



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).

These predictions assume a Poisson model with animals randomly encountering the resource. An alternative and realistic perspective is that the distribution of animals competing for the resource is more clumped, for instance, if animals are less likely to compete for a resource when many others are already competing and more likely to compete when one or few animals are already competing. In the extreme, the number of alliances competing for a resource is fixed at an integer m . In this case, $\alpha = 0$ if $m = 1$ and $\alpha = 1$ if $m \geq 2$. Thus, with these highly clumped distributions, alliances start to form when the number of animals competing for a resource increases from one to two.

This suggests that, as long as the results of competition between alliances are based upon net competitive ability, alliances should start to form when the mean number of animals competing for a resource increases above about 0.7–2.0. More complex individual-based simulations, which incorporate additional features such as costs of changing alliances, intrinsic costs of large alliances and transactional allocation of resources within alliances confirm this general result (Whitehead & Connor 2005).

The mean number of animals competing for a resource, m , is approximately the resource utilization time, τ , multiplied by the rate at which resources are encountered by animals, μ . Thus, a doubling of resource utilization time or a doubling of encounter rate is equally likely to push m over the threshold at which alliances are favoured. Here we see how the model has utility for understanding sex differences in alliance formation. If males and females are found at the same density and travel at the same velocities, a difference in resource utilization time will favour alliances in one sex but not the other. Similarly, if resource utilization time is constant, a sex difference in encounter rates could favour alliances in one sex but not the other.

Our model thus extends the logic of the explanation for interpopulation differences in male–male alliances in bottlenose dolphins offered by Connor et al. (2000b) to sex differences within populations. The key lies in the rate at which members of each sex utilize the resource that is most important to them: oestrous females for males and food for females. Odontocetes typically consume individual prey items quickly, whereas oestrous females must be defended for longer periods (Connor et al. 1996). Thus, we can understand why alliance formation will be favoured in males at a lower population density than in females. Even if increasing population density results in similar increases in the overall encounter rates for each sex, there will be a disproportionately greater increase in the rate of competitive encounters in the sex that has the longest resource utilization time.

Territoriality and the Resource Utilization Model

A key consequence of territoriality is that winning contests, regardless of whether resources are present, increases territorial control and thus reduces the proportion of resources for which individuals compete. Thus,

α , the proportion of resources for which individuals compete, declines as λ , the proportion of contests won, increases. This creates a negative feedback on alliance formation: forming an alliance increases the proportion of contests won (λ), thereby lowering the proportion of resources for which individuals compete (α), and thus decreasing the chance that alliance formation pays (equation 1). This is a complex situation, but, luckily, if we are just concerned about the cut-off at which alliances start to form, things are simpler.

Alliance formation is likely to be the most profitable for the lowest-ranking animal (see above). When alone, this animal wins no contests ($\lambda = 0$) and so α is not reduced by territorial considerations. The expected success of the single lowest-ranking animal is $S(1) = (1 - \alpha)$, as in the nonterritorial model. In an alliance, α is likely to be reduced by the territorial effect, to α' , so

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

But, just as in the nonterritorial case, $\lambda' \leq 1$, and $q \leq 0.5$, so

$$S(2) \leq 0.5k + (1 - k) \times (1 - \alpha).$$

As in the nonterritorial case (equation 1), alliance formation only pays if $S(1) > S(2)$ and so $\alpha > 0.5$. However, in this case, α , the proportion of resources for which individuals compete, refers only to the situation of the lowest-ranking individual who has no territorial success when alone.

Thus, as in the case of the nonterritorial model, the lowest-ranking individual should consider forming an alliance when at least half of its resources are subject to competition.

DISCUSSION

We have presented the first general model of sex differences in alliance formation in fission–fusion societies, irrespective of the degree of territoriality. While other authors have not explicitly invoked an encounter rate model that distinguishes competitive from noncompetitive interactions, a number have suggested that density differences might help to explain differences between species or populations in alliance formation. McNab (1963, page 138) pointed out that ‘the establishment of elaborate social behaviour within a population depends on a relatively high population density’. The link to our model is obvious; other factors being equal, increases in population density will increase the rate at which individuals encounter each other. First we review these earlier arguments, all based on territorial animals, then we explore the potential of our model to explain patterns of sex-specific alliance formation in nonterritorial mammals.

Territorial Species

Three arguments have been advanced relating population density (and thus encounter rates) to alliance formation in territorial species: high densities of females drive

the evolution of both male alliances and female alliances, and high densities of males favour the formation of male–male alliances.

Male density and male–male alliances

Density-based explanations have been offered to explain why male territory holders in some species may accept satellite males (e.g. waterbuck, *Kobus ellipsiprymnus*: Wirtz 1981, 1982). Caro (1994) observed an increase in territory holding by single male cheetahs relative to alliances over the latter half of a multiyear study. He attributed this shift to a reduction in litter size, possibly caused by an influx of predators. With reduced competition (=encounter rate) from alliances, single males were more often able to establish territories.

Female density and male–male alliances

In his review of group living in felids, Caro (1994) found that males are not more likely to live in groups in species where females have overlapping ranges or live at high densities. However, in two of three species in his sample, in which female ranges overlapped and population density was above the median, male groups were found, suggesting that this combination of factors favours, but does not ensure, male alliance formation.

Female density and female–female alliances

Packer (1986) suggested that a combination of high density, large prey and open habitat would favour female grouping because large carcasses last for some time, and are more visible in open habitats where they are more likely to be seen by rival females. Under these conditions, found only in lions, females are better off sharing with relatives than risking losing the prey to unrelated rivals. Caro (1989, 1994, page 330) argued that density is not a critical factor but that abundant large prey size is. Most felids live in areas where large prey (defined as one to two times the size of the cat) are scarce. Caro (1994) points out that several felids live at high population densities but do not form groups, whereas lions form groups of the same size at both low and high densities. Caro's conclusions about the importance of large prey anticipates the key notion in our model that it is not merely encounter rates with conspecifics that are critical, but encounter rates with conspecific competitors during resource utilization (large prey that take more time to consume than small prey).

Primate social groups

Socioecological models of sex differences in primate bonds have focused less on encounter rates than on the value of defending encountered resources. What can be called the 'standard primate model' is based on the general observation that one sex disperses and the other is philopatric and that females have priority in the 'philopatry decision' (Wrangham 1980; van Schaik 1989; van Hoof & van Schaik 1994). If interference competition for resources favours female alliances, then males will be forced to disperse. In one model, female alliances are

favoured by resource competition between groups (Wrangham 1980); while in another, predation favours group formation, and female alliances derive from within-group resource competition (van Schaik 1989; see also Sterck et al. 1997). If group defence of resources is not profitable, then selection on female philopatry is relaxed and the philopatry option switches to males. In this case, if male philopatry is profitable, females will be forced to emigrate.

The classic primate fission–fusion societies of chimpanzees and spider monkeys (*Ateles* spp.) show strong male–male bonds and philopatry. Alliance formation and male mating strategies are better understood in chimpanzees. Male chimpanzees form alliances primarily to increase rank. High-ranking males often attempt to guard females nearing ovulation. Mate guarding is usually performed by solitary males, but in one unusually large community (Ngogo), high-ranking pairs of males cooperate to guard females (Watts 1998), a behaviour Watts related to the larger number of competitors at Ngogo. Another mating strategy in chimpanzees is the formation of consortships between individual males and females (Tutin 1979). During chimpanzee consortships, females are led and kept away from other males in the community, effectively reducing the encounter rate. Because chimpanzee consortships include aggressive herding (Goodall 1986), they are similar to the consortships by male dolphin alliances (Connor et al. 1992), so why do male chimpanzees not use alliances to consort females as male dolphins do? Individual male chimpanzees may be able to conceal consortships more effectively than dolphins, whose greater dependence on vocalizations (e.g. during foraging) would make it more difficult to hide from other males who, with relatively low costs of locomotion compared with chimpanzees (Connor 2000), can more easily afford to seek them out.

There are other factors that devalue male alliances in fission–fusion societies. Striking differences in resource holding power (e.g. Noë 1994) and female choice can render alliances ineffective, and alliances may be more effective in conflicts that occur in three dimensions compared with two (Connor et al. 2000a; Whitehead & Connor 2005).

In two prominent terrestrial fission–fusion societies, female choice is suggested to trump male strategies that might include alliance formation. The New World murre monkey *Brachyteles arachnoides* shows male philopatry and female dispersal. Male murre have hostile between-group relations, but unlike chimpanzees, relatively egalitarian within-group relations (Strier 1994). Strier suggested that differential male mating success is determined by the choice of females who are not dominated by males and who actively initiate and avoid copulations.

Spotted hyaenas, *Crocuta crocuta*, also live in fission–fusion societies and individual males and females apparently form consortships (Szykman et al. 2001). Females are dominant to males so these associations might reflect choice by males, females or both (Szykman et al. 2001). Male alliances are likely to be ineffective against females or female alliances in this species.

Nonterritorial Species

Teasing apart the roles of encounter rate and resource utilization time is difficult for fission–fusion species such as chimpanzees that show pronounced sex differences in travel rates (Wrangham 2000) as well as resource utilization time (and the value of resource defence). However, this is possible with a different type of primate fission–fusion society. Hamadryas, *Papio hamadryas*, and gelada baboons, *Theropithecus gelada*, both live in nonterritorial fission–fusion societies in which the ‘fission’ and ‘fusion’ occurs between stable bisexual subunits (one male with one or more adult females: Dunbar 1983, 1986; Stammbach 1987) rather than individuals. The contrast between these two species illustrates the potential of our model to explain patterns of alliance formation in species that are not territorial and for which the two sexes do not differ appreciably in encounter rates. Unlike most other fission–fusion primate species, when bands of hamadryas and gelada baboons fission into subunits during daily foraging trips, the one-male units remain intact, thus males and females have basically equivalent ranging patterns. It follows that encounter rates alone cannot account for the patterns of sex-specific bonds found in the two species: hamadryas show stronger alliances between males whereas gelada are female-bonded. The standard primate model would lead us to expect that gelada females feed on defensible food patches whereas hamadryas do not, which would favour female alliances in geladas and permit male–male alliances in hamadryas. If true, the different social structures of hamadryas and gelada baboons is explicable by the model presented here, in combination with the primate ‘rule’ that one sex must emigrate and females have priority in dispersal decisions.

The Odontocetes and Alliance Formation

Odontocetes are of special interest for models of alliance formation because they may be relatively unencumbered by two conceptual issues that have constrained models of alliance formation in primates. The first is the ‘primacy of females’ in primate models, which itself derives from the requirement that one sex or the other must disperse from their natal group to avoid inbreeding. Natal geographical philopatry by both sexes may be widespread in odontocetes; the important distinction being the degree to which social philopatry is maintained (Connor et al. 2000a). In the extreme case of ‘resident’ killer whales, *Orcinus orca*, both sexes remain with their mother into adulthood (Baird 2000).

The second issue, frequently contested among primatologists, is the relative importance of within- versus between-group interactions in structuring social alliances. This distinction may be of little or no importance for some fission–fusion odontocete societies that do not live in closed or semiclosed bisexual groups. In Shark Bay, for example, there is no evidence of a closed or semiclosed bisexual group among the hundreds of bottlenose dolphins, *Tursiops aduncus*. Rather, there appears to be a more or less

continuous social network along the 50 km of coast where the population has been studied (Connor et al. 2000b).

Given that odontocetes generally feed on single food items that are quickly consumed (or patches of food that are soon dispersed) relative to female oestrous periods, our model predicts that alliances among males will be more widespread than alliances among females in odontocete fission–fusion societies. While male alliances are well documented only in bottlenose dolphins, evidence of strong male–male associations and alliances are emerging in a number of species in which territoriality appears not to be a factor (reviewed in Connor et al. 2000a).

One species that does not form male alliances is the sperm whale, *Physeter macrocephalus*. Female choice for the largest males in this species may preclude male alliance formation by smaller individuals (Whitehead 2003). A similar explanation might apply to the African elephant, *Loxodonta africana*, whose social system is strikingly similar to that of the sperm whale (Weilgart et al. 1996).

The results of our model suggest that differences in encounter rate or resource utilization time may produce sex differences in alliance formation. However, males and females may differ in other ways that impact alliance formation, such as the ability of an alliance to defeat a higher-ranking individual, the value of doing so, and the cost of alliance formation. Future empirical studies should attempt to assess the relative importance of these factors in different populations and species.

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