Inclusive fitness

"I will not here enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory."
Charles Darwin, 1859

Brian O'Meara
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Learning objectives

- Why helping appears problematic
- Hamilton's rule
- Inclusive fitness

If a working ant or other neuter insect had been an animal in the ordinary state, I should have unhesitatingly assumed that all its characters had been slowly acquired through natural selection; namely, by an individual having been born with some slight profitable modification of structure, this being inherited by its offspring, which again varied and were again selected, and so onwards. But with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection?

This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end. Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety; breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family. I have such faith in the powers of selection, that I do not doubt that a breed of cattle, always yielding oxen [castrated bulls] with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind. Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification. And I believe that this process has been repeated, until that prodigious amount of difference between the fertile and sterile females of the same species has been produced, which we see in many social insects.

Box 1

Glossary.

Actor: the focal individual performing a behaviour.

Altruism: a behaviour that is costly to the actor and beneficial to the recipient. Cost and benefit are defined on the basis of the lifetime direct fitness consequences of a behaviour.

Cheaters: individuals who do not cooperate or who cooperate less than their fair share, but are potentially able to gain the benefit of others cooperating.

Cooperation: a behaviour that provides a benefit to another individual (recipient), and the evolution of which has been dependent on its beneficial effect for the recipient.

Direct fitness: the component of fitness gained from producing offspring; the component of personal fitness due to one's own behaviour.

Greenbeard: a hypothetical gene that causes in carriers both a phenotype that can be recognised by conspecifics (a 'green beard') and a cooperative behaviour towards conspecifics who show a green beard.

Inclusive fitness: "the effect of one individual's actions on everybody's numbers of offspring [...] weighted by the relatedness [10]; the sum of direct and indirect fitness; the quantity maximised by Darwinian individuals.

Indirect fitness: the component of fitness gained from aiding related individuals.

Kin selection: process by which traits are favoured because of their beneficial effects on the fitness of relatives.

Mutual benefit: a benefit to both the actor and the recipient.

Mutualism: two-way cooperation between species.

Recipient: an individual who is affected by the behaviour of the focal individual.

Relatedness: a measure of the genetic similarity of two individuals, relative to the average; the statistical (least-squares) regression of the recipient's breeding value for a trait on the breeding value of the actor.

West et al. 2007

Hamilton's rule

$$r\,b > c$$

r: degree of relatedness (probability of sharing a given gene)
b: benefit to recipient
c: cost to donor

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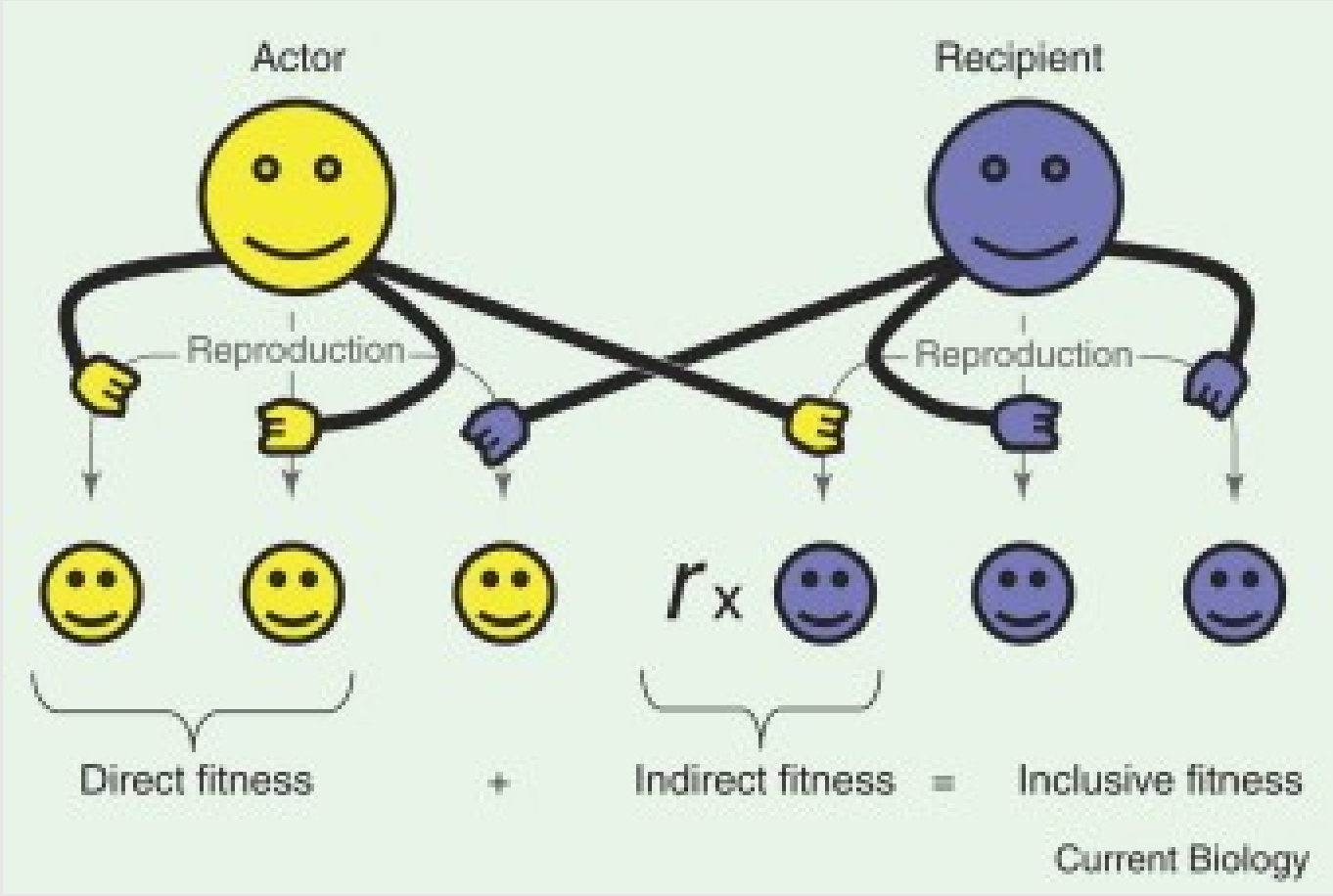

West et al. 2007

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"[L]egend has it that in a pub one evening Haldane told his friends that he would jump into a river and risk his life to save two brothers, but not one, and that he would jump in to save eight cousins, but not seven." Dukatkin 2007

Table 1 | Inclusive fitness theory has been important in understanding a range of behavioural phenomena

Research area	Correlational?	Experimental?	Theory–data interplay
Sex allocation	Yes	Yes	Yes
Policing	Yes	Yes	Yes
Conflict resolution	Yes	Yes	Yes
Cooperation	Yes	Yes	Yes
Altruism	Yes	Yes	Yes
Spite	Yes	Yes	Yes
Kin discrimination	Yes	Yes	Yes
Parasite virulence	Yes	Yes	Yes
Parent–offspring conflict	Yes	Yes	Yes
Sibling conflict	Yes	Yes	Yes
Selfish genetic elements	Yes	Yes	Yes
Cannibalism	Yes	Yes	Yes
Dispersal	Yes	Yes	Yes
Alarm calls	Yes	Yes	Yes
Eusociality	Yes	Yes	Yes
Genomic imprinting	Yes	Yes	Yes

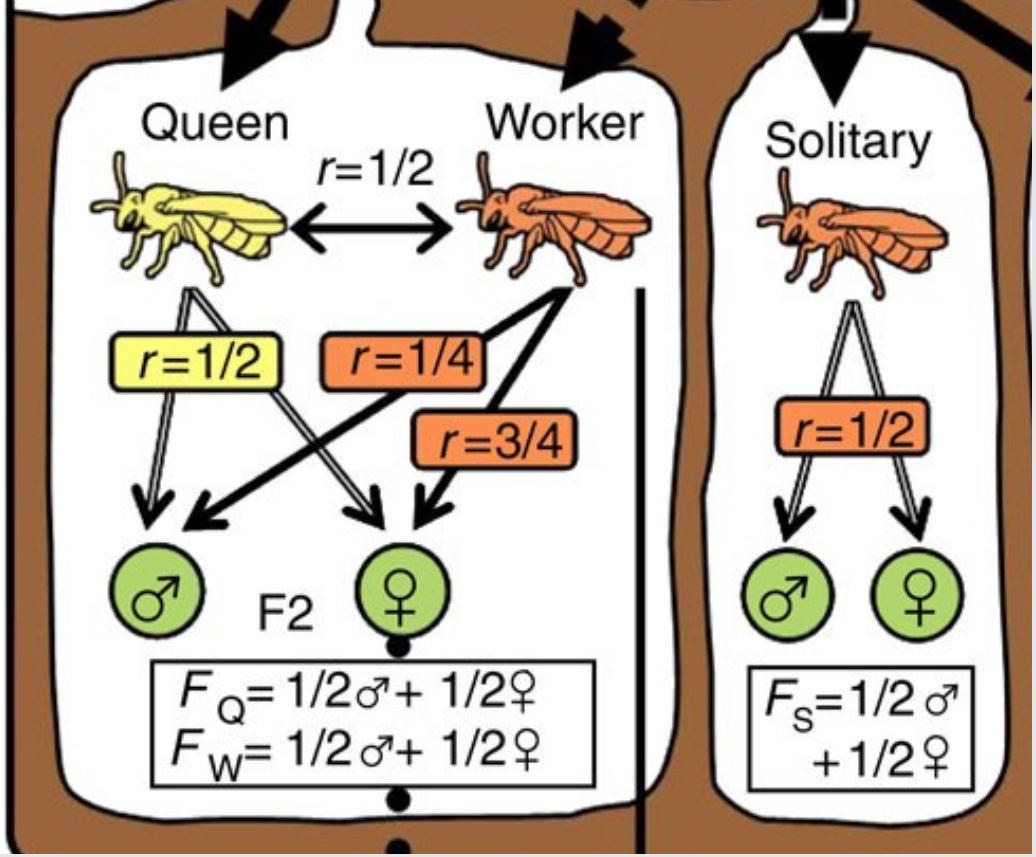
Data are taken from refs 9–11. Correlational studies test predictions using natural variation in key variables, whereas experimental studies involve their experimental manipulation. Interplay between theory and data means that theory has informed empirical study, and vice versa. Inclusive fitness is not the only way to model evolution, but it has already proven to be an immensely productive and useful approach for studying eusociality and other social behaviours.

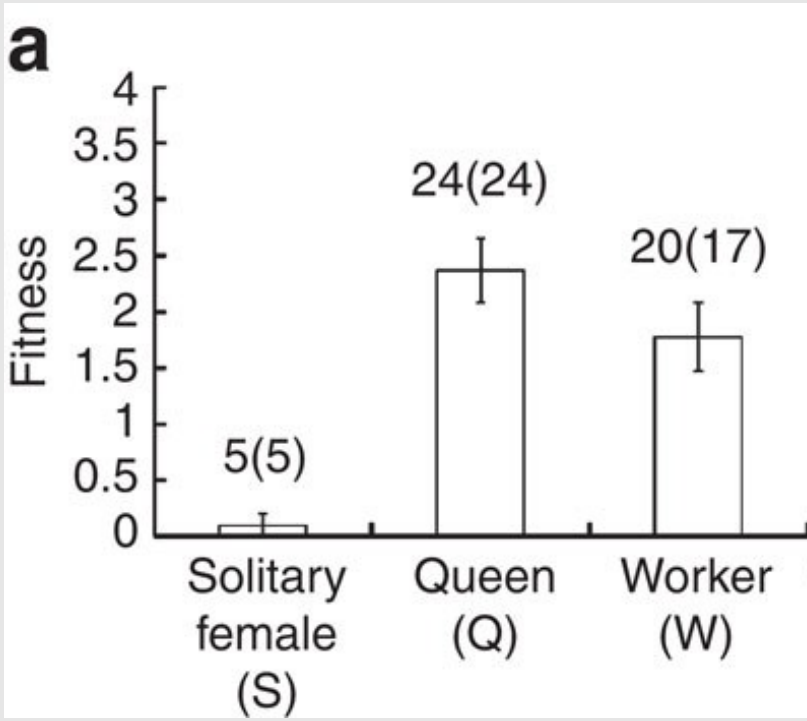
Table 2 | Areas in which inclusive fitness theory has made successful predictions about behaviour in eusocial insects

Trait examined	Explanatory variables	Correlational studies?	Experimental studies?	Interplay between theory and data?
Altruistic helping	Haplodiploidy versus diploidy	Yes	No	Yes
Worker egg laying	Worker policing	Yes	Yes	Yes
Policing	Relatedness	Yes	Yes	Yes
Level of cooperation	Costs, benefits and relatedness	Yes	Yes	Yes
Intensity of work	Need for work and probability of becoming queen	Yes	Yes	Yes
Sex allocation	Relatedness asymmetries due to variation in queen survival, queen number and mating frequency	Yes	Yes	Yes
Sex allocation	Resource availability	Yes	Yes	Yes
Sex allocation	Competition for mates between related males	Yes	Yes	Yes
Number of individuals trying to become reproductive	Presence of old queens	Yes	Yes	Yes
Workers killing queens	Presence of workers, reproductives or other queens	Yes	No	No
Exclusion of non-kin	Colony membership	Yes	Yes	Yes

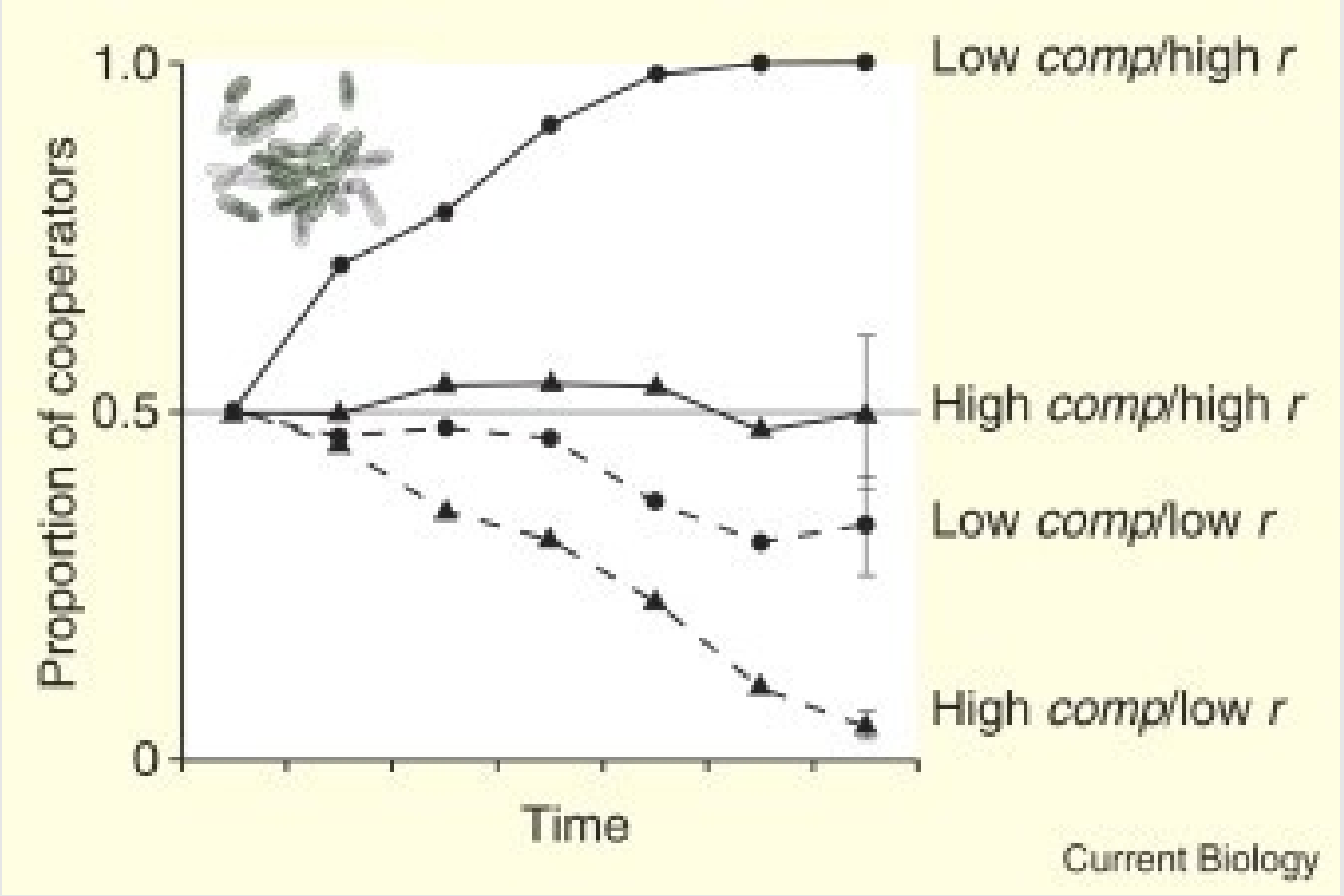
Data are taken from refs 12–16.

Patrick Abbot[1], Jun Abe[2], John Alcock[3], Samuel Alizon[4], Joao A. C. Alpedrinha[5], Malte Andersson[6], Jean-Baptiste Andre[7], Minus van Baalen[7], Francois Balloux[8], Sigal Balshine[9], Nick Barton[10], Leo W. Beukeboom[11], Jay M. Biernaskie[5], Trine Bilde[12], Gerald Borgia[13], Michael Breed[14], Sam Brown[5], Redouan Bshary[15], Angus Buckling[5], Nancy T. Burley[16], Max N. Burton-Chellew[5], Michael A. Cant[17], Michel Chapuisat[18], Eric L. Charnov[19], Tim Clutton-Brock[20], Andrew Cockburn[21], Blaine J. Cole[22], Nick Colegrave[23], Leda Cosmides[24], Iain D. Couzin[25], Jerry A. Coyne[26], Scott Creel[27], Bernard Crespi[28], Robert L. Curry[29], Sasha R. X. Dall[17], Troy Day[30], Janis L. Dickinson[31], Lee Alan Dugatkin[32], Claire El Mouden[5], Stephen T. Emlen[33], Jay Evans[34], Regis Ferriere[35], Jeremy Field[36], Susanne Foitzik[37], Kevin Foster[5], William A. Foster[20], Charles W. Fox[38], Juergen Gadau[39], Sylvain Gandon[40], Andy Gardner[5], Michael G. Gardner[41], Thomas Getty[42], Michael A. D. Goodisman[43], Alan Grafen[5], Rick Grosberg[44], Christina M. Grozinger[45], Pierre-Henri Gouyon[46], Darryl Gwynne[47], Paul H. Harvey[5], Ben J. Hatchwell[48], Jürgen Heinze[49], Heikki Helantera[50], Ken R. Helms[51], Kim Hill[52], Natalie Jiricny[5], Rufus A. Johnstone[20], Alex Kacelnik[5], E. Toby Kiers[53], Hanna Kokko[21], Jan Komdeur[54], Judith Korb[55], Daniel Kronauer[56], Rolf Kümmerli[57], Laurent Lehmann[15], Timothy A. Linksvayer[58], Sébastien Lion[59], Bruce Lyon[60], James A. R. Marshall[61], Richard McElreath[62], Yannis Michalakis[4], Richard E. Michod[63], Douglas Mock[64], Thibaud Monnin[7], Robert Montgomerie[65], Allen J. Moore[17], Ulrich G. Mueller[66], Ronald Noë[67], Samir Okasha[68], Pekka Pamilo[69], Geoff A. Parker[70], Jes S. Pedersen[58], Ido Pen[71], David Pfennig[72], David C. Queller[73], Daniel J. Rankin[74], Sarah E. Reece[23], Hudson K. Reeve[33], Max Reuter[75], Gilbert Roberts[76], Simon K. A. Robson[77], Denis Roze[78], Francois Rousset[79], Olav Rueppell[80], Joel L. Sachs[81], Lorenzo Santorelli[5], Paul Schmid-Hempel[82], Michael P. Schwarz[41], Tom Scott-Phillips[83], Janet Shellmann-Sherman[33], Paul W. Sherman[33], David M. Shuker[84], Jeff Smith[73], Joseph C. Spagna[85], Beverly Strassmann[86], Andrew V. Suarez[87], Liselotte Sundström[50], Michael Taborsky[88], Peter Taylor[30], Graham Thompson[89], John Tooby[90], Neil D. Tsutsui[91], Kazuki Tsuji[92], Stefano Turillazzi[93], Francisco Úbeda[94], Edward L. Vargo[95], Bernard Voelkl[96], Tom Wenseleers[97], Stuart A. West[5], Mary Jane West-Eberhard[98], David F. Westneat[99], Diane C. Wiernasz[22], Geoff Wild[100], Richard Wrangham[101], Andrew J. Young[17], David W. Zeh[102], Jeanne A. Zeh[102] & Andrew Zink[103]





Yagi & Hasegawa, 2012



West et al. 2007

Table 1. Correlational evidence[a] for an effect of helpers[b] on breeder fitness

Species	Correlation	*P*	Refs
Dwarf mongoose (*Helogale parvula*)	0.53	<0.001	18
Lion (*Panthera leo*)	–	<0.01[c]	10
Silverbacked jackal (*Canis mesomelas*)	0.89	<0.01	46
Golden jackal (*Canis aureus*)	0.36	<0.05	46
African wild dog (*Lycaon pictus*)	0.85[d]	0.06	35
Coyotes (*Canis latrans*)	Positive	NS[e]	47

[a]The correlation is usually between the number of helpers (or group size) and the number of infants surviving to a biologically meaningful age, such as mean age at weaning.
[b]Breeders that allosuckle other females' infants are also classified as helpers (e.g. lion).
[c]Based on an ANOVA of per capita reproductive success. Medium size groups had the highest success, suggesting an upper limit, beyond which the effects of 'helping' are outweighed by other factors.
[d]Excluding litters where no offspring survived.
[e]NS, not significant.

Jennions and MacDonald, 1994

Jennions and MacDonald, 1994

Table 3. Hypotheses to explain helping (with mammalian examples)[a]

Benefit to helper due to increased:	Proposed mechanism[b]	Mammalian examples	Refs
Survivorship	Group size improves vigilance, anti-predator behaviour or feeding success.	In evening bats (*Nycticeius humeralis*), females allosuckle unrelated pups (predominantly females), increasing colony size and future access to information about feeding sites.	22
	Helping is 'payment' for access to the natal territory.	In naked mole-rats (*Heterocephalus glaber*), there is conflict between the queen and workers over the amount of work performed, suggesting that some 'payment' is extracted (although conflict may occur for other reasons as well).	44,45
Future probability of territory holding	Larger groups expand their territories.	Naked mole-rat colonies probably divide by fission. The likelihood that the daughter colonies will succeed is probably related to size of the workforce.	44
Future probability of breeding	Helping results in coalitions between donors and recipients, and coalitions are more likely to acquire vacant territories than are lone individuals.	In dwarf mongooses (*Helogale parvula*), recipients and donors of help may disperse together. In lions (*Panthera leo*), mothers increase the likelihood of their offspring obtaining coalition partners by allosuckling. Larger coalitions are more successful (but also tend to comprise closely related males due to the increased skew in mating success).	10,18,39
	Helpers form bonds with opposite-sex breeders and are more likely to be chosen as future mates than non-helpers.	Little or no evidence for this in mammals, although Rasa has suggested that in dwarf mongooses, males that help more are more likely to be future breeders.	48
Reproductive success	Helpers gain breeding experience, which increases their own breeding success.	In many mammals, more experienced individuals have increased success in raising young. However, it remains to be shown that helpers are more successful than non-helpers when they first breed.	
	Helpers are more likely to gain the support of recipients of help as future helpers.	In dwarf mongooses, many helpers eventually breed in their natal group. Given that delayed dispersal is common, helpers will thus gain a future direct benefit. However, it remains to be shown that this benefit is greater than the initial cost of helping which requires a comparison between helpers and non-helpers.	18,31
Production of non-descendent kin	Increased survival of related breeders, hence higher reproductive success for breeders.	Breeders have higher survivorship when helpers are present in dwarf mongooses and lions.	10,18
	Increased survival of recipients of help which are related to the helper.	In most cooperatively breeding mammals, helpers and donors are closely related and substantial indirect benefits may be realized.	2,3,37,39

[a]See Ref. 3.
[b]Larger group size is assumed to be a consequence of helping.

How to assess relatedness?