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UNC-60$^{Cofilin\ 9}$ (Figure 1). Tian *et al.* show that ANI-1^{Anillin} is an important regulator of Q neuroblast migration and neurite formation, two processes required for the establishment of a functional nervous system. Interestingly, Anillin expression has been found to be upregulated in certain cancers and its expression level correlates with the metastatic potential of many types of cancers [7,20]. These new results suggest a function for Anillin in metastasis: it could regulate cell migration by inhibiting Cofilin and stabilizing F-actin. Future work will uncover whether Anillin plays a similar role in the cytokinetic contractile ring and, conversely, whether any of Anillin's interactors in the cytokinetic ring contribute to its roles in cell migration in metazoan development or cancer metastasis.

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Human Cooperation: The Race to Give

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An analysis of online charity donations reveals that, when males make large donations to attractive female fundraisers, other males respond in kind, providing field evidence for 'competitive altruism' in which helpful acts are used as a display to attract partners.

How can it be adaptive for one organism to help another? This is an enduring question, and one that becomes especially challenging in cases such as charitable donations, where there may be no obvious return to a benefactor. One potential answer comes from viewing helpful behaviour as a display to potential interaction partners. If individuals differ in their qualities as social or sexual partners, and if helping provides an honest signal of these qualities [1], then those who help more may be more likely to be chosen. As a result, we can expect competition between individuals

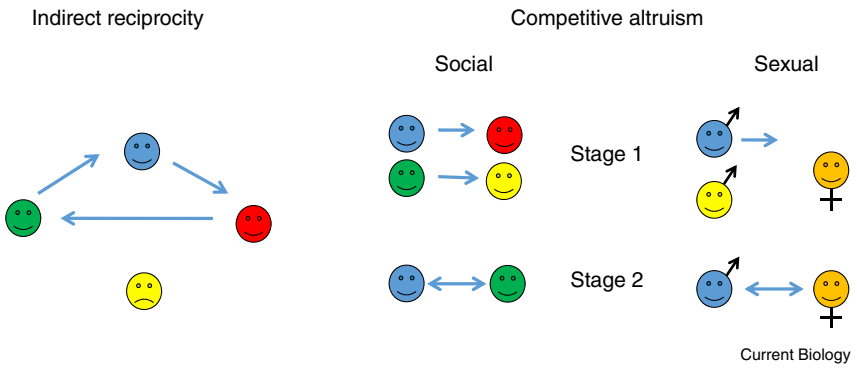

Figure 1. Mechanisms of reputation-based cooperation.
In indirect reciprocity, individuals donate to others who have previously donated (blue arrows) and therefore have a positive reputation. In competitive altruism, there are two distinct stages. First, individuals have an opportunity to donate and build a reputation; secondly, those who have donated have preferential access to either social or sexual partnerships. It is this process of competition for partnerships that is hypothesized to drive costly displays such as charitable donation.

to display their generosity and consequently be chosen by the most desirable partners, a process called competitive altruism [2]. Until now, evidence for this theory has been largely limited to laboratory experimental games [3–5]. In a recent issue of *Current Biology*, Raihani and Smith [6] report an analysis of a large data set of donations on a fundraising website which shows that males compete with other males in giving exceptionally large donations to attractive female fundraisers. Their finding provides field evidence for competitive altruism and in doing so highlights the role of sexual selection as one driver of human cooperation.

Behaviours such as donating to charity are interesting because they involve a cost to the donor and a benefit to a recipient. Behavioural scientists typically refer to such acts as altruistic when the behaviours themselves are associated with putative fitness costs [7,8]. They then seek to determine how the responses by recipients and third parties provide a counteracting fitness benefit making the behavior adaptive. When these responses of other individuals that lead to a net fitness benefit are identified, some evolutionary biologists would not consider altruism to have occurred [9]. For many behavioural scientists though, the term altruism is useful in highlighting when adaptive strategies involve an intrinsically costly behaviour, which benefits the individual through the responses of others.

An intuitively appealing way in which the responses of others may lead to adaptive outcomes is through reciprocation, but such behavior can only work if the act of cooperating leads to an increase in the chance of receiving [10]. This is true whether the reciprocity is direct or indirect [11], yet donors to charity are not giving to other givers, they are giving to people or institutions that will use their money because of their need. So theory would say indirect reciprocity is a poor candidate explanation for charitable giving, notwithstanding experimental evidence that charity donors are rewarded [12]. The theory of competitive altruism resolves this problem of conditional giving by suggesting that donors benefit, not through getting a reciprocal return, but from access to profitable partnerships.

Competitive altruism theory assumes that individuals vary in quality as potential social or sexual partners; that altruistic behaviour provides public information about quality and/or intentions; and that individuals can choose their partners for further interactions (Figure 1). It then makes the inferences that those seen to be most altruistic will either assortatively partner with each other (in the case of social selection), or will be preferentially selected by sexual partners (in the case of sexual selection). Where individuals are competing for access to partners, the theory proposes that displays of increasingly costly behaviour will be used as signals to attract the best partners.

Evidence for competitive altruism comes from laboratory experimental economic games which implement the two stage structure with an opportunity for reputation building in a game where cooperating is individually costly, followed by an opportunity for choosing partners for a mutually beneficial cooperative game. People are more cooperative when they are in public; they are more generous still when they are told they will have an opportunity to choose a partner; more generous partners pair assortatively, and they receive more from their chosen partners in a mutual benefit game [3,4].

Raihani and Smith [6] tested for evidence of competitive altruism in the field by analysing a large database of charitable donations. They focus on the specific prediction of competitive gift giving by asking whether people respond dynamically to the donations of others. On the basis of sexual selection theory, they reason that competition will be strongest amongst males in the context of donations to attractive female fundraisers. In order to simplify their analysis, they defined donations as large when they are more than twice previous donations to the fundraiser and over £50, and then examined responses to these. As predicted, they found that responses to large donations were greater by males following large donations by other males, in the condition where they were giving to an attractive female fundraiser. Women showed no evidence of competing with large donations by others.

What can we conclude from these results? The study provides striking field support for the prediction from competitive altruism theory that donations are used to 'show off' generosity in a competitive context. But as one would expect from an opportunistic field study, there is much we do not know. In particular, are competitive donations by males strategic in the sense that the donors actually benefit through being more desirable partners? Further, we do not know what donations might signal about an individual's quality and intentions and why recipients and/or observers might then behave in a manner beneficial to the signaller. In these

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regards, we can only refer to other results which have found a link between charitable donation and status [12,13] and between blood donation and generosity [14]. Assembling these strands of evidence it is reasonable to speculate that reputational benefits may outweigh donation costs. Interestingly, a model suggests courtship gifts should be costly (and so signal quality or intentions) yet intrinsically worthless to the recipient (to overcome the 'gold-digger' problem) [15], so charitable donations via a fundraiser may be a nice example of this.

Are the results surprising? On the one hand they fit well with existing examples where generosity is displayed publicly [16]. Furthermore, generosity is well known to be a desirable trait in mate choice [17]. A few experimental studies have also found evidence that altruism is used as a display to attractive members of the opposite sex [18,19]. Yet despite all this, sexual selection is rarely invoked in explaining cooperation, and a high profile review does not include it as one of the routes to cooperation [20]. The stimulating work of Raihani and Smith [6] serves to highlight the potentially rather overlooked role of sexual selection in driving displays of altruism. It is well established that aggression may be used in male–male competition over access to females, but this shows that cooperation may also be used in competitive contexts. More generally the results should stimulate further work on how we benefit from being seen to be cooperative, and how explanations for reputation-building extend beyond indirect reciprocity.

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Plant Sex Chromosomes: Lost Genes with Little Compensation

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In many animals, gene loss on Y chromosomes is compensated through altered expression of their X-chromosome homologue. Now, however, a new study in plants finds that even genes deleted from the Y show no dosage compensation.

In species with an XY sex-determination system, such as mammals, genes in the sex-determining region (SDR) on the Y chromosome are never exposed to selection in females, while those on the X will spend twice as much time in females as in males. The same principle applies in species with Z and W chromosomes, such as birds and butterflies, where the