



Alliances I. How large should alliances be?

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Males of a number of species form alliances with other males during competition for access to females. There is a great deal of variation in alliance sizes between and within populations. Using individual-based models in which alliances with greater net competitive ability outcompete those with less, and males can switch between alliances based on their expected success, we examined the distribution of alliance sizes that result from different assumptions about how males compete and cooperate. In many runs of the model, the distribution of alliance sizes was quite similar to the distribution of the number of males competing for a receptive female. Results were little affected by the number of males in the population, their range of competitive abilities, how expected success within alliances was allocated, whether there were costs to switching alliances, whether males were able to switch alliances with a partner, or whether a kinship structure was added to the population. However, adding a separate cost of being in larger alliances, or allowing males to leave large alliances as pairs, could reduce mean alliance size. Thus, males would be expected to form alliances except when the number of males competing for a receptive female is very few, there are substantial costs to being in an alliance, or alliances do not outcompete single males. Alliances were found to be quite dynamic except when a cost of switching alliances was introduced.

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Males of numerous mammalian species form alliances to gain access to, or defend, females (e.g. bottlenose dolphins, *Tursiops* spp.: Connor et al. 1996; lions, *Panthera leo*: Packer et al. 1991). They may also use alliances in competition for territory (cheetahs, *Acinonyx jubatus*: Caro 1994) or to increase rank (chimpanzees, *Pan troglodytes*: Goodall 1986). There are also species, such as elephants, Elephantidae, and sperm whales, *Physeter macrocephalus*, in which males do not form alliances, although there is no obvious factor preventing this (Whitehead 2003).

In some species, male alliances are found in one geographical area but not in another (e.g. mate guarding alliances in chimpanzees and bottlenose dolphins: Watts 1998; Connor et al. 2000b), and even where alliances are found, some males may continue to behave singly. Alliance sizes also vary between areas, and between alliances in the same area (e.g. Connor et al. 2000b).

To try to make some sense of all this variation, we model the adaptive advantages of different alliance sizes for

males in situations where males, alone or in alliances, move among females looking for receptive mates and where those alliances attending a receptive female compete with one another for access. We define an alliance as two or more animals behaving so that they encounter resources together and cooperate in competition for these resources with other conspecifics, or alliances of conspecifics. In the case of this paper, the resources are mating opportunities with females. The general approach follows previous models of the behaviour of roving males (Whitehead 1990, 1994), in which the interactions between receptive females and males are the result of a Poisson process. We also consider the case where the number of males competing for a female has less variance, as might result, for instance, from a situation in which animals have individually distinctive home ranges, as well as the possible influence of kinship on the distribution of alliance sizes (Packer et al. 1991). However, some situations in which males use alliances, such as during territorial disputes and to increase rank, are excluded.

This modelling is designed to examine overall emergent patterns, the distributions of alliance sizes. It contains some of the elements used by Noë (1994) to model coalition formation in savanna baboons, *Papio cynocephalus*. This model and others, such as those of Dugatkin (1998)

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and Johnstone & Dugatkin (2000), investigate the details of who forms coalitions with whom. Ours is more general.

Initial considerations suggest that there may not be a simple solution to the question, 'What is the optimum alliance size for a male?' For instance if all other males are in alliances of size four, an alliance of size five might win all contests and do better, while a single male might also do well because, although he would lose all contests, if he met an unescorted female he would not have to share her attentions with his alliance partners. If male competitive abilities vary, then optimal alliance choice might differ for low- and high-ranking males, and depend on what alliances were available for joining and were to be competed against. This suggests that optimal alliance formation for males may be dynamic in many cases.

Thus we use individual-based models (DeAngelis & Gross 1992) in which each male is represented separately in the model, and males are allowed to switch alliances. We can then see what distribution of alliance sizes results from each set of model parameters.

The models are aimed at answering the following questions: when should we expect males to form alliances; what distribution of the sizes of alliances would we expect to find; and how dynamic should alliance formation be? A companion paper (Connor & Whitehead 2005) addresses the issue of when alliances should start to form using analytical models, and is particularly aimed at questions of sex difference in alliance formation.

METHODS

Assumptions of the Model

(1) Each male, j , has a competitive ability, $c(j)$, constant through time.

(2) Males form alliances; and $C(i)$, the net competitive ability of alliance i , is the sum of the competitive abilities of its members: $C(i) = \sum c(j; j \in i)$.

(3) Of the alliances that compete for a receptive female, the alliance with the greatest net competitive ability fertilizes her. Assumptions 2 and 3 do not mean that an alliance with net competitive ability of four is twice as strong as one with net competitive ability of two, just that the alliance with greater competitive ability outcompetes the other.

(4) If alliances are of equal net competitive ability, they have an equal probability of fertilizing a receptive female.

(5) The mean number of males competing for a receptive female is m , which will itself depend upon the length of time that a female is receptive, the density of males, and the movement behaviour of both sexes.

(6) The number of alliances competing for a female is either

(a) Poisson distributed (as would result from totally random encounters); or

(b) clumped at exactly $\mu = m/(\text{mean alliance size})$ rounded up to the nearest integer (a fixed number).

(7) The success of an alliance in fertilizing females is divided among its members either:

(a) in proportion to their competitive ability; or

(b) in proportion to their squared net competitive ability, so that dominant individuals exert a proportionally greater influence on within-alliance allocation of success than during competitions between alliances; or

(c) after transactions among its members, as they join the alliance (see below).

These are approximations to likely realistic scenarios in which reproductive success within alliances is skewed towards males with more competitive ability, because they are likely to achieve more matings. In 7b the skew is greater than 7a, while in 7c there is a 'historical inertia' so that alliance members tend to maintain their relative expected reproductive success as new members join alliances.

The Model

Suppose there are n males in the population (which could be a closed 'group' of primates). Let N be the total number of alliances, and $s(i)$ be the number of more powerful alliances than i (i.e. with $C > C(i)$). The probability that none of these more powerful alliances compete for a particular female that is being attended by alliance i is, under assumption 6a (Poisson):

$$f(i) = e^{-m \times s(i)/n}$$

Alternatively, under assumption 6b (clumped):

$f(i) = 1$ if $\mu = 1$ (i.e. only one alliance attends each female, so the alliance is always the most powerful);

$f(i) = 0$ if $N - s(i) < \mu - 1$ (i.e. there are not enough alliances of equal or less competitive ability to make up the number of competitors, so there will always be a more powerful alliance present);

$f(i) = \frac{(N - s(i) - 1)C_{(\mu - 1)}}{(N - 1)C_{(\mu - 1)}}$ (i.e. the probability that when choosing $\mu - 1$ other competing alliances, none of the more powerful $s(i)$ alliances is selected).

Then, if $r(i)$ is the number of alliances that have equal competitive ability (i.e. with $C = C(i)$), the probability that alliance i fertilizes the female is, under assumption 6a (Poisson):

$$X(i) = f(i) / ((m \times r(i)/n) + 1)$$

and under assumption 6b (clumped):

$$X(i) = f(i) / ((\mu - 1) \times r(i) / (N - s(i) - 1) + 1)$$

Then the expected success of individual j in alliance i is:

$$x(j, i) = c(j) \times X(i) / \sum c(k; k \in i)$$

under assumption 7a; or

$$x(j, i) = c(j)^2 \times X(i) / \sum (c(k; k \in i))^2$$

under assumption 7b.

In these situations, males have the opportunity to join the alliance within which they gain the maximum expected success (maximum x). At each time step, a potential joiner, j , is randomly chosen, and he joins the

alliance I that maximizes $x(j,i)$, which could be his original alliance.

In the transactional models (assumption 7c), which follow the ideas of transaction theory (see reviews by Keller & Reeve 1994; Emlen 1997), the joining of an alliance by an animal is the result of a 'transaction' between the joiner and the previous members of the alliance. The male, as before, joins the alliance within which he will gain the most benefit, but this benefit is allocated by the current members of that alliance. They will benefit if they can induce him to join their alliance, but allocate him less than the net increase in expected success that results from his addition to their numbers. There are a number of systems by which such arrangements could be determined, depending on the social systems within alliances, the knowledge available to alliance members and potential joiners, and so forth (e.g. Keller & Reeve 1994; Emlen 1997; Reeve & Emlen 2000). We adopt a moderately simple perspective.

As in the nontransactional models, at each step, a potential joiner is randomly chosen. The current expected success (expected probability of fertilizing a female) of the potential joiner j is $x(j)$, and the current expected successes of all the alliances are $\{X(i)\}$. After he has joined alliance k , these become modified to $\{X'_k(i)\}$, and his expected success to $x'_k(j)$. So how much expected success should alliance k offer him as an incentive for joining? To make it worth the while of the members of alliance k :

$$x'_k(j) < X'_k(k) - X(k)$$

(i.e. they offer the joiner less than their total gain in expected success due to his joining).

Thus, the alliances that would benefit most from his membership can offer him most. There is then the potential for a bidding war to open up. We assume that the joiner joins the alliance k that has maximum net increase in expected success ($X'_k(k) - X(k)$) resulting from his joining, because it can offer him the most. We also assume that he is offered expected success $x'_k(j) = (X'_h(h) - X(h))$, where h is the alliance with the second greatest increase in expected success resulting from his joining (unless he goes solo, joining an alliance, k , with no previous members, in which case $x'_k(j) = X'_k(k)$). In other words, he is offered marginally more than it would pay any other alliance to offer him. If $x'_k(j) > x(j)$, he joins alliance k , otherwise remaining in his original alliance. If he joins alliance k , the net increase in the expected success of the alliance due to his joining ($X'_k(k) - X(k) - x'_k(j)$) is allocated to the original members in proportion to their previous individual expected success. The total expected successes of all other alliances, $X(i)$, are recalculated, and individual expected successes, $x'(j)$, allocated among alliance members in the same proportions as previously.

This transactional system is a generalization of models in which individuals only have the possibility of either joining (or staying with) a particular alliance or operating solitarily (Reeve & Emlen 2000), because in our model, a male can potentially join any alliance. It is also a generalization of models in which single dominant individuals 'bid' for an alliance with a subordinate (Reeve

1998), because the alliances that males may join can already have several members. These generalizations, which are perhaps more realistic than those of previous transactional models, are possible with the use of stochastic, individual-based models.

Running the Model

We initially assumed a population of $n = 30$ individual males. At the start of each run, males were in alliances of size one (by themselves) and then, at each step, n randomly chosen males, in turn, had an opportunity to change to the alliance that gave them the greatest expected success. For each set of assumptions and parameters, 10 runs were made with 100 steps each. The distribution of alliance sizes was noted at the end of each run, and combined to give average proportions of each alliance size at the end of the 10 runs with that combination of parameters and assumptions. Sets of runs were made with all combinations of m ranging from 0.5 to 5.0 in steps of 0.5, Poisson (assumption 6a) and clumped (assumption 6b) distributions of the number of males competing for a female, and three ranges of competitive abilities among males: (1) all males equally competitive; (2) male competitive abilities chosen randomly from a uniform distribution over the narrow range of 0.9–1.1; (3) male competitive abilities chosen randomly from a uniform distribution over the wide range of 0.4–1.6. In addition, we used each of the three methods, proportional, squared and transactional, to allocate expected reproductive success within alliances (assumptions 7a–7c).

Additional runs were made by making changes, or adding additional elements, to the set of runs that used proportional allocation of expected reproductive success within alliances and a Poisson distribution of the number of alliances competing for a female as follows.

We added a linearly increasing cost of increased alliance size equal to $0.05 \times$ alliance size (also run with clumped distribution of number of alliances competing for a female). This could, for instance, be caused by feeding competition or disease transmission.

We added a cost of changing alliances, so that males only changed alliances if the increase in expected success when competing for a female (x) was greater than 0.05. In many cases this would be equivalent to a cost of alliance choice.

We changed the number of males from $n = 30$ to $n = 10$ or $n = 60$.

We allowed members of alliances containing four or more animals to leave with a partner (run with competitive abilities in narrow (0.9–1.1) and broad (0.4–1.6) ranges and $m \geq 3.5$; also run with a clumped distribution of the number of alliances competing for a female). When a male's opportunity came to change alliances, he could stay, transfer to another alliance singly, or transfer to another alliance with any one of his current partners, choosing whichever of these options gave him the greatest expected success. This option was also run with a cost to switching alliances singly, but not in partnership.

We added a kinship structure to the population of males, and allowed switching males to choose the alliance that gave them the greatest expected inclusive fitness (sum of expected success of all males multiplied by their relatedness to the switching male; Hamilton 1964). Two relatedness patterns were used: that estimated for the 20 male bottlenose dolphins at Port Stephen, Australia by Möller et al. (2001) using microsatellite genetic analysis, and perhaps representative of a population in which litter size is one and contains few full brothers ('bottlenose pattern'); and a population of 20 males made up of six sets of full brothers (with 6, 5, 4, 2, 2, and 1 males in each set) so that relatedness between males of the same set was 0.5, and that between males of different sets was 0.0, a pattern more representative of a species with large litter sizes ('lion pattern'). This option was also run with squared allocation of resources within alliances.

RESULTS

Distribution of Alliance Sizes

The results of the simulations are summarized in Table 1, which gives the mean alliance size for each set of runs, and in Figs 1–4, which plot the distribution of alliance sizes against the mean number of males competing for each receptive female (m). Each plot summarizes the results of all runs with a particular set of parameters and assumptions, but varying m . Results assuming a Poisson distribution of the number of males are shown in Figs 1, 2, and those assuming a clumped distribution in Figs 3, 4. Each column of three plots has the same set of assumptions and parameters except that the upper plot represents runs with no variance in male competitive ability ($c = 1$), the middle plot represents runs with a narrow range ($c = 0.9$ – 1.1), and the bottom plot those with a wide range ($c = 0.4$ – 1.6) of competitive abilities.

Few alliances were much larger than the mean number of males competing for a female (m), with the mean alliance size often approximating m (Table 1), except of course when $m < 1$, when animals were almost invariably single. However, variation in the assumptions and parameters had a range of effects on the distribution of alliance sizes.

Number of males

Changing the number of males in the model from 30 to 10 or 60 had virtually no effect on the distribution of alliance sizes, so only the results of runs using 30 males are presented here.

Range of competitive abilities

The range of males' competitive abilities (c) had generally little effect on the distribution of alliance sizes (compare vertically arranged plots in Figs 1–4), with the exception of the case of the clumped distribution of males competing for a female, and changes from equal competitive abilities to some variance in competitive ability (cf. Fig. 3a, b, Fig. 4a, b). This is because of the (probably biologically spurious) effects of requiring all males to have

exactly the same competitive ability. For instance, consider the case when $m = 2$ with the clumped distribution, so that exactly two males compete for each female. Then, if all males are single, they will have a mean expected success of 0.5 as they gain access to exactly half the females for which they compete. In this situation a male who pairs with another male to form an alliance of two will also have an expected success of 0.5, as they gain access to all females for which they compete, but have to share the benefits, so there is no benefit to forming an alliance and males stay single with $m = 2$ (Fig. 3a, b). However, keeping these general circumstances, but adding some variance in male competitive abilities, the lowest-ranking male will have no expected success when alone (there is always a more powerful male competing), so it pays him to form an alliance and alliances of pairs result when $m = 2$ (Fig. 3c, d).

Allocation of expected success within alliances

There is little difference to the formation of alliances whether the expected success within alliances is allocated in proportion to the members' competitive ability or to their squared competitive ability (Table 1, Figs 1, 3). When alliances are the result of transactions concerning the distribution of expected success among alliance members, then they tend to be rather larger than in the simpler case if the number of males competing for a female is Poisson distributed (Table 1, Figs 1, 2), but rather smaller if the distribution is clumped (Table 1, Figs 3, 4), although these differences are not very substantial.

Cost of alliance size

When an additional cost of increased alliance size is added (linearly proportional to the size of the alliance), then, as would be expected, alliances tend to be smaller (Table 1, Figs 2, 4).

Cost of changing alliances

When a cost of changing alliances was added so that males only changed alliances if the increase in expected success when competing for a female (x) was greater than 0.05, the distributions of alliance sizes with narrow ($c = 0.9$ – 1.1) and wide ($c = 0.4$ – 1.6) ranges of male competitive ability were virtually identical to the runs without these costs (Table 1). In the fairly unrealistic case when all males had identical competitive abilities ($c = 1$), resulting alliances were a little smaller (Table 1).

Transferring with a partner

When males in quartets or larger alliances were permitted to transfer as pairs, the resultant distribution of alliance sizes was almost identical to those runs in which this was not possible when using a Poisson distribution for the number of males competing for a female (Table 1), although this option was frequently exercised (during 22–25% of alliance transfers when $m = 5.0$). Adding a cost to changing alliances singly, but not with a partner, slightly lowered mean alliance size at the largest values

Table 1. Mean alliance sizes from model runs with different sets of parameters and assumptions

Distribution of alliances with female	Range of competitive ability (c)	Allocation within alliances + cost?	Mean alliance sizes for different values of <i>m</i>									
			0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0
Poisson	1–1	Proportional	1.0	1.0	1.4	1.7	1.9	2.3	2.5	2.8	3.0	3.3
Poisson	0.9–1.1	Proportional	1.0	1.3	1.5	1.6	1.9	2.1	2.4	2.4	2.7	3.1
Poisson	0.4–1.6	Proportional	1.0	1.2	1.5	1.6	1.8	1.9	2.1	2.3	2.5	2.8
Poisson	1–1	Squared	1.0	1.0	1.4	1.7	1.9	2.3	2.5	2.8	3.0	3.3
Poisson	0.9–1.1	Squared	1.1	1.5	1.7	1.9	2.0	2.2	2.3	2.4	2.6	2.8
Poisson	1–1	Transactional	1.0	1.0	1.4	1.7	2.0	2.3	2.5	3.0	3.5	3.6
Poisson	0.9–1.1	Transactional	1.0	1.3	1.6	1.9	2.3	2.6	3.1	3.3	3.7	3.9
Poisson	0.4–1.6	Transactional	1.0	1.1	1.4	1.6	2.0	2.4	2.7	3.1	3.4	4.0
Poisson	1–1	Pr+SC	1.0	1.0	1.2	1.4	1.6	1.7	1.9	2.0	2.0	2.1
Poisson	0.9–1.1	Pr+SC	1.0	1.2	1.4	1.5	1.6	1.8	2.0	2.0	2.1	2.3
Poisson	0.4–1.6	Pr+SC	1.0	1.2	1.4	1.5	1.5	1.5	1.7	1.8	2.0	1.9
Poisson	1–1	Pr+CC	1.0	1.0	1.2	1.4	1.7	1.9	2.1	2.4	2.7	2.7
Poisson	0.9–1.1	Pr+CC	1.0	1.4	1.5	1.7	1.9	2.1	2.2	2.6	3.0	3.2
Poisson	0.4–1.6	Pr+CC	1.0	1.1	1.5	1.5	1.8	1.9	2.1	2.3	2.5	2.7
Poisson	0.9–1.1	Pr+PL	—	—	—	—	—	—	2.4	2.4	2.7	3.0
Poisson	0.4–1.6	Pr+PL	—	—	—	—	—	—	2.1	2.3	2.5	2.8
Poisson	0.9–1.1	Pr+PL+CC	—	—	—	—	—	—	2.3	2.5	2.6	2.6
Poisson	0.4–1.6	Pr+PL+CC	—	—	—	—	—	—	2.0	2.2	2.5	2.6
Poisson	0.9–1.1	Pr+bnd kin	1.0	1.2	1.4	1.7	1.7	1.9	2.1	2.2	2.6	2.8
Poisson	0.4–1.6	Pr+bnd kin	1.1	1.3	1.4	1.6	1.7	1.8	2.2	2.4	2.5	2.7
Poisson	0.9–1.1	Pr+lion kin	1.0	1.2	1.4	1.6	1.8	2.0	2.3	2.5	2.7	2.8
Poisson	0.4–1.6	Pr+lion kin	1.0	1.2	1.3	1.7	1.9	2.0	2.2	2.5	2.4	2.9
Poisson	0.9–1.1	Sq+bnd kin	1.1	1.2	1.4	1.6	1.8	1.9	2.2	2.4	2.7	2.9
Poisson	0.4–1.6	Sq+bnd kin	1.1	1.2	1.5	1.6	1.7	2.0	2.2	2.4	2.7	2.7
Poisson	0.9–1.1	Sq+lion kin	1.0	1.3	1.3	1.6	1.8	2.0	2.2	2.4	2.5	3.0
Poisson	0.4–1.6	Sq+lion kin	1.0	1.2	1.4	1.7	1.9	1.9	2.3	2.3	2.6	2.8
Clumped	1–1	Proportional	1.0	1.0	1.0	1.0	2.6	3.0	3.4	3.8	3.9	4.5
Clumped	0.9–1.1	Proportional	1.0	1.0	1.7	2.0	2.6	3.0	3.4	3.8	4.3	5.0
Clumped	0.4–1.6	Proportional	1.0	1.0	1.7	2.1	2.6	3.1	3.4	3.9	4.4	5.1
Clumped	1–1	Squared	1.0	1.0	1.0	1.0	2.6	3.0	3.4	3.8	3.9	4.5
Clumped	0.9–1.1	Squared	1.0	1.0	1.7	2.0	2.6	3.0	3.4	3.8	4.3	5.0
Clumped	0.4–1.6	Squared	1.0	1.0	1.8	2.4	2.9	3.4	3.7	4.2	4.7	5.3
Clumped	1–1	Transactional	1.0	1.0	1.6	1.9	2.0	2.0	3.2	3.0	4.1	2.9
Clumped	0.9–1.1	Transactional	1.0	1.0	1.6	2.3	2.8	3.3	3.3	4.1	3.7	4.9
Clumped	0.4–1.6	Transactional	1.0	1.0	1.7	2.1	2.7	3.1	3.5	3.6	2.8	3.4
Clumped	1–1	Pr+SC	1.0	1.0	1.0	1.0	1.4	2.4	2.5	2.7	2.7	2.9
Clumped	0.9–1.1	Pr+SC	1.0	1.0	1.6	1.7	1.7	2.0	2.1	2.5	2.6	3.1
Clumped	0.4–1.6	Pr+SC	1.0	1.0	1.7	2.0	2.6	2.4	2.1	2.3	2.6	2.5
Clumped	0.9–1.1	Pr+PL	—	—	—	—	—	—	2.4	2.5	2.6	2.8
Clumped	0.4–1.6	Pr+PL	—	—	—	—	—	—	2.5	2.5	2.6	2.7
Clumped	0.9–1.1	Pr+PL+CC	—	—	—	—	—	—	2.3	2.4	2.7	2.8
Clumped	0.4–1.6	Pr+PL+CC	—	—	—	—	—	—	2.4	2.4	2.6	2.8

m = the mean number of males competing for a receptive female; Pr = proportional allocation of resources within alliances; Sq = squared allocation of resources within alliances; SC = additional costs of alliance size; CC = additional cost of changing alliances; PL = males allowed to leave alliances as pairs or singly; PL + CC = males allowed to leave alliances as pairs or singly, but an additional cost was added only when they left singly; bnd kin = males choosing their alliance based upon the maximum increase in inclusive fitness, and the kinship structure of the male bottlenose dolphins (bottlenose pattern) in the study of Möller et al. (2001); lion kin = males choosing their alliance based upon the maximum increase in inclusive fitness, and a kinship structure based upon sets of full brothers (lion pattern).

of *m* (Table 1). This might be expected, as the incentive for the larger alliances to split is increased. With the clumped distribution of competing males, the possibility of transferring with a partner reduced mean alliance sizes, with alliances often containing two to three males when *m* = 3.5–5 (Table 1). This too is not unexpected. If, say *m* = 4 and animals were forming foursomes with just one foursome competing for each female, then the highest-ranking pair of any quartet could split off and increase their expected success (as they would have access to almost the same number of females, but only have to share her attentions between two rather than

four). This would then trigger other splittings of foursomes into two pairs.

Kinship structure

Adding kinship structures to the population of competing males had no discernible effect on the distribution of alliance sizes (Table 1), whether we used the milder version representative of populations with single litter size (bottlenose pattern) or the version with sets of full brothers (lion pattern). In both cases, males tended to form alliances with related males (as indicated by a higher mean relatedness within alliances than between alliances) if

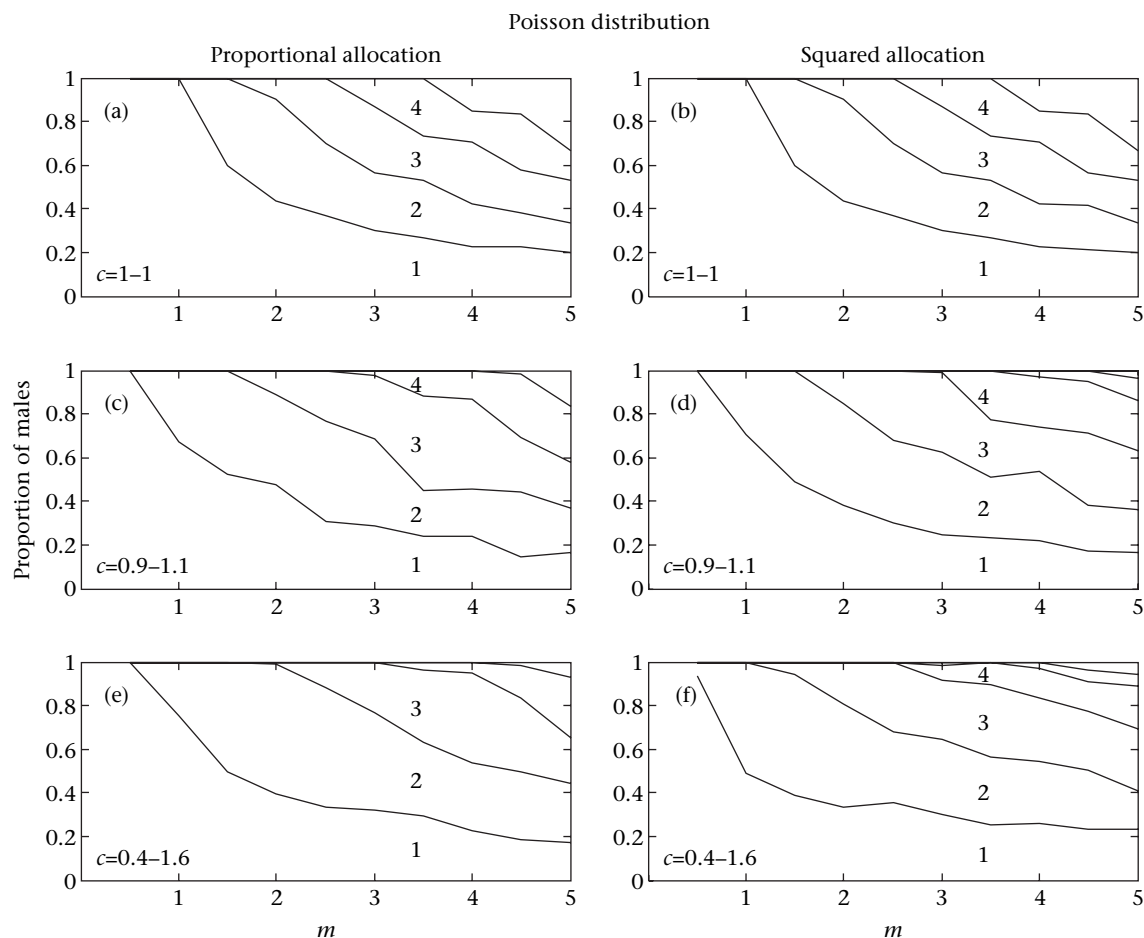


Figure 1. Results of runs of individual-based models of alliance formation showing the distribution of alliance sizes as a function of the mean number of males competing for each receptive female (m), when the number of alliances competing for each female is Poisson distributed and males' competitive ability is equal ($c = 1$; a, b), varies within a small range ($c = 0.9-1.1$; c, d) and varies over a wide range ($c = 0.4-1.6$; e, f). Reproductive success of an alliance is allocated among members in proportion to their competitive abilities (a, c, e), and in proportion to their competitive abilities squared (b, d, f).

$m > \sim 2.5$, but at lower values of m , relatedness patterns were inconsistent between runs, and many males were solitary.

Distribution of number of alliances competing for a female

Changing the distribution of alliances competing for a female from Poisson to clumped, while it has rather little effect on mean alliance sizes (Table 1), greatly affects the distribution of these alliances: when the number of alliances competing for a female is clumped, so is the distribution of alliance sizes (indicated by nearly vertical contours in Figs 3, 4), whereas when the number of competing alliances varies, so do the alliance sizes (indicated by the more horizontal contours in Figs 1, 2). This is as might be expected. When numbers of alliances competing for a female vary considerably, then a single male has opportunities even when in a population of larger and more powerful alliances: the cases when he encounters a female by himself. When the number of alliances competing for a female is fixed, he will almost always be outcompeted and so would do better to join one

of the larger alliances. In the case of proportional or squared allocation of resources within alliances, small differences in male competitive abilities and no additional cost of larger alliances, then the distributions of alliance sizes can be quite closely approximated by the following simple rules.

(1) If the number of alliances competing for a female is Poisson distributed, then roughly equal numbers of males are in all alliance sizes from 1 (single males) to m (the mean number of males competing for a female).

(2) If the number of alliances competing for a female is clumped, then most males will be in alliances of size m (the mean number of males competing for each female), unless males can leave larger alliances as pairs.

Dynamics of Alliance Formation

If all males have equal competitive abilities ($c = 1$), with proportional allocation of expected success within alliances, the distribution of alliance sizes stabilizes rapidly (within one or two time steps) to the equilibrium distribution. However, when the competitive abilities of males

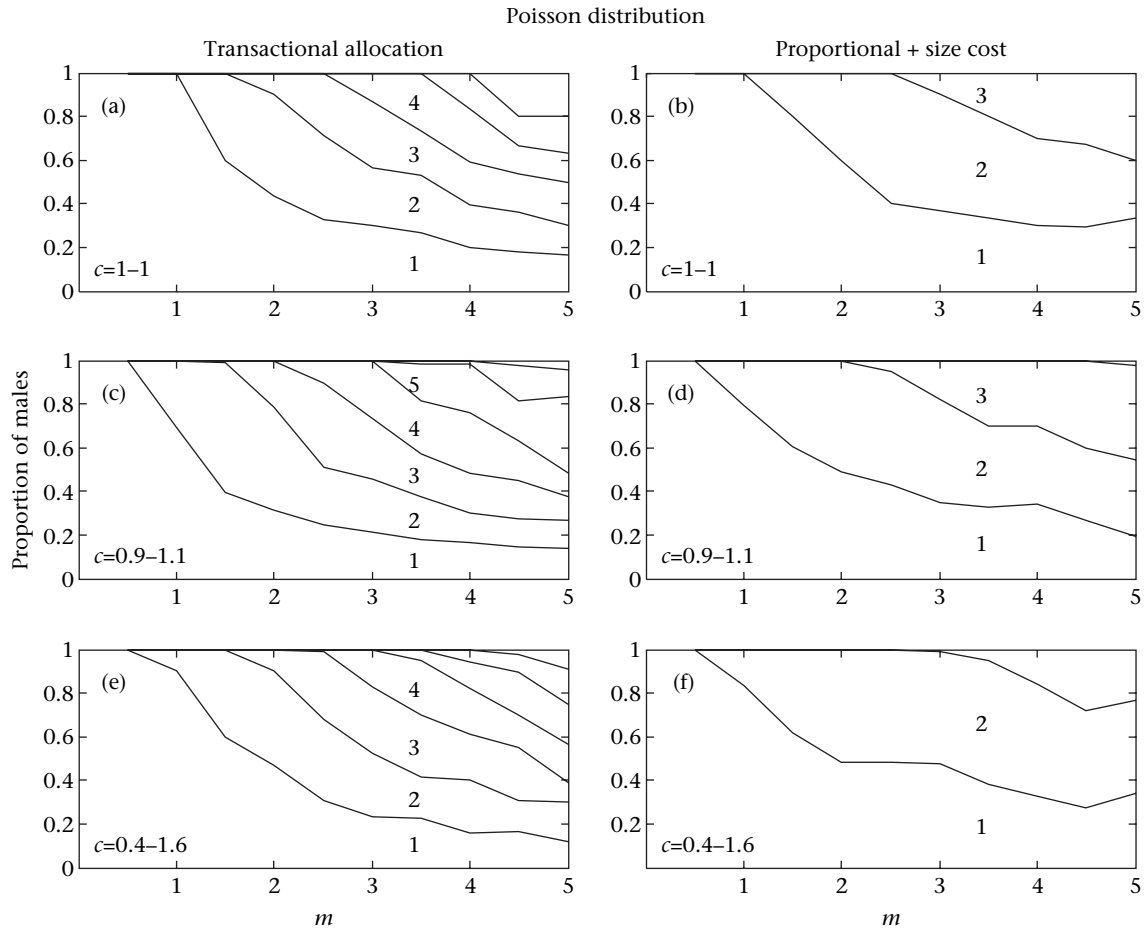


Figure 2. Results of runs of individual-based models of alliance formation showing the distribution of alliance sizes as a function of the mean number of males competing for each receptive female (m), when the number of alliances competing for each female is Poisson distributed and males' competitive ability is equal ($c = 1$; a, b), varies within a small range ($c = 0.9-1.1$; c, d) and varies over a wide range ($c = 0.4-1.6$; e, f). Reproductive success of an alliance is allocated among members using a transactional model (a, c, e), and in proportion to their competitive abilities with an added linearly increasing cost of alliance size (b, d, f).

vary, alliances are much more dynamic: individuals use 77–86% of their opportunities to switch alliances ($m \geq 2$, excluding the first two steps, with both $c = 0.9-1.1$ and $c = 0.4-1.6$) compared with 0–35% when competitive abilities of all males are equal ($c = 1$). When competitive abilities vary, the distribution of alliance sizes also varies considerably through time (Fig. 5). However, when we added a cost of changing alliances to the models, with the mean expected success increasing by at least 0.05 before a male could switch, alliances became less dynamic, with individuals using only 17–48% of their opportunities to switch alliances ($m \geq 2$, excluding the first two steps, with both $c = 0.9-1.1$ and $c = 0.4-1.6$).

DISCUSSION

We used individual-based, stochastic models to look at equilibrium distributions of alliance sizes, as these are particularly flexible, and thus can deal with quite complex models (DeAngelis & Gross 1992), such as the transactional systems explored here. At the start of this investigation we examined the distribution of alliance

sizes using game-theoretic optimality models with males of equal competitive ability: finding distributions of alliance sizes in which all males had equal fitness, and no movement by any male increased his fitness. The results were identical to those from the individual-based models with equal male competitive ability, and are not presented here.

The results of running the individual-based models give preliminary answers to the questions posed in the Introduction.

(1) When should we expect to find roving males form alliances? The results of the simulations, summarized in Table 1 and Figs 1–4, as well as a separate paper using analytical models to investigate the conditions under which alliances should start to form (Connor & Whitehead, 2005), identify only one circumstance in which no males should form alliances: when the rate at which receptive females encounter males is low, with the average number of males per receptive period being less than one. Yet males do not form alliances in many species and populations. An average of at least one male probably competes for each female in most. Therefore, there must

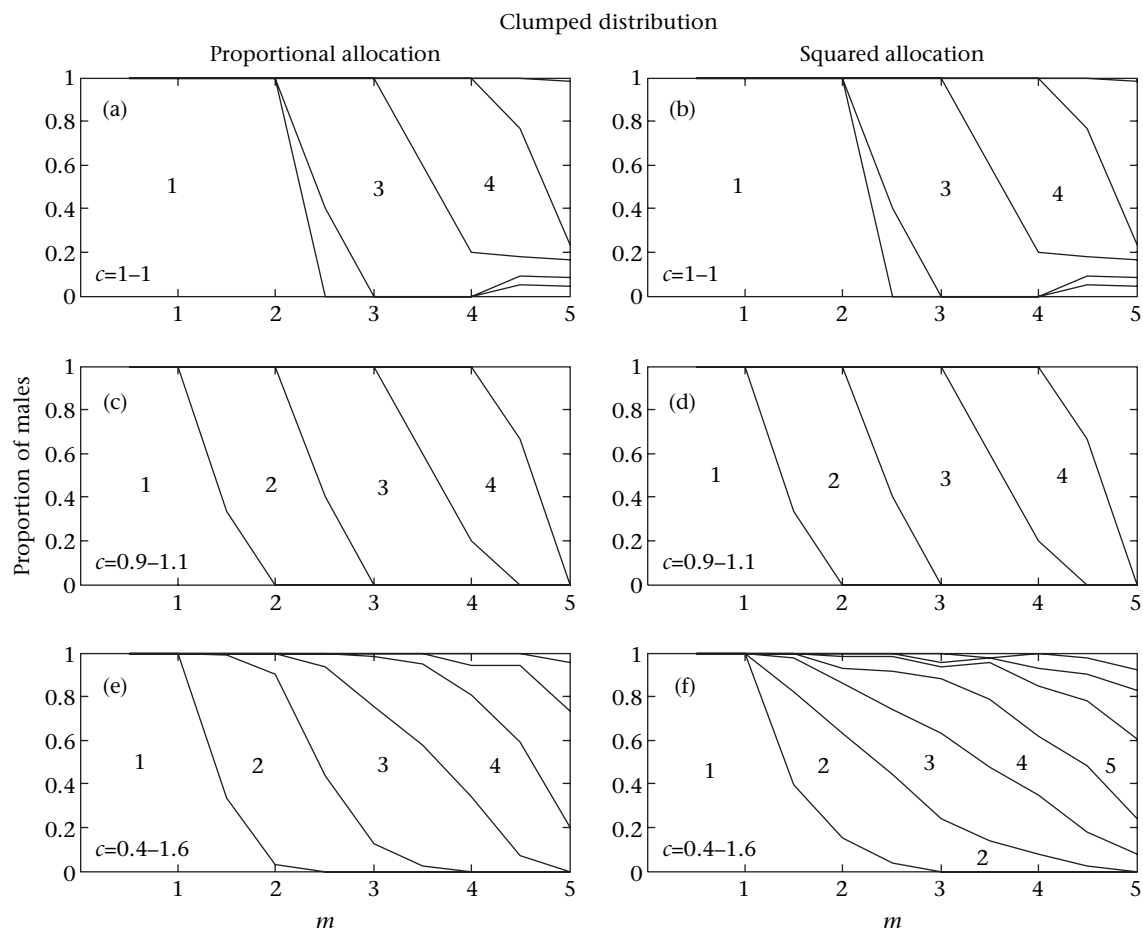


Figure 3. Results of runs of individual-based models of alliance formation showing the distribution of alliance sizes as a function of the mean number of males competing for each receptive female (m), when the number of alliances competing for each female is clumped and males' competitive ability is equal ($c = 1$; a, b), varies within a small range ($c = 0.9-1.1$; c, d) and varies over a wide range ($c = 0.4-1.6$; e, f). Reproductive success of an alliance is allocated among members in proportion to their competitive abilities (a, c, e), and in proportion to their competitive abilities squared (b, d, f).

be factors acting against the formation of alliances that are not included in our models. There are a number of possibilities. First, the models show that an additional cost of larger alliances, for instance, due to feeding competition or disease, reduces mean alliance size (Table 1). If this cost were increased sufficiently, then only single males would be found. Second, the benefits of alliance formation may be lacking; simply, alliances need not necessarily outcompete single males. There are several reasons for this. Large discrepancies in resource holding power among males could render alliances ineffective (e.g. Noë 1994), as could a lack of effective male dominance over females combined with female choice for particular males. Alliances would also be disfavoured if females mate promiscuously (perhaps with cryptic choice), favouring sperm competition between males rather than female defence strategies. Finally, the success of alliances may also depend on the ability of individuals to manoeuvre around a solitary more powerful opponent, and this may be greater when contests are conducted in three dimensions (water) rather than two (land) indicating a greater likelihood of marine alliances (Connor 2001).

(2) What distribution of the sizes of alliances would we expect to find? The simulations suggest that, under many circumstances, the distribution of alliance sizes should roughly approximate the distribution of the number of males competing for each female. Thus, if males rove randomly among females, producing a roughly Poisson distribution of the number competing for any female, then males should be found in a range of alliance sizes from singletons up to roughly the mean number of males competing for a female. In contrast, when the number of alliances competing for a female is more clumped, for instance, when the number of alliances whose home ranges overlap that of a female is fairly fixed, or alliances avoid females who are already attended by a number of others, then the alliance sizes may also be more clumped, with, for instance, most males being members of trios. In fact, the number three shows up frequently in male alliances. In bottlenose dolphins and cheetahs it seems to be a maximum size for alliances consorting with females (Caro 1994; Connor 2001), and also for male lion alliances containing a nonrelative (Packer et al. 1991). When there is a clumped distribution of males competing

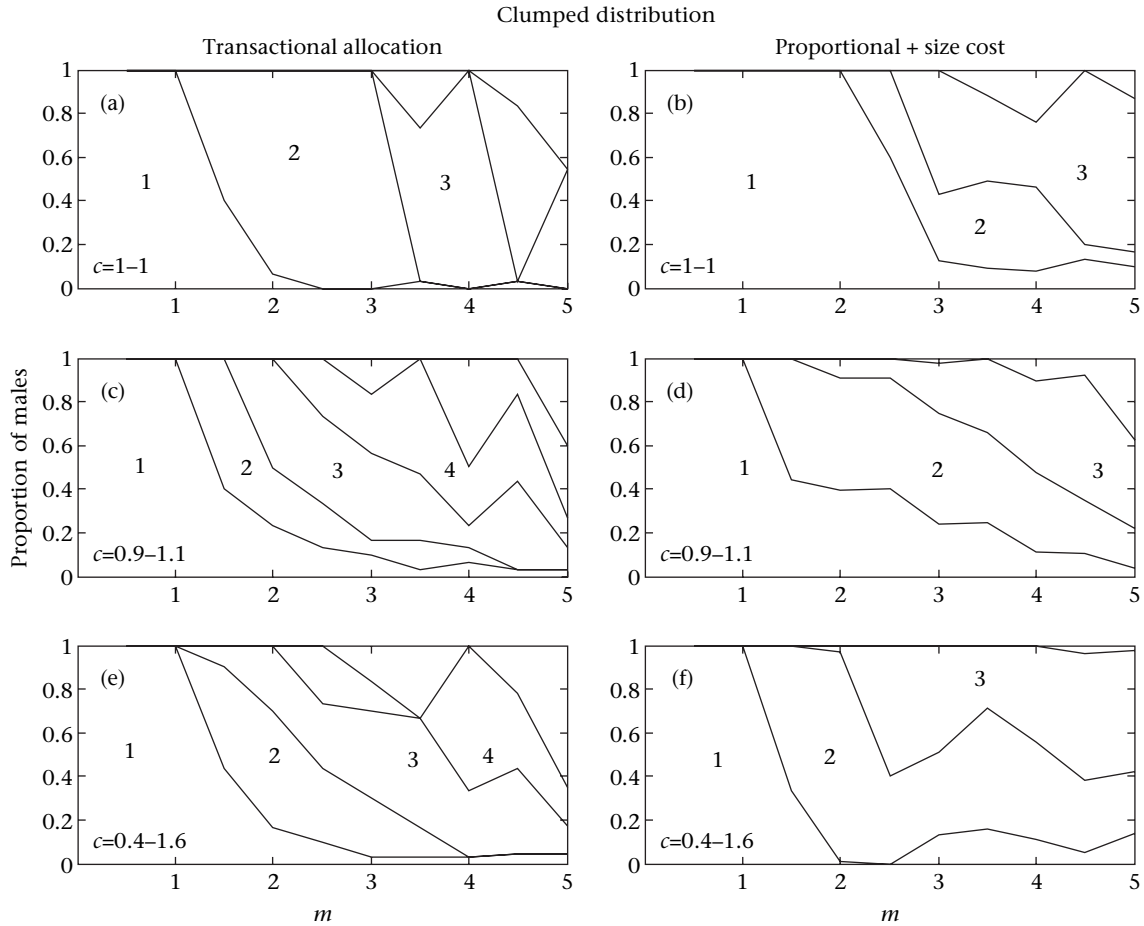


Figure 4. Results of runs of individual-based models of alliance formation showing the distribution of alliance sizes as a function of the mean number of males competing for each receptive female (m), when the number of alliances competing for each female is clumped and males' competitive ability is equal ($c = 1$; a, b), varies within a small range ($c = 0.9-1.1$; c, d) and varies over a wide range ($c = 0.4-1.6$; e, f). Reproductive success of an alliance is allocated among members using a transactional model (a, c, e), and in proportion to their competitive abilities with an added linearly increasing cost of alliance size (b, d, f).

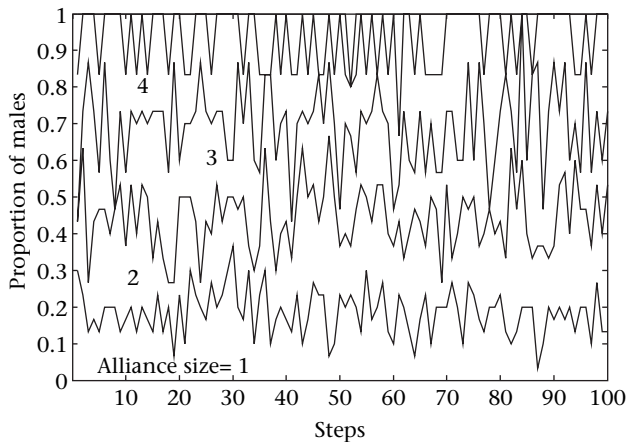


Figure 5. Variability in the distribution of alliance sizes through 100 time steps, with proportional allocation of resources within alliances and high variance in male competitive ability ($c = 0.4-1.6$) and the mean number of males competing for a female is five.

for a female, and males are able to leave larger alliances as pairs, realistic assumptions in many circumstances, then alliances of two or three become particularly common (Table 1).

In many terrestrial species, males may rove for a time but then establish and defend territories. Thus, Packer et al. (1991) discovered that, in lions, larger than normal (> 3) alliances occur when there are numbers of highly related males. The large alliances of male lions have great variance in reproductive success, containing low-ranking animals that are virtually nonreproductive (Packer et al. 1991). In our model of roving males, such animals would do better to join smaller alliances of nonrelatives or operate alone. In the territorial world of lions, however, the habitat can become saturated, favouring a strategy of helping relatives for low-ranking animals. This option is closed to male lions without close kin.

(3) How dynamic should alliance formation be? Except in the, probably unrealistic, case in which all males are of equal competitive ability, the models predict that alliances should be dynamic with males frequently switching alliances to improve their expected reproductive success, although introducing a cost of changing alliances (in,

for instance, choosing a suitable new alliance, sorting dominance relationships or learning to work together) slows this down somewhat.

The results of our models are strongly affected by m , the mean number of males competing for a female. Thus, factors that impact m predictably will strongly affect the likelihood of males forming alliances, and the sizes of the alliances. Three such factors are the time duration for which the female is available, the density of females and the operational sex ratio (OSR). m will be higher, and predicted alliance sizes larger, when females are receptive for long periods, when they are close together, so males spend relatively little time searching, when females are detectable at long range, when one or both sexes are highly mobile, and when the number of males who can potentially mate at any time is much greater than the number of females. Thus, our results support Connor et al.'s (2000a) suggestion that differences in alliance formation between bottlenose dolphin populations might be explained by differences in the rates at which males interact in competition over females. Much variation in the OSR may be explained by variation in the interbirth interval, which generally increases with body size in mammals (Harvey & Read 1988). In species where males rove and cannot effectively monopolize more than one female, we might compare species that vary significantly in interbirth interval. We can thus predict that, other factors being equal, alliances will be less common in porpoises, which have interbirth intervals of 1–2 years, versus delphinids, with intervals of 3 or more years (reviewed in Whitehead & Mann 2000).

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References

- Caro, T. M. 1994. *Cheetahs of the Serengeti Plains*. Chicago: University of Chicago Press.
- Connor, R. C. 2001. Social relationships in a big-brained aquatic mammal. In: *Model Systems in Behavioral Ecology* (Ed. by L. A. Dugatkin), pp. 408–432. Princeton, New Jersey: Princeton University Press.
- Connor, R. C. & Whitehead, H. 2005. Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, **69**, 127–132.
- Connor, R. C., Richards, A. F., Smolker, R. A. & Mann, J. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*, **133**, 37–69.
- Connor, R. C., Read, A. J. & Wrangham, R. 2000a. Male reproductive strategies and social bonds. In: *Cetacean Societies* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 247–269. Chicago: University of Chicago Press.
- Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. 2000b. The bottlenose dolphin. Social relationships in a fission–fusion society. In: *Cetacean Societies* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 91–126. Chicago: University of Chicago Press.
- DeAngelis, D. L. & Gross, L. J. *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. New York: Chapman & Hall.
- Dugatkin, L. A. 1998. A model of coalition formation in animals. *Proceedings of the Royal Society of London, Series B*, **265**, 2121–2125.
- Emlen, S. T. 1997. Predicting family dynamics in social vertebrates. In: *Behavioral Ecology*. 4th edn (Ed. by J. R. Krebs & N. B. Davies), pp. 228–253. Oxford: Blackwell.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.
- Harvey, P. H. & Read, A. F. 1988. How and why do mammalian life histories vary? In: *Evolution of Life Histories: Pattern and Process from Mammals* (Ed. by M. S. Boyce), pp. 213–232. New Haven, Connecticut: Yale University Press.
- Johnstone, R. A. & Dugatkin, L. A. 2000. Coalition formation in animals and the nature of winner and loser effects. *Proceedings of the Royal Society of London, Series B*, **267**, 17–21.
- Keller, L. & Reeve, H. K. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, **9**, 98–102.
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G. & Krützen, M. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London, Series B*, **268**, 1941–1947.
- Noë, R. 1994. A model of coalition formation among male baboons with fighting ability as the crucial parameter. *Animal Behaviour*, **47**, 211–213.
- Packer, C., Gilbert, D. A., Pusey, A. E. & O'Brien, S. J. 1991. A molecular genetic analysis of kinship and co-operation in African lions. *Nature*, **351**, 562–565.
- Reeve, H. K. 1998. Game theory, reproductive skew, and nepotism. In: *Game Theory and Animal Behavior* (Ed. by L. Dugatkin & H. K. Reeve), pp. 118–145. Oxford: Oxford University Press.
- Reeve, H. K. & Emlen, S. T. 2000. Reproductive skew and group size: an N-person staying incentive model. *Behavioral Ecology*, **6**, 640–647.
- Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, **44**, 43–55.
- Whitehead, H. 1990. Rules for roving males. *Journal of Theoretical Biology*, **145**, 355–368.
- Whitehead, H. 1994. Delayed competitive breeding in roving males. *Journal of Theoretical Biology*, **166**, 127–133.
- Whitehead, H. 2003. *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.
- Whitehead, H. & Mann, J. 2000. Female reproductive strategies of cetaceans. In: *Cetacean Societies* (Ed. by J. Mann, R. Connor, P. L. Tyack & H. Whitehead), pp. 219–246. Chicago: University of Chicago Press.