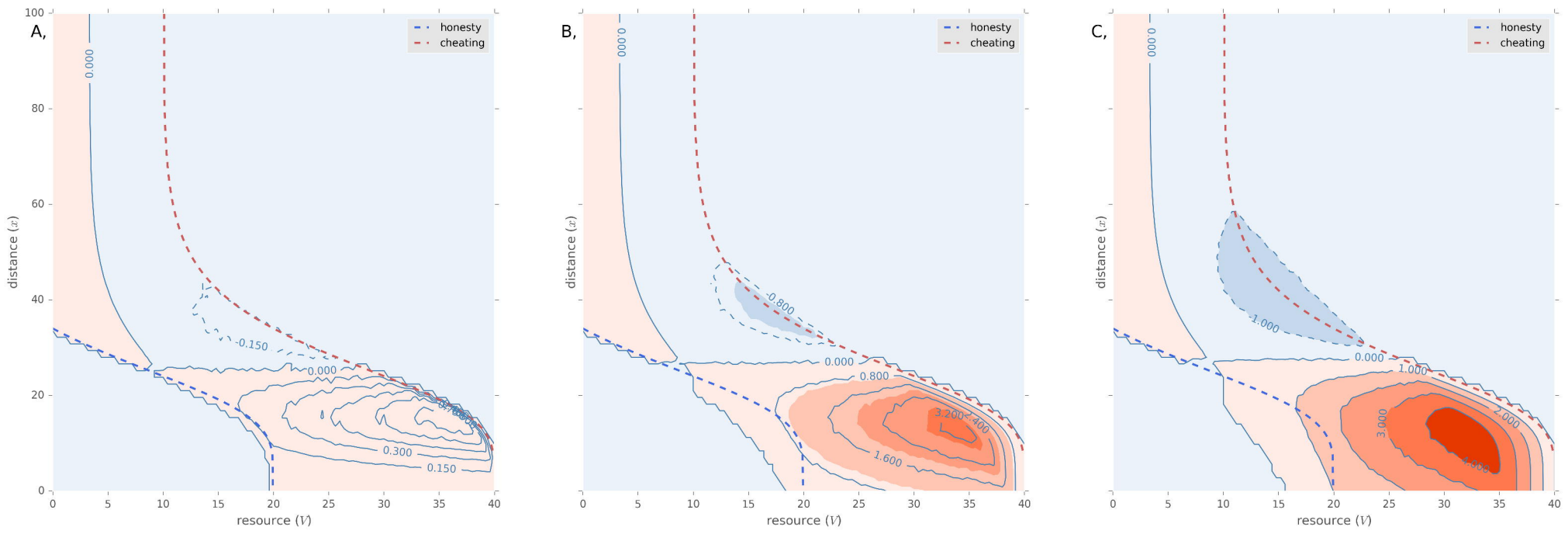
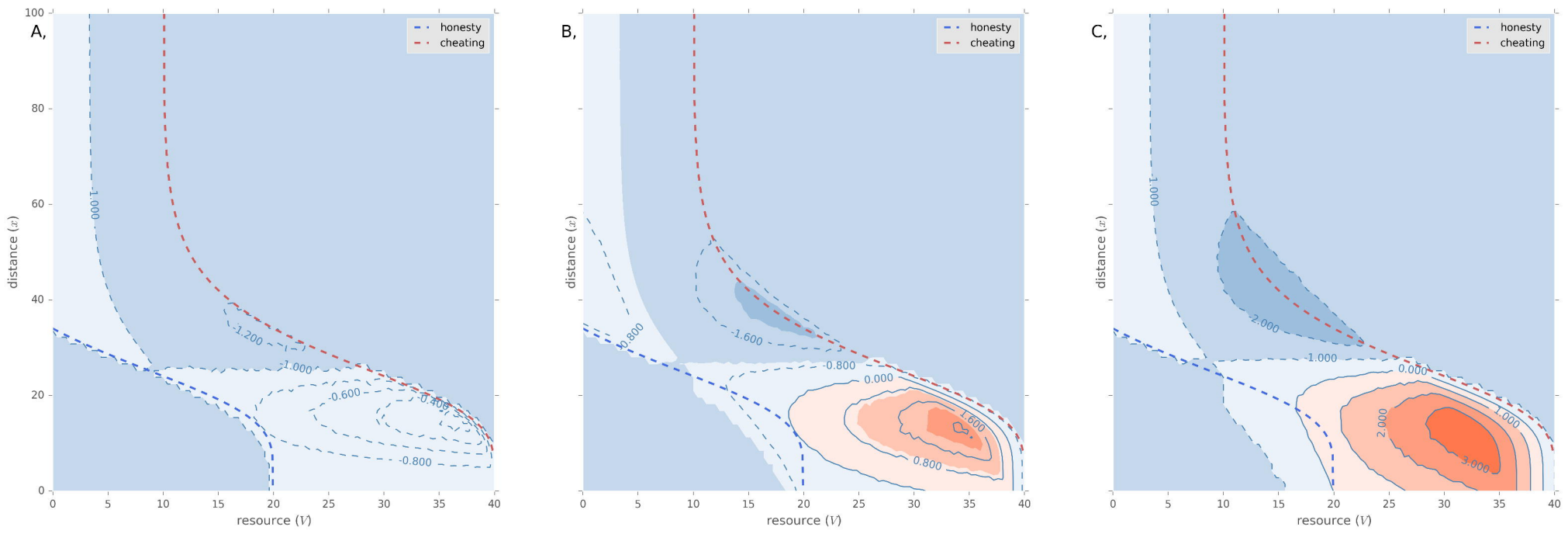
0.300
0.100


A,
B,
C,
honesty
cheating
distance (x)
resource (V)
0.000
-0.150
0.300
0.150
-0.800
0.800
1.600
2.400
3.200
-1.000
1.000
2.000
3.000
4.000


A,
B,
C,
honesty
cheating
distance (x)
resource (V)
-1.000
-1.200
-1.000
-0.600
-0.400
-0.800
-0.800
-1.600
-0.800
0.000
1.600
0.800
-1.000
-2.000
-1.000
0.000
2.000
1.000
3.000