

Visual Communication and Social Structure – The Group Predation of Lions

Alwyn Barry and Hugo Dalrymple-Smith

University of Bath

Department of Computer Science

Claverton Down, Bath, UK.

a.m.barry@bath.ac.uk

Abstract

[Creel, 1997] in a study of african hunting dogs suggested that, where the maximisation of net energy gain from hunting requires cooperation, cooperative hunting becomes an important part of the sociality of the hunting dogs. When considering Lion cooperative hunting [Scheel and Packer, 1991] suggested, in contrast, that Lions do not form groups to increase the intake of food for the group but for the individual, implying that cooperative behaviour in hunting has very little impact on the formation of prides. In using simulation to investigate the role of visual location in the group hunting behaviour of Lions it is shown that a minimal communication simulation can be derived if the dominance of pride members is taken into account. We conclude that agreed dominance permits the reduction of visual cues required to coordinate complex cooperative simulated behaviour.

1 Introduction

Cross-disciplinary engagement between behavioural biology and computer science has generated valuable insights and new directions for both biological and computer science research [Boden, 1996], such as in the understanding of flock formation [Reynolds, 1987] or fish schooling [Tu and Terzopoulos, 1994]. For example in [Zaera *et al.*, 1996] biologists had proposed several different hypotheses regarding schooling behaviour, but these presented contradictory opinions about the reasons for schooling behaviour. Artificial life models of fish behaviour and schooling have provided new tools with which to evaluate the plausibility of biological hypotheses, and have provided computer scientists with valuable models of behaviour and control.

Considerable progress has been made in the modelling of aspects of behaviour in animals with relatively limited cognitive abilities (such as ants, spiders and fish). The modelling of higher animals is more problematic. With lower animals limited cognitive capabilities rule out consideration of complex models. The discovery of a simple mechanism to describe a behaviour in a higher animal does not rule out the use of a more complex mechanism by the animal, and the cognitive capabilities of the animal provide a large search space for

plausible models. Nonetheless, the search for simple models of complex behaviour in higher animals is important not only for the Behavioural Biologist but also for the Computer Scientist. For example, in robotic control it is more likely that few robots with considerable computing power will be available. Behavioural algorithms based on the behaviour of tens or hundreds of simple animals will not necessarily scale down in useful ways with orders of magnitude fewer robots. In contrast, behavioural models derived from the smaller groups of higher animals may be a better fit.

[McFarland, 1994] distinguishes between ‘eusocial’ and ‘cooperative’¹ behaviour where the latter is a behaviour selected intentionally by selfish agents to maximise individual utility in contrast to the former which is innate (genetically encoded). Whilst many large predators are lone hunters, some demonstrate selective behaviour – utilising lone hunting in certain environmental situations and small group cooperative hunting in others. However, there has been debate over when seemingly cooperative behaviours can be considered cooperative or are merely an extension of the selfish behaviour of agents forced by circumstance to be part of a group.

In their study of the hunting behaviour of Serengeti lions, [Scheel and Packer, 1991] noted that when cooperative behaviour does happen it appears more likely to occur in situations when the prey is larger, more difficult to kill or in long distance hunts. Using success of the hunt as a criteria, they suggest that lions do not form groups to increase the intake of food for the group but for the individual, implying that cooperative hunting does not exist but rather that opportunistic hunting is being displayed. The observation that amongst the lions there are some which take a less active role in hunting, a behaviour they define “cheating”, is used to support this hypothesis.

From a study of African hunting dogs [Creel, 1996; 1997] have suggested that cooperative hunting should not be judged on the success of the hunts, but on the food intake per day against the energy spent during the hunt. Using this criteria, [Creel, 1997] was able to show that the packs formed by the African hunting dogs were optimal for pack sizes of 8 – 11. They suggest that cooperative hunting plays an important part

¹[Cao *et al.*, 1994] defines “cooperative” behaviour as follows: ‘a [multi-agent] system displays cooperative behaviour if, due to some underlying mechanism, there is an increase in the total utility of the system’.

in the sociality of african hunting dogs. [Creel, 1997] extends this argument to prides of lions. [Griffin, 1984] suggests that there must be some form of conscious decision making behind the hunting behaviour of the lions. Although this opinion is largely based upon on a single observation, he argues that it is difficult to believe that with the success that cooperative hunting brings the lions are not at some level aware of the benefits of planning such attacks. In contrast [Scheel and Packer, 1991] seem to hold the position that cooperative hunting has little impact on pride formation. [Schaller, 1972; Stander, 1991] do not commit to such an opinion. Stander notes that the question exists, and that the research simply shows the benefits of cooperative hunting. Schaller is satisfied with a statement of two possible positions, either that pre-planned cooperative hunting is taking place or that the lions are simply making use of the opportunities afforded by the presence of other lions.

We have conducted a preliminary investigation of these claims using a simplified simulation of group predation. From a review of lions' group hunting behaviour (see section 2) we hypothesised that the use of attraction / repulsion dynamics would lead to emergent group dynamics that simulates this behaviour. Our results demonstrate that to achieve the observed behaviour in simulation the addition of a dominance hierarchy between the simulated predators is required.

2 The Predators and their Prey

There are surprisingly few academic sources on the hunting methods used by lions, but those that are available provide a useful level of detail. The research available focuses on two different lion societies; from the Etosha National Park [Stander, 1991] and from the Serengeti National Park [Schaller, 1972].

2.1 Prey

Lions from the Etosha National Park were observed to have hunted and killed 16 different species of prey. Three species accounted for 83% of the hunting activity ... springbok, zebra and wildebeest. The Serengeti lions were mainly observed hunting warthog, zebra, gazelle wildebeest and buffalo. This slight difference has an effect on the cooperative behaviour of the lions at these locations.

There are two primary elements in the relationship between lions and their prey that affect hunting behaviour – size and speed. Schaller, in discussing the speed relationship between a lion and its prey, notes that of all prey only the warthog has a lower speed than the lion, whilst the buffalo can achieve the same speed in escape as a lion. Schaller identifies the lion's top speed as 48 to 59 km/hr while Thomson's gazelle average 70 to 80 km/hr and the wildebeest 80 km/hr. Thus, when hunting the majority of prey, lions cannot rely on speed alone to achieve their goal. Interestingly, the buffalo does not need to use speed because a buffalo can cause a large amount of damage to a lion.

In general the prey's reaction to the presence of lions is not one of fear and panic. Schaller observed that the majority of the time when the lions were not hunting the prey was prepared to keep a reasonable distance from the lions and keep

them under observation. The response to being attacked by a lion is for the herd to simply scatter, which can cause general confusion to lions. Schaller observed that sometimes the lions were unable to select an individual from the scattering herd resulting in the failure to achieve a kill. Lions use sight as the primary sense during hunting, although sound and smell may contribute to the initial location of prey in the Etosha national park where the biomass of potential prey is considerably lower. Schaller shows that group hunts that occur up-wind from the prey have about 33% greater chance of success than those that occur down-wind from the prey.

Since lions are at a disadvantage when chasing most of their prey, they make use of the cover available to increase their chance of success. Schaller's observations of Serengeti lions shows that, although the majority of kills are in the open, prey are generally killed near areas that offer the greatest cover. The Etosha National Park is a flat arid plain with much less cover than the Serengeti plains, and yet even here the short grass is essential for the lions, for without some element of cover the lions have very little chance of gaining the advantage of surprise or the ability to ambush possible prey. The majority of hunts take place at night so that greater cover can be gained by use of the darkness.

2.2 The Predators

There are a number of factors that determine the use of group hunting in different prides of lions. For example, the environment that the lions live in has an effect. On the Serengeti plains, solitary hunts occur for approximately 48% of hunts, whilst in the Etosha National Park solitary hunting only occurred in 1% of hunts. This disparity is attributed to the difference in the environment and type of prey available in the two areas. The Etosha National Park is a vast semi-arid plain with little natural cover whilst the Serengeti National Park is a rich habitat. Faced with a reduction in cover those lions from Etosha seem to be forced into a situation where cooperative hunting provided a greater kill rate. The type of prey also has an effect on cooperative hunting. Over over 80% of the diet of the lions of the Etosha national park is made up of large and/or fleet-footed prey. Serengeti lions have a greater variety of prey that includes animals, such as the warthog (the greatest occurrence of solitary hunting occurring in the Serengeti was upon the small warthog). In the Serengeti National Park, those prey which are hard to catch are hunted using group methods.

The available studies of the methods and tactics of group hunting adopted by lions give a similar basic plan of the hunting process. It starts when the group spots the prey, sometimes initiated by a single lion identifying the prey and looking at it, to which the other lions respond by looking in the same direction – the only clear form of “communication” evidenced in the hunting process. The group fans out, with certain lions stalking at a greater distance to encircle the prey. The encircling lions launch the *attack*, seemingly to drive the prey towards the other lions who *ambush* the prey from their cover position. A failed ambush may cause a *rush* after the prey for a short distance.

Stander's observations showed that, in general, lions followed approximately the same patterns when hunting. He

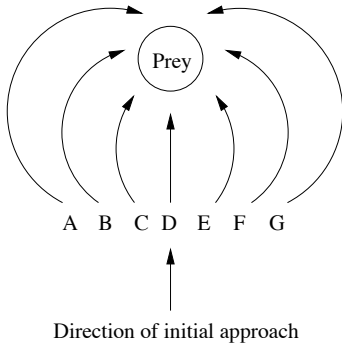


Figure 1: A schematic of generalised lion hunting behaviour.

divided the lions into seven different stalking roles, shown in Fig. 1, grouping these roles into Left Wing, Centre and Right Wing positions. Although no lions were exclusively fixed to any position and most hunts involve fewer lions than positions, Stander noted that the lions did seem to have a preference for certain positions, with ‘wings’ having a preferred angle of attack be it left or right. These positions would seem to be determined by the physical nature of the individual lions. The lions were measured and weighed, and it was discovered that the ‘centres’ were generally bigger, heavier and older than the ‘wings’. In general the ‘centre’ lions are more capable of assuming different positions, but his research also showed that in situations when the lions were hunting in their preferred roles the success of the group increased by 9%. The hunting success rate also increased with the size of the group – the greater the size of the group the greater chance the lions had of assuming their preferred positions. Recent video evidence would suggest that the younger lions approach the prey faster than the older lions, possibly due to lack of experience of the younger lions or due to the younger lions needing to move further to get into position.

In general Stander observed that the average distance that the ‘wings’ stalk would be about 320m. Once the lions are in position, the breakdown of the roles in the hunt occurs with the ‘wings’ initiating the majority of the attacks. The ‘centres’ are more likely to be involved in ‘ambushes’ than the ‘wings’. If the prey is not caught in an ‘ambush’ it would be the ‘wings’ that would become involved in the ‘rush’. The ‘rush’ part of the hunt is only a short distance – Schaller observed that in general the lions could maintain a fast run for only a few hundreds meters before having to stop and pant.

3 Hypothesis

Although the details of the behaviour are known, the mechanism by which such behaviour is coordinated (if it is at all) is unknown. [Stander, 1991] suggests that the ‘wings’ could keep, as a 3rd point, the prey on an imaginary straight line between them, enabling the Lions to ‘model’ the locations of the other lions. Unfortunately, it is difficult to conceive that the Lions should need to locate lions on the other side of the encirclement in order to coordinate behaviour, since this would raise the possibility that the stalking lions could be spotted by the prey. However, Stander’s proposals were the seeds of an

alternative possible mechanism.

[Reynolds, 1987] used links of attraction and repulsion to produce the emergent group behaviour seen in flocking and herding, since applied to many other forms of emergent behaviour. We hypothesised that, through initial repulsion from the prey during stalking representing the need to remain unseen, attraction to the prey during stalking representing the need to get within range of the prey to attack, repulsion from other lions representing the need to obtain coverage of the prey’s lines of escape, and attraction to other lions representing the need to close off possible escape between lions, an encircling behaviour during stalking would be seen. This hypothesised mechanism would require sight of the two neighbouring lions and the prey alone. Thus, no global knowledge and minimal local knowledge is required, and the behaviour would be an emergent property of the interaction of the agents involved.

The initial algorithm using this simple attraction-repulsion approach can be expressed simplistically as follows:

```
repeat until movement > chaseDistance or kill:
  if noticedMovement(sight) or lions.tracking < 2:
    lions = closestTwoLions
    if prey == null: prey = closestPrey
    if lions.tracking != 0 or prey != null:
      attractOrRepel(lions,prey)
    else: wander
  sight = vision(lions,prey)
```

4 Simulation

To investigate the proposed hypothesis a simulation was built in which distributed algorithms describing the action-selection and behavioural response of predators (the ‘lions’) and prey could be investigated. The intent of the simulation was to capture key aspects of the coordinated behaviour of the lions in the approach, stalk, rush and kill. Thus the simulation developed was intentionally simplistic, in marked contrast to the realism obtained from a complex simulation such as that of [Tu and Terzopoulos, 1994]. This decision is readily justified by recourse to a consideration of the nature and purpose of *simulation*; the oft-discussed consequences that such a decision implies are acknowledged.

In the simulation the following implementation decisions were made:

- The predators and prey are represented by a point-and-spread method, occupying a small circular area on a large 2-D torus simulation surface.
- Vision is the primary means of location of prey and other predators by the lions, and therefore must be modelled more accurately than simple line-of-sight. Vision is modelled as a cone extending forward from the location of the predator with a predefined spread. An animal in the cone is seen if $\lceil \frac{d}{d_{max}} g \rceil + (\frac{s_{max}}{2} - s + 1) + c < g$, where d is the distance to the target, g is the granularity of vision, s_{max} is the maximum speed of the animal, s is the current speed, and c is a current cover value, thereby trading-off visual acuity with distance, movement and cover. Peripheral vision is modelled as a second cone, overlaying the first, with less distance and a wider spread. Peripheral vision is sensitive to movement detection, but objects in peripheral vision will not

be ‘recognised’. Prey have two main and peripheral vision cones directed 90 and 270 degrees from the direction the prey is facing. These are have less distance but are wider than those of the predator.

- Although scent is a factor in the prey locating predators, vision is the key component in identifying the close location of a predator and avoiding an attack. Similarly, scent is only a small factor in prey location by the predator and is not a primary factor in the final approach-stalk-rush behaviours. Therefore, scent is not modelled in the simulation.
- The predators are provided with four basic behaviours — *rest* - wandering as a part of a group in search of prey, *approach* - where the predator approaches a prey to observe it, *stalking* - where the predator uses cover and crouched movement to close the distance to the prey without detection, and *rush* - where the predator chases (for a short distance) and seeks to bring down the prey.
- A number of pre-determined triggers for behaviours are included that correspond to known single animal behaviour. The *approach* behaviour will be triggered when a predator spots a prey within attacking distance, or when a predator sees another predator approaching the prey. The *rush* behaviour will always be triggered when the prey flees away from a predator ([Schaller, 1972] identifies that lions launch a ‘rush’ opportunistically if they stumble upon a prey at close range or if the prey being stalked spots the predator and flees).
- The prey are provided with two basic behaviours — *grazing* - moving around a specific area looking for potential predators whilst eating, and *fleeing* - if a lion is spotted within a simulated distance of 50m [Schaller, 1972] or is spotted stalking or rushing, then the prey will turn away from the predator and flee. Fleeing is always away from the detected predators, although it is recognised that more complex fleeing strategies could be adopted [Cliff and Miller, 1996].
- It is assumed that the prey is always faster than the predators.
- In order to provide a measure of attraction / repulsion for use in the simulation the Lennard-Jones Potential was employed. Normally describing the relationship between water molecules, it provides a useful means of expressing the degree of attraction or repulsion as a function of distance between two points and is expressed as: $y = a * (\frac{b}{d})^{12} - (\frac{b}{d})^6$, where a is the rate of attraction/repulsion, b is the distance where the forces are in balance and d is distance between the animals. Although this could be used to vary the speed of approach to the balance point, we simply use it for the binary decision to approach or move away from an animal.

A simulation will start with predators placed spatially close to one another and within range for at least one of the predators to immediately detect the prey (i.e. there is no requirement within the simulation for the larger task of prey location). Each agent in the simulation (predator or prey) is independent, without any global coordination once the simulation

starts and until the prey is killed or escapes. No global information is available to any agent in the simulation.

5 Investigation of the proposed algorithm

The algorithm identified in section 3 uses peripheral vision to identify when new movements are seen when the predator is looking at the prey or another predator. In testing it was found that since a predator has to turn to sight the prey or a predator, it can lose sight of a predator it was aware of and find another predator instead. This can cause the predator to spend its time searching for and trying to align with neighbouring predator (who are all moving) and seemingly lose interest in the prey.

A modification was made to the algorithm to prioritise stalking of the prey and to provide memory of the prey’s last position so that the lion can re-locate the prey after it has turned. This version performed better, producing encircling behaviour at the desired attract/repel distance with a good distribution of predators around the prey. However these changes also introduced occasional problems. Where a predator B was directly between predator A and the prey, predator A would seek to move a back from predator B whilst being attracted towards the prey. Similarly predator B would seek to move towards the prey to get away from predator A whilst being repelled by the predator. This would result in a deadlock.

Although partially successful, it was also clear that the algorithm was not simulating some of the fundamental behaviour observed. The algorithm allowed predators no preference for position in the circle and did not normally show the younger predators covering larger distances. Rather than continue to modify the initial algorithm with additional constraints, an alternative approach seemed possible.

Lions within a pride display a form of dominance hierarchy, with older heavier lions typically dominant over younger lighter lions. In section 2.2 it was noted that [Stander, 1991] observed a preference for positions, with the ‘wings’ usually taken by the younger lions and the ‘centre’ taken by older and heavier lions. We hypothesised that this structure could be constructed using the same attraction / repulsion mechanisms if the mechanism included weighting for dominance (which might be argued to correlate with either a fear of more dominant lions, or a wish to avoid dispute over dominance) within a stalking area around the prey. We further identified that the faster movement of the wing lions was required to encourage rapid resolution of the dominance order without excessive ‘shuffling’ of positions.

Introducing this change in the algorithm not only demonstrated the desired encircling behaviour, but it was discovered that each predator only needs to be aware of the location of one immediate neighbour at a time in order to create the encircling behaviour. Since the maintenance of cover is important during stalking, this reduction in the requirements of sight suggests that the algorithm identified is plausible.

No information is available from the literature about how the final attack is initiated. This is an important matter, since early initiation will cause the prey to be chased into a location before the ambush is set. However, with the less dominant predators now being pushed to the wings and the more

dominant predators settling into position first it becomes easy to devise a trigger. The solution is in two parts. Firstly no predator can rush until the correct attract/repel distance with the prey and other predators is found, and secondly the distance away from the prey at which it is acceptable to initiate the ‘rush’ is weighted by dominance. Thus, less dominant predators will start the ‘rush’ as soon as they are in-place, at which time the other predators will also be in place. The older predators will not ‘rush’ until the prey is within a smaller distance, thereby creating the ambush. The final algorithm² was thus:

```
repeat until movement > chaseDistance or kill:
  prey, lion = closest(sight, memory)
  memory = [lion, prey]
  if distance(pre) in stalkBoundary and (fleeing(pre)
    or movement > stalkDistance(dominance)): rush
  elseif prey != null and lion != null:
    if collisionLikely(lion): moveAway(lion)
    elseif distance(pre) in stalkBoundary:
      attractOrRepelMax(lion, prey)
    else: attractOrRepel(lion, prey)
  elseif lion != null or prey != null:
    attractOrRepel(lion, prey)
  else: wander
  sight = vision(memory)
```

6 Results

Initial tests ran the final algorithm simulating the lions hunting behaviour ten times to identify whether the encirclement behaviour with appropriate distribution based on ‘dominance’ was consistently displayed. In these tests four lions were simulated, the average number involved in Stander’s observations. In every test the predators were started in close proximity to one another and within sufficient distance to sight the prey. Parameters were set as follows: $d_{max} = 900$ (lion), 140 (prey); $g = 12$; $c = 5$ (lion stalking), 1 (prey and lion not stalking); $s_{max} = 5$; $s = 2$ (lion wandering and stalking), 4 (lion rush), 1 (prey wander), 5 (prey fleeing), $a = 5$; $b = 100$ (prey) and 150 (lions). The encircling and rush behaviour is illustrated in figure 2, with the (randomly generated) dominance setting for the predator identified beside the corresponding plotted pathway.

The results in the plots show several different patterns depending on the success of the hunts. Successful hunts tended to look like those shown in plot (a) and (b). The correspondence between the ‘dominance’ of the simulated predators and the pathways shown on these plots illustrates the emergent order of the lions in the encircling behaviour. The initial rush behaviour by low dominance lions who drive the prey towards the more dominant lions, one of whom makes the kill, can also be seen in the plots.

A failed kill is illustrated by plot (c), which shows the situation where the prey notices the lions before any encirclement could be performed so that the prey flees from the lions. This example shows that a dominant lion does not give chase to the prey but the less dominant lions chase the prey for a distance. This behaviour emerges as a result of the lower distance to ‘rush’ for more dominant lions that otherwise provides the lion ‘ambush’ behaviour, and is similar to observed

²For a detailed discussion of the algorithm and its development, the reader is referred to [Dalrymple-Smith, 2003].

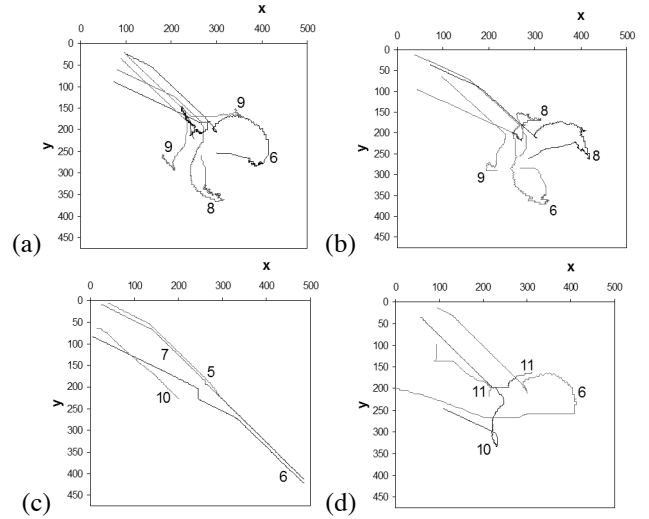


Figure 2: The encircling and rush of lions - (a) & (b) Successful hunts; (c) A hunt where the prey spotted a stalking predator; (d) A hunt where the prey escaped the ambush. Only the lion traces are shown, with the ‘dominance’ value indicated by each lion trace.

Table 1: Percentage of hunts with kills (a) for each dominance level, including the number of simulated hunts lions of that dominance were involved in, and (b) for each group size.

Dom	Hunts	Kill%
11	34	56
10	40	48
9	42	43
8	41	34
7	39	49
6	39	56
5	31	42

(a)

Lions	Kill%
6	53
5	60
4	27
3	40
Any	45

(b)

behaviour. Plot (d) also shows a failed kill. In this case the low dominance lion starts the chase and the prey flees, as expected. However all the remaining lions have a similar high dominance and therefore none will join the ‘rush’ until the prey is close. This allows the prey to run away from the single chasing lion, past the ambush and get away.

Another result (not shown on the plots) occurs on the occasions when the lions are out of position with the dominant lions on the ‘wings’ rather than the low dominance lions. In this situation the low dominance lions ‘rush’ from the central position enabling the prey to flee away from any ambush. This behaviour is interesting in relation to the observations discussed earlier that the probability of the lions having a successful hunt is dependant on the lions encircling at their preferred position.

A further investigation simulated 60 hunts with group sizes ranging from 3 to 6 predators (chosen to reflect the average group size of 4 lions, observed by Stander). The results are shown in table 1a and 1b.

Table 1a also shows that the percentage of successful hunts in relation to the hunts in which predators of a particular dom-

inance are involved. No clear pattern can be identified. It was hypothesised that this could be because the success or otherwise of a group hunt is dependant on the mix of dominance in the group. An analysis of the individual simulation results revealed that groups with more low dominance or more high dominance predators were less successful. This is readily explained by the observation that with a preponderance of low dominance predators it is unlikely that an ambush would be set up correctly, whilst with a preponderance of high dominance predators the prey is more likely to find a pathway of escape (see Figure 2d). Unfortunately no literature was available that would allow these findings to be compared with observed behaviour.

There is no clear pattern in the results shown in table 1b. It is interesting to note that [Stander, 1991] gives the success of hunts in the Etosha National Park at 27%, which is the same success rate seen in all simulations run with only four predators. Furthermore, Stander noted that the success of the hunt is increased with the group size, which is also seen with the overall kill rate in the simulation of 45%. However, in order to obtain statistically valid results a larger experimental run is necessary, and a fuller exploration of the parameter space of the simulator is required.

7 Conclusions and Further Work

The results presented in this paper represent the output of preliminary investigations of a highly simplified simulation to test the hypothesis that the group predatory behaviour of lions can be mimicked using attraction / repulsion between the lions and their prey. Although a full investigation, particularly of the parameterisation of the simulation, has yet to be conducted, the results demonstrate that many of the observed behaviours in the group hunting of lions are replicated in the simulation.

It would be inappropriate to claim that the proposed mechanism is therefore the mechanism deployed by lions in group hunting. However, it is important to note that the complex cooperative behaviour demonstrated here emerges from the deployment of very simple dynamic interactions. It is of particular interest that the introduction of dominance relations was not only key to producing behaviour that correctly mimicked observed stalking, rush and ambush behaviour, but was also key to an important simplification in the visual communication required for agent coordination. This finding opens an avenue of further research for multi-agent coordination.

We hypothesise that such 'cooperative' behaviour within a group hunting situation could arise from the 'selfish' behaviour of lions, and be deployed in a coordinated manner, when use is made of group dominance relations. Verification of this hypothesis from further live observations would help to resolve the debate on the nature of the 'cooperation' seen in lion hunting, and would provide further insights into the role of dominance in animal groups.

Further work is required to investigate the parameterisation of the model used and then to use the simulator to obtain a wider range of results to which statistical analysis can be applied. Future work will seek to explore the role of dominance in multi-agent coordination in distributed computer

applications, and the identification of dominance agreement algorithms for fault tolerant systems.

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