Exploring Knowledge Dissemination as a Selective Force for Aggregation: Preliminary Results from Modelling Wild Asiatic Asses

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Aggregation is a costly strategy for any species, because individuals must compete for resources such as food, shelter and mating opportunities. Hamilton (1971) provides the best-established explanation of aggregation, which is security. For reasons ranging from increased vigilance to cooperative mobbing of aggressors, living in a group can provide benefits as well as costs.

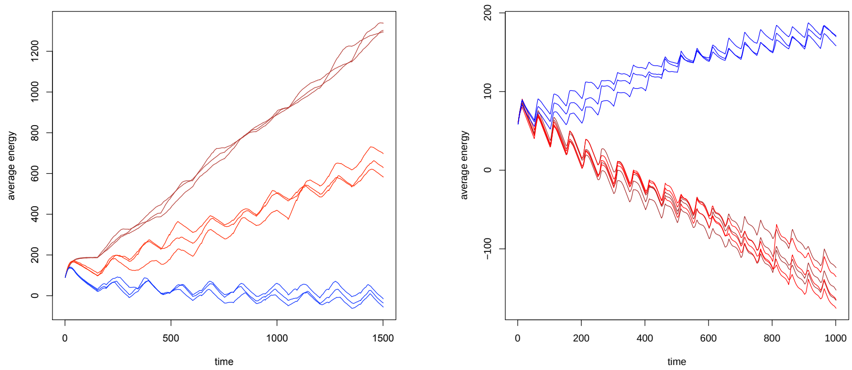
But security may not be the only explanation for aggregation. Aggregation can also occur by chance rather than choice, as individuals may come to the same location simply be seeking the same resources, and it may not be worth effort of driving others away from these.

One strong indication that there may be more than one selective pressure for aggregation is when a group can be described at multiple levels of hierarchy. A fission-fusion (FF) society is characterised this way. FF societies consist of both *parties* — relatively small groups travel together, and a *community* or troop from which parties are drawn. Party size may well be determined by security, but in some species it is not clear that the entire community ever aggregates at the same time.

Lehmann et al. (2007) suggest that *knowledge exchange* may be one selective pressure for community-level aggregation in fission-fusion species where party composition is flexible. This is an attractive theory in species like great apes where some communities are known to posses behaviour not seen in other communities. Such 'culture' is particularly obvious when the communities are completely isolated from each other by geographic features such as rivers, but otherwise live in identical ecosystems (Whiten et al., 1999).

Here we present new preliminary results concerning aggregation in Asiatic wild asses *Equus hemionus*. In examining available data simulating multiple hypotheses on their social behaviour, we have identified potential new costs as well as benefits. Our collaboration began because Kaczensky and colleagues were looking for a mechanism that could explain the exceptional ability of Asiatic asses to exploit unexpected resource bonanzas in the form of transient oases caused by rainfall in the Gobi desert.

Mongolian or Asiatic wild asses are primarily adapted to arid desert steppes and semi-deserts of the Gobi. They can venture well away from water sources and are able to exploit resources that vary in space and time. Asiatic wild asses also live in



(a) Individual Strategy Dominating (b) Territorial Strategy Dominating

Figure 1: Figure showing the utility of three different strategies under two different conditions; see text for details. Each line represents the average energy for a fixed number of asses in one simulation, there are three runs per strategy per condition. Brown lines are simulated asses pursuing individual strategies, any aggregation is coincidental. Red lines indicate asses that chase other asses that seem to be moving with intent. Blue lines represent asses that also chase, but when sufficiently well-fed become territorial. In both figures, the X axis is time in simulation cycles, the Y is the energy (see text).

fission-fusion societies. This may be due to the unreliable nature of the distribution of their required resources (Kaczensky et al., 2008). The species is reported to be particularly adept at discovering good foraging opportunities following rain.

We have developed a series of agent-based models. Each can be seen as embodying a different hypothesis of social and ecological dynamics for this species (Bryson et al., 2007). The simulations are standard spatial models with animals moving across a very large torus. An oasis is created at regular time intervals but random locations. After some exploration of possible model types, we decided to evaluate our models by the average energy held by every individual in a population of fixed size. Energy increases when the agents eat, and increases more when they eat food that's recently been rained on. It decreases as they move, and decreases more if they move quickly. During this first, exploratory stage, the only simulation details which are even roughly grounded in real data is the visual and motion range of the agents.

We have been able to build models showing any of three strategies might be "most adaptive", depending on the true nature of the ecological context and the metabolic costs. There are three agent strategies. First, an independent strategy relies on free-range grazing and the accidental individual discovery of the temporary oases. If asses see an oasis, they will run to it immediately. The second strategy is like the first, accept that agents chase conspecifics that they see running. The third strategy is like the second, except that when not chasing other asses and when relatively well fed, the asses form networks of regularly-spaced 'territorial' asses. In the wild, some male asses temporarily defend featureless and resourceless areas of desert, standing at regular intervals within view of the next territorial male (Rubenstein et al., 2007). Non-territorial males, females and juveniles all move in parties through these territories.

We began running experiments comparing the utility of our three strategies after it became visually apparent that more asses converged on the transient oases in the second condition than the first, and in the third than in the second. Nevertheless, success at *finding* the oases did not necessarily indicate that doing so was adaptive.

The figure shows the outcome of two sets of experiments. Note that since the simulations are not metabolically-grounded, there is no significance to whether average energy is positive or negative, only in the relative amounts of energy between strategies. In the first simulation (figure 1(a)), the costs of aggregation far outweigh the benefit of finding the oases, so the individual strategy dominates. These costs include the energy of running to the oases before it disappears, and being near many other asses after the oases dries up. For a second condition (not shown) we decreased the amount of food in the ordinary desert and increased the energy benefit of recently rained-on food. This results in equivalent energy levels for all three strategies.However, this similarity masks both increased benefit and costs in the social strategies. In particular, chasing other asses becomes expensive when the oases are fully exploited — animals may chase each other in circles or across the desert.

For the third condition (figure 1(b)), we refined the method programmed for establishing territories, and also set limits on how long the asses were willing to run. The advantage of the territorial strategy is probably exaggerated since it comes not only from the extra information gained from having a regular network of territorial animals, but also because territoriality provides an alternative behaviour that helps terminate unnecessary chasing.

Without data, theory tells us nothing about reality, and simulations are only theory. We must now turn back to observations to examine the metabolic advantages and costs of the asses' behaviours. Only then will we know whether we have found a species that supports the hypothesis that some aggregation occurs due to social communication of knowledge.

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