Negotiating a stable solution for vigilance behaviour

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Commentary

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Most, if not all, animals are highly responsive organisms that are capable of adjusting their behaviour during the course of their interactions with others [1]. This observation may seem obvious, yet evolutionary theory has traditionally modelled cooperation and conflict as a 'sealed bid', assuming that both parties decide on a fixed strategy without any knowledge of the other's behaviour [2]. Recently, theoreticians have started to consider the so-called negotiation rules animals use to respond to, and potentially manipulate, each other in real time, but so far this work has focused exclusively on family conflicts over offspring care [3]. A new study by Sirot [4] applies this method for the first time to group foraging, exploring how the threat of predation may drive patterns of vigilance behaviour.

Anti-predator vigilance is key to survival in many animal species and clearly falls within the scope of negotiation models because individuals living in groups are known to adjust their vigilance patterns depending on the behaviour of their companions [5,6]. A striking illustration of this is the sentinel behaviour seen in some social vertebrates, where group members suspend foraging, adopt a raised position and look out for danger [7–9]. Sentinel bouts within groups are tightly coordinated, with individuals typically taking turns and there rarely being more than one or two engaging in this activity at any one time [8,9]. In such situations, vigilance decisions are anything but a sealed bid.

Recognizing the high degree of responsiveness in these interactions, Sirot modelled vigilance in a pair of foraging animals that continuously monitor each other's behaviour. At any given time, each animal could choose either to feed or to scan for predators, but in contrast to previous models they could flexibly adjust this decision depending on the current behaviour of their companion. Sirot then varied the mode of predatory attack, to see how this influenced the evolutionarily stable vigilance pattern of the foragers. If predators randomly target either one of the pair, both benefit equally from the other's vigilance behaviour, which favours separate bouts of scanning with no overlap ('coordination'). By contrast, if predators direct their attacks towards a non-vigilant animal when its companion is vigilant, it is too risky to be the only one feeding. In this situation, when one animal starts scanning its companion immediately follows suit, resulting in long bouts of scanning together interspersed with long bouts of feeding together ('synchronization').

The model therefore predicts that the extent to which vigilance behaviour is coordinated in a group depends on how predation risk is spread across those individuals that are vigilant and those that are not (see [10,11]). In general, one might expect that actively scanning individuals are in less danger, given that they will normally be the first to spot an approaching predator. According to Sirot's model, this differential risk forces groupmates to copy each other's vigilance, generating a contagious spread of vigilance that seems consistent with evidence from a variety of mammal and bird species [4]. Interestingly though, the opposite pattern (coordination) of vigilance seen in some cooperative vertebrates suggests that in these systems the risk might be spread more evenly between sentinels and non-sentinels (but see [7,10]).

Sirot's study provides an important first step in building behavioural interactions into models of animal vigilance, but also raises some intriguing issues for future consideration. For example, what are the exact processes that allow groups of foragers to 'negotiate' their levels of vigilance? The model assumes that individuals are constantly aware of the activities of their companions. While it is now apparent that foraging does not necessarily prevent individuals from gathering some visual information about predators and/or conspecifics, it is likely that scanning is compromised to some extent [12]. In many social species, individuals use continuous quiet vocalizations to stay in contact with one another, both when foraging [13,14] and when being vigilant [9,15]. There is growing evidence that these 'close' calls can be used by other group members to assess the need for vigilance [16–18], although it remains unclear precisely how much information is directly conveyed about the caller's current behaviour. Moreover, while both empirical and theoretical work (including the new model by Sirot) has so far tended to focus on pairs of foragers, there is the possibility that individuals are simultaneously negotiating with multiple groupmates [17]; this added complexity needs addressing for a full understanding of how negotiation and cooperation are linked.

It is also known that hunger levels have a critical influence on vigilance decisions [7,8]. A rich body of theory on optimal state-dependent behaviour shows that investment in foraging and vigilance must strike a delicate balance between minimizing the twin risks of predation and starvation [19]. To keep things simple, Sirot's negotiation model ignored the risk of starvation, focusing only on the goal of maximizing the amount of time spent feeding while avoiding being killed by a predator. An obvious next step would be to track the hunger levels of the foragers and allow their vigilance levels to depend on this. Such state dependence is likely to reduce the benefit of the long, synchronized bouts of vigilance predicted by Sirot's model.

Combining these ideas, there is the potential that negotiations over vigilance may be considerably more complex than the passive process considered by Sirot, in which individuals monitor and respond to the current behaviour of their foraging companions. Recent work has demonstrated

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that groupmates actively communicate with each other about their energetic state and thus their need to forage, and that such information influences their decisions about individual vigilance levels [17]. This raises the intriguing possibility that the signalling of future intentions may play a crucial role in negotiations over vigilance in group-living animals. Sirot's model sets the stage for a new body of theoretical work exploring how the rich potential for information exchange between interacting animals may influence their patterns of behaviour.

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