

# Electronic Supplementary Material

Incentives in the family II: Behavioural dynamics and the evolution of non-costly signaling

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## ESM 1 Player and strategy sets for the behavioral and evolutionary game

The behavioral game is played between a single parent and her offspring, and is analogous to a limit of an infinitely repeated game where the time between each stage game goes to zero. Each time point is characterized by a state consisting of the current begging  $c$  and provisioning  $p$ . At each time point, the offspring decides how much to change its begging level  $c$ . This (infinitesimal) amount is denoted by  $dc$ , and is a continuous real variable. Conversely, the parent decides how much to increase or decrease the provisioning  $p$ , which is denoted by  $dp$ , also a continuous real variable.

The two-tiered model construction means that behavior at the behavioral game is under the control of decision rules that are fixed at this level. The parent's decision rule is given by equation (5) in the main text, which maps  $dc$  onto  $dp$  (the inverse of this function comprises the "payment scheme"), whereas the offspring's decision rule is given by equation (3) in the main text.

The evolutionary game (that includes offspring evolution, see below), on the other hand, is defined between a genetic locus that affects the parent's objective and another locus that affects the offspring's objective. This is because over the course of the entire life-history an individual becomes both offspring and parent, one cannot take the individuals as players in the evolutionary game. Nonetheless, I refer to the two strategies as the parent's and offspring's traits in the text, since they are expressed in these individuals. The parental locus' strategy  $\delta$  is assumed to be a positive real number, specifically  $\delta \in [\max\{r_s, \kappa\}, \infty)$ . Likewise, offspring locus strategy,  $\kappa$ , is also a positive real number, with  $\kappa \in (0, \delta]$ . The lower and upper constraints for  $\delta$  and  $\kappa$ , respectively, stem from the condition that the cost function cannot become negative.

Both the behavioral and evolutionary games are defined over pure strategies only.

## ESM 2 Evolution of the parental objective

### Second order ESS condition for $\delta$

The second order evolutionarily stability condition for the parental trait  $\delta$  in the model of section 3 is simply:

$$\frac{d^2}{d\delta^2} E[W_p] < 0 \quad (\text{ESM 1})$$

Evaluating, rearranging and canceling the relevant terms, we arrive at:

$$\begin{aligned} E \left[ \left( \frac{dp^*}{d\delta} \right)^2 \left( \frac{\partial^2 g}{\partial p^2} - (1 - \delta + r_s) \frac{d^2 f}{dp^2} \right) - (1 + r_s) \frac{df}{dp} \frac{d^2 p^*}{d\delta^2} \right. \\ \left. + (r_s - \delta) \left( \frac{d^2 f}{dp^2} \Big|_{p=p_0} \left( \frac{dp_0}{d\delta} \right)^2 + \frac{df}{dp} \Big|_{p=p_0} \frac{d^2 p_0}{d\delta^2} \right) - 2 \frac{df}{dp} \Big|_{p=p_0} \frac{dp_0}{d\delta} \right] < 0, \end{aligned} \quad (\text{ESM 2})$$

where the derivatives of  $f$  and  $g$  are evaluated at  $p = p^*(\delta, n)$ , except when noted.

### The critical value of relatedness for cost-free signaling

To find the lowest value of relatedness  $r_s^*$  that satisfies  $\delta^* = r_s$ , we can use equation (17) in the main text and set it equal to  $r_s$ . Solving this equation, we obtain:

$$r_s^* = \frac{20bn_0^2 - 10n_0\Delta n(a - 2b) - 3\Delta n^2(a - 2b)}{b(20n_0^2 + 30n_0\Delta n + 9\Delta n^2)} \quad (\text{ESM 3})$$

We can then differentiate  $r_s^*$  with respect to  $a$ ,  $b$ ,  $n_0$  and  $\Delta n$ :

$$\frac{\partial r_s^*}{\partial a} = - \frac{10n_0\Delta n + 3\Delta n^2}{b(20n_0^2 + 30n_0\Delta n + 9\Delta n^2)} \quad (\text{ESM 4})$$

$$\frac{\partial r_s^*}{\partial b} = \frac{a\Delta n(10n_0 + 3\Delta n)}{b^2(20n_0^2 + 30n_0\Delta n + 9\Delta n^2)} \quad (\text{ESM 5})$$

$$\frac{\partial r_s^*}{\partial n_0} = \frac{40n_0\Delta n(a + b)(5n_0 + 3\Delta n)}{b(20n_0^2 + 30n_0\Delta n + 9\Delta n^2)^2} \quad (\text{ESM 6})$$

$$\frac{\partial r_s^*}{\partial \Delta n} = - \frac{40n_0^2(a + b)(5n_0 + 3\Delta n)}{b(20n_0^2 + 30n_0\Delta n + 9\Delta n^2)^2} \quad (\text{ESM 7})$$

Since  $a$ ,  $b$ ,  $n_0$  and  $\Delta n$  are all positive real numbers, the signs of the right-hand sides of the preceding equations are negative, positive, positive, and negative, respectively. Hence,  $r_s^*$  increases with  $b$  and  $n_0$  but decreases with  $a$  and  $\Delta n$ .

### ESM 3 Evolution of the offspring objective

In this section, I consider the co-evolution of parental and offspring objectives. In particular, I model the possibility that the offspring might also place a different valuation on the survival of the parent,  $f$ , so that the offspring's objective is given by:

$$x_o = g(p, n) + \kappa f(p), \quad (\text{ESM 8})$$

where  $\kappa > 0$  is analogous to the parent's trait,  $\delta$ . In an interaction between an offspring carrying a resident trait  $\kappa$  and parent carrying  $\delta$ , the signaling costs are given by:

$$c(p) = (\kappa - \delta)(f(p) - f(p_0(\delta))), \quad (\text{ESM 9})$$

Note that here,  $\kappa$  must represent the parent's estimate of the offspring's trait, which might be different than the offspring's true trait value. In particular, I assume that in a population fixed for a given value of  $\kappa$ , the parent's estimate of the offspring  $\kappa$  corresponds to this resident value. When a focal offspring carries a mutant trait,  $\dot{\kappa}$ , the parent will not be able to discern this from the offspring's begging alone, as she would not know whether a change in the begging behaviour is due to different need or different  $\kappa$ . Hence, the cost function imposed by the parent is only based on the resident value of  $\kappa$ . Therefore, the equilibrium demand of a mutant offspring with trait  $\dot{\kappa}$  in a population with resident value  $\kappa$  is given by:

$$\frac{\partial g}{\partial p} + (\dot{\kappa} - \kappa + \delta) \frac{df}{dp} = 0 \quad (\text{ESM 10})$$

To model the co-evolution of parent and offspring trait, I construct a simple life-history model. Following example 4 of Taylor and Frank [1], I assume a sexually breeding population of hermaphrodites where each parent contributes genetically to  $2m$  offspring every year, but care for  $m$  of them only (the other  $m$  are cared by their other parent). Offspring, as a function of the care they receive, survive to adulthood with probability  $G$ , and parents, as a function of the care they supply, survive to breed again with probability  $F$ . The functions  $G$  and  $F$  correspond to expected values of the offspring growth minus signal costs, and parental survival, i.e.  $g - c$  and  $f$  at the signaling equilibrium. Hence,  $F$  and  $G$  are functions of the offspring and parent traits,  $\dot{\kappa}$  and  $\delta$ , as well as the parent's perception of the offspring's trait,  $\kappa$ . For a mutant population fixed for  $\kappa$ , we can summarize the life-history of a lineage with traits  $\dot{\kappa}$  and  $\delta$  in a simple projection matrix:

$$\mathbf{A} = \begin{pmatrix} 0 & m \\ G(\dot{\kappa}, \kappa, \delta) & F(\dot{\kappa}, \kappa, \delta) \end{pmatrix}. \quad (\text{ESM 11})$$

In this matrix, even though  $m$  can be greater than 1, I assume that each parent cares for only a single offspring at a time; i.e. there are no direct sib-sib interactions.

In a life-history model such as this, the relevant fitness measure is the population growth rate  $\lambda$ , calculated as the first eigenvalue of the matrix  $\mathbf{A}$  [2]. Changes in  $\mathbf{A}$  that increase  $\lambda$  will be favored by selection, and hence life-history evolution will maximize  $\lambda$ . Consider a rare mutant offspring with trait  $\dot{\kappa}$  in a population that is fixed for  $\kappa$ . The projection matrix the mutant induces is:

$$\mathbf{A}' = \begin{pmatrix} 0 & m \\ G(\dot{\kappa}, \kappa, \delta) & (1 - r_s)F(\kappa, \kappa, \delta) + r_s F(\dot{\kappa}, \kappa, \delta) \end{pmatrix}, \quad (\text{ESM 12})$$

where  $r_s$  is the average sib to sib relatedness among all broods of a given individual, corresponding to the probability that the future brood of the parent will carry the mutant trait  $\dot{\kappa}$ . Here, the adult survival probability term accounts for the fact a mutant offspring's caring parent will on average have a fraction  $r_s$  of her other offspring carry the mutant gene. However, the relatedness between sibs plays no role in the change in the parental trait  $\delta$ , because the parent and all her broods will experience the same  $\delta$ . Furthermore, while the offspring trait "plays" against the resident offspring trait (because of the parent's perception of  $\kappa$ ), the mutant parent trait does not play against the resident parent trait, since we assumed that each parent cares for the offspring alone.

Due to the simplicity of the model, we can compute the first eigenvalue of the projection matrix with both parent and offspring mutations directly and deal with its maximization. The first order ESS conditions for the parent and offspring traits (assuming no genetic linkage between  $\kappa$  and  $\delta$ ) are then:

$$\left. \frac{\partial \lambda}{\partial \dot{\kappa}} \right|_{\dot{\kappa}=\kappa} = 0 \quad (\text{ESM 13})$$

$$\left. \frac{\partial \lambda}{\partial \delta} \right|_{\dot{\kappa}=\kappa} = 0 \quad (\text{ESM 14})$$

These conditions are equivalent to [1]:

$$\left[ \frac{\partial G}{\partial \dot{\kappa}} + \frac{r_s \lambda(\kappa, \dot{\kappa}, \delta)}{m} \frac{\partial F}{\partial \dot{\kappa}} \right]_{\dot{\kappa}=\kappa} = 0 \quad (\text{ESM 15})$$

$$\left[ \frac{\partial G}{\partial \delta} + \frac{\lambda(\kappa, \dot{\kappa}, \delta)}{m} \frac{\partial F}{\partial \delta} \right]_{\dot{\kappa}=\kappa} = 0 \quad (\text{ESM 16})$$

The factor  $\lambda/m$  accounts for the difference in the reproductive value of offspring compared to the parents [1]. Models of parent-offspring conflict usually do not deal with this effect of the life-history explicitly, instead positing that the parent and offspring traits maximize  $G+F$  and  $G+r_s F$ , respectively [e.g. 3, 4].

## Evolutionarily stable $\dot{\kappa}$

Expanding the first-order condition (ESM 15) in terms of the growth and survival functions  $g$  and  $f$ , we obtain:

$$\frac{\partial G}{\partial \dot{\kappa}} + \frac{\lambda r_s}{m} \frac{\partial F}{\partial \dot{\kappa}} = \text{E} \left[ \frac{dp^*}{d\dot{\kappa}} \left( \frac{\partial g}{\partial p} - (\kappa + \delta - \frac{\lambda r_s}{m}) \frac{df}{dp} \right) \right] = 0, \quad (\text{ESM 17})$$

with the derivatives evaluated at the behavioural equilibrium (ESM 10) and  $\dot{\kappa} = \kappa$ . Under these conditions,  $\frac{\partial g}{\partial p} + \delta \frac{df}{dp}$  vanishes, and we are left with:

$$\text{E} \left[ \frac{dp^*}{d\dot{\kappa}} \frac{df}{dp} \left( \frac{\lambda r_s}{m} - \kappa \right) \right] = 0. \quad (\text{ESM 18})$$

We can find  $\frac{dp^*}{d\dot{\kappa}}$  from the behavioural equilibrium condition as:

$$\frac{dp^*}{d\kappa} = - \frac{\frac{df}{dp}}{\frac{\partial^2 g}{\partial p^2} + (\dot{\kappa} - \kappa + \delta) \frac{d^2 f}{dp^2}}, \quad (\text{ESM 19})$$

which is negative at  $\kappa = \dot{\kappa}$ . Since  $\frac{df}{dp} < 0$  by assumption, and  $m$ ,  $\lambda$  and  $r_s$  are constants with respect to  $n$  over which the expectation is taken, equation (ESM 18) can only be satisfied when the term in the parenthesis vanishes. Hence, the only value of  $\dot{\kappa}$  that satisfies the first order ESS condition (ESM 13) is

$$\dot{\kappa} = \frac{r_s \lambda}{m}. \quad (\text{ESM 20})$$

In other words, the offspring's ES objective has it maximizing its real fitness given from the life-history model. This result contrasts with that of the parent, which says that the parent in general will evolve an objective function different than the fitness function. This result comes about because the parent cannot know the offspring's actual objective, and therefore cannot react to changes in the focal offspring's  $\dot{\kappa}$ . Under these circumstances, there is no indirect cost or benefit through a change in the parent's payment schedule [5], and hence the best the offspring can do in the behavioural time-scale is to try to maximize its actual fitness given the payment schedule for the resident  $\kappa$ . Note, however, the parent's trait  $\delta$  does influence  $\kappa$  indirectly through changing  $\lambda$ . Note also that whenever  $\lambda/m < 1$ , the ES  $\kappa < r_s$ , meaning that the offspring will evolve to be more "selfish" than predicted from a simple inclusive fitness maximization. The reason is that the offspring discounts its future siblings with the population growth rate, compared to itself.

Figures ESM 1 and ESM 2 show that with parent-offspring co-evolution, a pattern similar to that of Section 3 holds. Figure ESM 1 is the counterpart to figure 1 in the main text, and shows how the ES values of the offspring trait  $\kappa$  and the parent trait  $\delta$  change with the relatedness  $r_s$  for a given parameter set. As in Figure 1, we see that the ES  $\delta$  decreases in with  $r_s$ . We can also see that the ES  $\kappa$  is increasing in  $r_s$ . Note that for this parameter set,  $\lambda/m > 1$  at equilibrium, and hence  $\kappa > r_s$ , meaning that the offspring values the parental survival more than based purely on its relatedness to future sibs  $r_s$ . At around  $r_s \approx 0.4$  for these parameter values,  $\delta$  comes up against the lower bound of  $\kappa$ . For higher relatedness values, the signaling between the parent and offspring is non-costly.

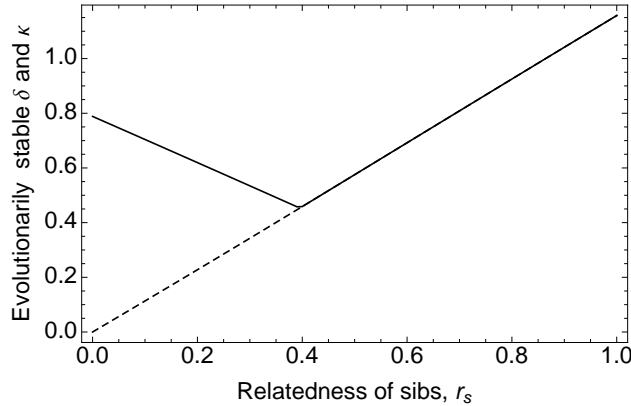


Figure ESM 1: The evolutionarily stable values of the parental  $\delta$  and offspring  $\kappa$  traits as a function  $r_s$ . Solid line depicts  $\delta$ , dashed line  $\kappa$ , and the dotted line shows  $r_s$ . At  $r_s \approx 0.4$ ,  $\delta$  comes up against the lower bound of  $\kappa$ , and they increase together for higher values of the relatedness. Parameters for this plot are same as in Figure 1:  $a = 2$ ,  $b = 1$ ,  $n_0 = 1$  and  $\Delta n = 1$ , with the additional parameter  $m = 1$ .

Figure ESM 2 depicts how this critical value of  $r_s$  varies the marginal rate parameters  $a$  and  $b$  and for different offspring needs. The pattern shown in Figure ESM 2 is essentially identical to Figure 3 in the main text: with increasing  $a$ , the critical value of  $r_s$  decreases, whereas with increasing  $b$ , it increases. Additionally, for the same values of  $a$  and  $b$ , the critical value of  $r_s$  decreases slightly as the variation in offspring need ( $\Delta n - n_0$ ) increases. One noticeable difference between Figures 3 in the main text and ESM 2 here is that the latter shows higher critical values of  $r_s$  for a given parameter set. Thus, we might conclude that for these functional forms, the coevolution of parent and offspring traits in a life-history model makes it slightly harder to evolve cost-free communication between the parent and the offspring.

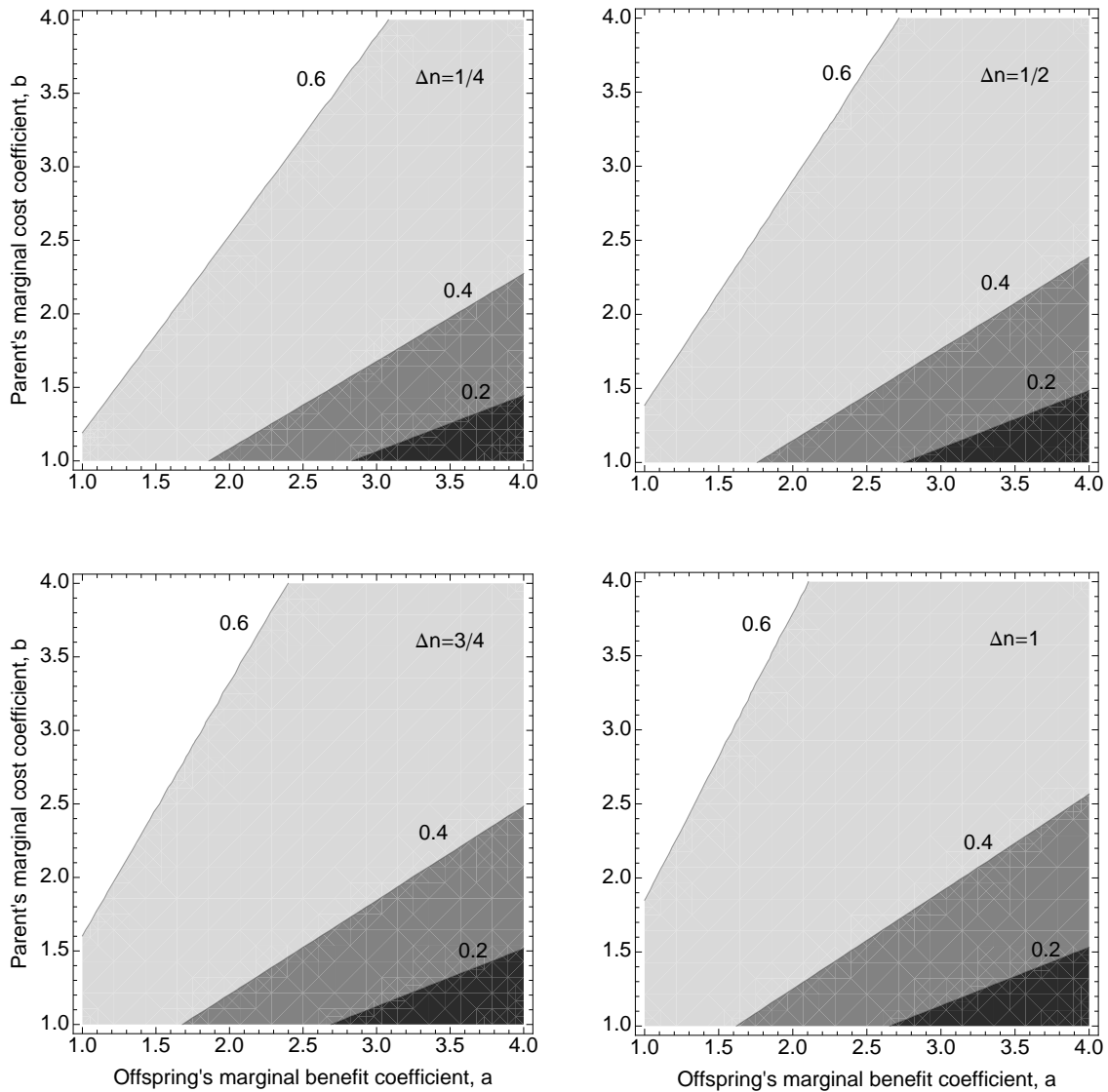


Figure ESM 2: The lowest value of  $r_s$  that sustains cost-free signaling as a function of the marginal benefit and cost parameters  $a$  and  $b$ , and for different spreads of offspring need. In all panels, the mean offspring need is equal to 1, and the fecundity  $m = 1$ .

## ESM 4 The Vickrey-Clarke-Groves auction

This section illustrates how mechanism design theory works by describing its canonical model, the Vickrey-Clarke-Groves (VCG) auction [6–8], and how it maximizes aggregate payoffs under imperfect information. The basic problem in a VCG auction is to assign a number of items ( $t_j$ ) to a set of bidders ( $b_i$ ), such that the total welfare of the set of bidders is maximized, i.e., achieve the “efficient” allocation. Each bidder has private information about their valuation of each item. In general, bidders will have incentives to misrepresent their valuations in order to be assigned their preferred items.

In the VCG auction, each bidder submits their valuations for each item to the auctioneer. The auctioneer then assigns items to maximize the total payoff given the messages he received, and charges each bidder an amount equal to the “harm” they cause to the aggregate welfare by participating in the auction. More precisely, let  $v_{ij}$  be  $b_i$ ’s valuation of item  $t_j$ . An allocation  $a$  is a map from the set  $T$  of items on to the set  $B$  of bidders, assigning a bidder  $b_i$  for each item  $t_j$ . Some bidders might be left without an item, but no bidder can get multiple items. The efficient allocation  $a^*$  maximizes  $\sum_j v_{a(t_j),j}$ . Now, call the total value achieved under an allocation  $a$  for every bidder except  $i$ ,  $V_{-i,a} = \sum_{k \neq j} v_{a t_k, k}$ . Suppose now that bidder  $b_i$  is removed from the auction, and consider the optimal allocation  $a'$  under this reduced set of bidders; i.e.  $a'$  maps from  $T$  onto  $B \setminus b_i$  and maximizes  $V'_{-i,a'} = \sum_j v_{a' t_j, j}$ , the total welfare that bidders other than  $b_i$  can achieve, if  $b_i$  had not showed up at the auction. Therefore, the difference between  $V_{-i,a}$  and  $V'_{-i,a'}$  is how much  $b_i$ ’s participation in the auction “hurts” other bidders’ payoff in the aggregate. Note that the difference is zero if  $b_i$  was not assigned an item under the efficient allocation.

To see how the VCG auction achieves incentive compatibility, fix a set of declared valuations by all bidders except  $b_i$ , and denote by  $a^*$  the efficient allocation for the set of declared valuations plus  $b_i$ ’s true valuation. Suppose when  $b_i$  tells the truth, he receives item  $t_j$  under  $a^*$ , and thus his payoff is:  $u_i = v_{ij} - (V_{-i,a^*} - V'_{-i,a'})$ . If instead  $b_i$  declares a different set of valuations and gets a different item  $t_k$ , his payoff is now:  $u'_i = v_{ik} - (V_{-i,a} - V'_{-i,a'})$ . If the difference  $u'_i - u_i \leq 0$  for all  $a \neq a^*$ , it is optimal for  $b_i$  to submit bids so as to get  $t_j$ . The difference is:  $u'_i - u_i = v_{ik} - (V_{-i,a} - V'_{-i,a'}) - v_{ij} + (V_{-i,a^*} - V'_{-i,a'}) = V_a - V_{a^*}$ , where  $V_a$  and  $V_{a^*}$  are the total valuations, including  $b_i$ ’s valuation, under the allocation rules  $a$  and  $a^*$ , respectively. Since by assumption  $a^*$  maximizes the total valuation,  $u'_i - u_i \leq 0$  for all  $a \neq a^*$ .

Note that this argument does not rely on other bidders having told the truth about their own valuations. Indeed, regardless of what others do, truth-telling is a dominant strategy in the VCG auction, which makes it quite robust for actual implementation. However, note also the sequence of events, which require the auctioneer to first declare (and commit to) the mechanism he is going to implement, then gather all messages, and finally calculate the charges to each bidder. While such a setup poses no problem for actual auctions, biological interactions may not allow such separation between messages and “payments” (e.g., when the messages themselves are the payments). Nonetheless, the underlying idea of the VCG auction can be implemented in biological interactions with behavioral dynamics, as my model shows.

## References

- [1] Taylor PD, Frank SA. How to make a kin selection model. *Journal of Theoretical Biology*. 1996;180:27–37.
- [2] Caswell H. *Matrix Population Models*. Sunderland MA: Sinauer Associates; 2001.
- [3] Godfray HCJ. Signalling of need by offspring to their parents. *Nature*. 1991;352:328–330.
- [4] Johnstone RA. Signaling of need, sibling competition, and the cost of honesty. *Proc Natl Acad Sci USA*. 1999;96(22):12644.
- [5] Akçay E, Van Cleve J, Feldman MW, Roughgarden J. A theory for the evolution of other-regard integrating proximate and ultimate perspectives. *Proc Natl Acad Sci USA*. 2009;106(45):19061–6.
- [6] Vickrey W. Counterspeculation, Auctions, and Competitive Sealed Tenders. *The Journal of Finance*. 1961 Jul;16:8–37.
- [7] Clarke EH. Multipart pricing of public goods. *Public Choice*. 1971 Sep;11(1):17–33.
- [8] Groves T. Incentives in teams. *Econometrica*. 1973;41(4):617–631.