



Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies

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Ecological explanations of sex-specific patterns of bond formation have focused primarily on resource defence and predation. Resource defence models of alliance formation had not, until recently, explicitly considered encounter rates between competing individuals. Here we present a general model for alliance formation in fission–fusion societies based upon the rates at which individuals encounter each other in competition for resources. Our model applies to both territorial and nonterritorial species. Given the prevalence of stronger bonds among female mammals, the occurrence of prominent male–male alliances in phylogenetically distant species with a fission–fusion grouping pattern is striking (e.g. chimpanzees, *Pan troglodytes*; bottlenose dolphins, *Tursiops* spp.). In our model, a sex difference in alliance formation emerges, even when encounter rates are the same for each sex, if there is a sex difference in the duration of resource defence. Thus, if the primary resources for which males compete (oestrous females) are defended for longer periods than the primary resources for which females compete (food), male alliance formation is expected to occur at lower encounter rates than female alliances.

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The ecological basis for sex-specific patterns of alliance formation has been explored extensively, especially for primate societies, beginning with Wrangham's (1980) resource defence model for female-bonded primates. We define an alliance of conspecifics as two or more animals behaving so that they encounter resources together and cooperate in competition for these resources with other conspecifics. Until recently, resource defence models of alliance formation have not explicitly considered encounter rates among potential competitors. A recent verbal model incorporated encounter rates to explain population differences in bottlenose dolphin *Tursiops aduncus*, male alliances (Connor et al. 2000a, b). There remains a need for a general encounter rate model that: (1) addresses sex differences in alliance formation and (2) applies to both

territorial and nonterritorial species. Here we offer a formal model, based on encounter rates during resource utilization, which accomplishes this task.

Encounter Rates and Alliance Formation in Male Bottlenose Dolphins

Bottlenose dolphins in Shark Bay, Western Australia, live in a classic fission–fusion society with marked sex differences in alliance formation (Connor et al. 2000b). The strongest alliances are between males who form alliances of two to three individuals that, in some cases, endure for years. However, the pattern of male–male associations differs between populations. In Sarasota, Florida, U.S.A., males are found alone or in pairs, while in the Moray Firth, Scotland, there is no evidence that males form strong alliances at all. Connor et al. (2000a, b) suggested that these differences might be due to the different rates at which males encounter each other in competition over oestrous females. Such differences might be due to differences in population density, operational sex ratio or the distance at which males detect oestrous females. As encounter rates increase, the cost of sharing copulations

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with alliance partners is outweighed by the benefits of cooperative female defence.

Connor et al.'s (2000a, b) model provides an explanation for why males might form alliances in one population and not in another but it also focuses attention on another problem. If the encounter rate is high enough to favour male alliance formation in a population, why do females not form alliances as well?

A GENERAL MODEL: RATES OF ENCOUNTER DURING RESOURCE UTILIZATION

Our basic model focuses on rates of encounter during resource utilization and assumes other encounters are not competitive, so they are not incorporated into the model. The model generates sex differences in alliance formation if there are sufficient differences in encounter rate or resource handling time; that is, even if overall encounter rates are identical, sex differences in resource handling time can favour the formation of alliances in one sex but not the other. A model based on territorial interactions would assume that all encounters are competitive. Our model can be extended to situations that are intermediate between territoriality and nonterritoriality. Territoriality thus emerges as a special case of a more general model.

The Model: Nonterritorial Species

Suppose there are no alliances and an animal gains a proportion α of its resources in competition with other animals, and $1 - \alpha$ noncompetitively. If an animal wins a proportion λ of its contests, then the rate of resource acquisition, if operating alone, $S(1)$, is proportional to

$$S(1) = \alpha \times \lambda + (1 - \alpha).$$

At what point will individuals begin to form alliances? If an animal forms an alliance with one or more colleagues a proportion k of the time, then it will gain at a rate proportional to

$$S(2) = k \times (\alpha \times \lambda' + (1 - \alpha)) \times q + (1 - k) \times (\alpha \times \lambda + (1 - \alpha)),$$

where q (≤ 1) represents the sharing of resources among alliance members, and λ' ($\geq \lambda$) represents the increased competitiveness of the alliance. Alliance formation is favoured if

$$S(2) > S(1)$$

or

$$k \times (\alpha \times \lambda' + (1 - \alpha)) \times q + (1 - k) \times (\alpha \times \lambda + (1 - \alpha)) > \alpha \times \lambda + (1 - \alpha)$$

In the case where animals are not too different in their competitive abilities, this is generally most likely to be true for the least competitive individual, because $\lambda = 0$ (i.e. no expected competitive success alone), and $\lambda' > 0$ (substantial expected competitive success in an alliance).

Thus, the lowest-ranking individual should form an alliance if

$$k \times (\alpha \times \lambda' + (1 - \alpha)) \times q + (1 - k) \times (1 - \alpha) > (1 - \alpha).$$

We can get a lower bound on α in which alliance formation is favoured, because $\lambda' \leq 1$ (i.e. λ' is a proportion) and $q \leq 0.5$ (i.e. the lowest-ranking member of an alliance will probably get less than half the alliance's resources). We set the parameters at values that are optimally favourable for a subordinate forming an alliance; the new alliance wins all of its contests ($\lambda' = 1$) and the subordinate gets fully half the spoils ($q = 0.5$). Thus, when

$$\begin{aligned} 0.5k + (1 - k) \times (1 - \alpha) &> (1 - \alpha), \text{ then} \\ 0.5 &> (1 - \alpha) \text{ and} \\ \alpha &> 0.5. \end{aligned} \quad (1)$$

Therefore, alliance formation can only be favoured if at least half the resources are obtained competitively. If parameter values were less ideal, so that the subordinate was awarded less than half the spoils and the alliance was not always victorious, α would have to be even higher to favour alliance formation. This result can be used to consider more specific situations.

Sex Differences in Alliance Formation

Consider a nonterritorial species in which members of the same sex encounter each other in the presence of a resource, for example, male bottlenose dolphins with an oestrous female or females with a fish.

We allow two parameters to vary between sexes: resource utilization time, τ , and the overall rate at which resources are attended by potential competitors, μ per unit time. Then the mean number of individuals present and competing for a resource during its utilization is about $m = \mu \times \tau$. (It might be somewhat less than this if later arriving animals have little will or ability to compete.) μ will itself depend upon the density of resources, resource behaviour (e.g. movement, patterns of availability) and the searching behaviour of the animals.

Suppose that the distribution of the number of alliances encountering a particular resource is Poisson (i.e. that the competition of any alliance for a resource is unaffected by the competition of others). Then

$$\alpha = (1 - e^{-m})$$

and, as $\alpha > 0.5$, alliances can only be favoured if

$$\begin{aligned} (1 - e^{-m}) &> 0.5, \text{ so} \\ m &> 0.693. \end{aligned}$$

So, in this scenario, alliances start to form when the average number of alliances or individuals competing for resources is greater than 0.693. Alliances generally start to form at higher m values than this (because the least competitive animal will not receive half the expected success of the alliance and/or the alliance may not outcompete the most powerful single animals).

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