Unravelling complexity in inter-species interaction through nonlinear dynamical models

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Abstract

Unraveling complex interactions between animal species is of paramount importance to understand competition, facilitation and community assembly processes. Using data from GPS positions of sheep (*Ovis aries*) and red deer (*Cervus elaphus*) grazing a moorland plot, we modeled the animal movement of each species as a function of the distance between individuals, with the aim to assess the role of animal interactions (i.e. attraction and repulsion) in their spatial movement. We used black-box based models. These models do not require making assumptions about the biological meaning of their parameters. They are data driven and use embedding complex algorithms that create nonlinear functions that estimate the behaviour of the system, in our case the movement of our animals, and its errors. We used an algorithm based on radial basis functions to build models of time series data, using minimum description length as the criteria for model optimization. Included in the model is a factor that captures the collective behavior of the animals based on the distance between individuals. The model emphasizes the spatial relationship between animals from the absolute navigational directions by attenuating the latter. Our simulations showed that animals of the same specie tend to group together, with sheep having a stronger grouping behaviour than deer. The dynamics of the model are density dependent, that is, the number of animals within range affects the strength of the interactions and their grouping behaviour. A strong swarm behaviour was detected by the model, the longer the distance between species, the stronger the attraction between them; and the shorter the separation between species, the stronger their repulsion, which suggests inter and intra competition for food and space resources. Our modeling approach is useful to interpret animal movement interactions between animals of the same or different species, in order to unravel complex cooperative or

competitive behaviors, or to make predictions of animal movement under different population scenarios.

Keywords: Animal behavior; computational modeling; social dynamics; *Ovis aries*; *Cervus elaphus*

Introduction

Collective animal movement refers to the unified motion of a group of animals, which aggregate and interact to form a cohesive unit, either influenced by individuals within the population or external effects caused by the environment or another animal group (Okubo and Levin 2001). The study of collective animal movement is of paramount importance to understand how the individuals interact with the environment and the role of social interactions in the speed and accuracy of decision making (Robbins 1993; Michelena et al. 2010; Ward et al. 2011). Positive and negative interactions within and between different species, mainly driven by processes of cooperation and competition for resources or niche partitioning (Ricklefs 2010) are used to explain patterns of animal distribution at different spatial scales, such as sexual and social segregation and species assemblages (Ruckstuhl and Neuhaus 2005; Whittaker and Fernández-Palacios 2010).

Interest in the study of animal movement has increased in the last few years, particularly because of the availability of newer precise technology to the field biologist, such as GPS and video recording systems (Ballerini et al. 2008; Nagy et al. 2010). These new advances allow

researchers to record large amounts of data, almost in real time, on the dynamics of the spatial movement of animals. The use of methods from statistical physics and network theory applied to real animal datasets have helped to unravel the complexity that drives some collective behaviors. For example, the role of leadership against collective decision making has been inferred from the complex interactions in the movement of individuals within a flock of birds and fish shoals (Nagy et al. 2010; Herbert-Read et al. 2011; Ward et al. 2011). Numerical analysis of the nature of bird flying movement has provide some evidence that local interactions in a flock can be better explained by a topological range (i.e. number of animals in the vicinity) than by the traditional metric range (i.e. distance between members of a group) (Ballerini et al. 2008). While analytical mathematical models (based on differential or difference equations) have been applied to various forms of animal collective behaviour (Reynolds 1987; Vicsek et al. 1995; Okubo and Levin 2001; Couzin et al. 2002), the aim of this paper is different. Such traditional analytical models are usually derived from the understanding of the physical or biological phenomenon combined with expert knowledge or intuition of the researcher. This typically leaves a small number of free parameters to be chosen, each of which has some biologically relevant meaning. For example, tuning models using fixed predefined mathematical functions based on classical structures and only estimating parameters has been used for simulated swarming data and for experimental data from surf scoters (Eriksson et al. 2010; Lukeman et al. 2010). Our approach is to build an arbitrary model of the dynamics from the data - avoiding the dependence on the “correct” intuitive understanding of the system. This new computational data-driven approach can automatically tune the model to replicate the data, but this necessarily means that the formulation of the model and its specific parameter values lack biological meaning. One of the advantages is that these data-driven approaches based on black box models

have less prior assumptions on the system they represent, e.g. using neural networks to make models of shoaling fish (Herbert-Read et al. 2011), or radial basis functions for homing pigeon flights (Dieck Kattas et al. 2011), in order to infer the essential local interaction rules that produce collective behavior without any assumption about how each individual has to behave. Hence, to extract meaning for the biologist from such a model we need to perform an extra step: the characterization of the model itself. In this study we do this by inferring the attraction-repulsion profiles for various animal interactions from the interaction forces evident in the model.

We propose to build mathematical models directly from experimental data movement of GPS marked sheep and deer using the methodology applied to modeling homing pigeon flocks (Dieck Kattas et al. 2011). We extend the methodology to consider two interacting species. The strength of this method lies in the usage of dynamical separation measures to infer the underlying attraction and repulsion tendencies that the individuals in the model follow, and thus the underlying interaction rules can be inferred.

We are interested in assessing (i) how well the models fit the observed data; (ii) which species drives the decision making movement of the other species; and (iii) how distance between animals (i.e. metric range) and animal density (i.e. topological range) affect the spatial interactions.

Based on previous studies of sheep and deer ecology and behavior we hypothesized that our species will show a swarming behavior (H1): repulsion at short distances, attraction at

medium ranges, and alignment of velocities (Reynolds 1987; Vicsek et al. 1995; Couzin et al. 2002). This is expected because these species compete for food and shelter, and therefore, it is predicted that they will use similar areas, so at long distances there will be an attraction between species. Within shorter separations, competition for resources will increase and so we expect a repulsion between species, with social factors as the underlying mechanisms that maintain tighter intraspecies grouping bonds (Bon and Campan 1996; Pérez-Barbería et al. 2005). (H2): sheep, the domestic species, will show stronger grouping behavior than deer (Price 1999); and (H3) the larger deer will drive the movement of the smaller sheep, as the larger and deeper bite size of deer facilitates sheep grazing in long swards (Bell 1970) (Farnsworth et al. 2002). Consequently, there will be attraction between species at long separation distances (i.e. sheep following deer movement), but at shorter distances the larger species can actively displace the smaller species and thus sheep will show spatial repulsion to deer (Perez-Barberia and Yearsley 2010).

Material and methods

Input data

The positional data used in this study was obtained from sheep (*Ovis aries*) and red deer (*Cervus elaphus*) in an experiment carried out at The James Hutton Glensaugh Experimental Field Station in Auchenblae (Aberdeenshire), North East Scotland (56° 29' 23.366" N, 2° 54' 41.273" W). Between August of 2010 and January of 2011, 17 red deer adult hinds (age = 5-13 yr, mean = 10 yr, mean weight = 92.2 kg) and 23 Scottish black face ewes (age = 3 yr, mean weight = 46.6 kg) fitted with GPS collars (LOTEK GPS3300) grazed a stock-proof fenced plot

of 1.04 km² located in a moorland area. Sheep and hinds were drawn from the field station animal stock kept in hill farming conditions. During this period human disturbance was reduced to the minimum husbandry required to ensure the welfare of the animals. Animals were not fed or supplemented throughout the duration of the study, they relied on the natural resources of the plot. The density of sheep in the plot was close to the maximum densities of hill sheep in the Scottish highlands (McLeod 2002), while the deer density was near the maximum for Scottish wild red deer recorded (Deer Commission for Scotland 2002). These two species have grazed extensively the Scottish glens, hills, and moorland for at least 200 years (Grant et al. 1976; Clutton-Brock and Albon 1989).

The GPS collars were programmed to record one location fix every 30 minutes, throughout the study period. Location data from the collars were downloaded at the end of the experiment and all records were differentially corrected to improve accuracy. Trials undertaken in our plot indicated that 95% of the differentially corrected fixes were within a 14 m radius of their actual position. The positional data of the sheep and the deer consisted of coordinates defined by Easting and Northing using the British National grid at 30 minute intervals. Missing positional data (due to radio collar malfunction) reduced the number of animals to 5 sheep and 4 deer per time interval. For the purpose of using simultaneous records for all animals, we broke down the dataset into continuous segments that include all of the 9 animals. This allowed the dataset to be treated as a collection of short dynamical sequences. Consequently all our analyses and comments apply to these 9 animals.

Modeling approach

In our modeling scheme, inspired by classical swarming approaches such as Boids and the Vicsek model (Reynolds 1987; Vicsek et al. 1995), we propose to use a single local interaction model followed by all the individuals of the same species. This approach was successfully used to model the collective movement of pigeon flocks (Dieck Kattas et al. 2011). Using discrete time intervals, the model estimates the change in position of an individual i of the group between times t and $t + 1$. Since we are considering two species, we require two models:

$$\Delta s_i(t+1) = f[z_i(t)] + e_i(t) \quad (1)$$

$$\Delta d_i(t+1) = g[w_i(t)] + \varepsilon_i(t) \quad (2)$$

where s_i and d_i represent the positions of a sheep and a deer respectively, f and g are nonlinear functions to be built from the experimental data, e and ε are the model prediction errors, which we assume to be independent and identically distributed. The vectors z and w contain the values from time interval t that are used to predict the change in position at time $t + 1$ for a sheep or a deer respectively, and will be referred to as the model embeddings. Both vectors contain information about individuals of both species in order to fully consider their influence in the dynamics of a single species. The models f and g actually consist of two (possibly nonlinear) functions each, since the positions are two-dimensional (x and y coordinates), and thus we have one function for each coordinate to predict. Each of the functions is constructed using a well tested algorithm that uses radial basis functions to build models of time series data, using the minimum

description length as the criteria for model optimization, which is known to prevent overfitting (Judd and Mees 1995; Small and Judd 1998; Small and Tse 2002).

The proper selection of embedding vectors $z_i(t)$ and $w_i(t)$ is essential for the adequate use of information at the current time interval to predict the next step in our models. They change for each individual and each time interval, and therefore we use instances from every animal to make the input samples for our model building algorithm. For each embedding, we defined the separation between individuals as the key factor to capture the collective behavior. Previous studies on flocking behaviour consider changes in velocity and position in the embedding (Ballerini et al. 2008; Eriksson et al. 2010; Lukeman et al. 2010; Dieck Kattas et al. 2011). However, because of the very slow sampling rate of the positions of our sheep and deer no velocity information was available and consequently was not included in the model.

First we define the positional difference between two sheep i and j , at a time interval t as $a_{ij}(t) = s_i(t) - s_j(t)$. The positional difference between a sheep i and a deer j is denoted by $b_{ij}(t) = s_i(t) - d_j(t)$, and relative positions of the deer population is given by $c_{ij}(t) = d_i(t) - d_j(t)$. In order to facilitate the presentation, the numbered indexes refer to the neighbor ranking of individuals, e.g. a_{i2} will symbolize the difference between sheep i and its second sheep nearest neighbor, while b_{3j} refers to the difference between deer j 's third sheep nearest neighbor and deer j .

Since we have a small number of sheep and deer, it is actually feasible to use the separations of every single animal in our model. This can help to capture the differences between

the influence exerted by nearer or farther neighbors of either species. With this in mind, the embedding for a sheep i at a time interval t is defined as:

$$z_i(t) = (a_{i1}(t), a_{i2}(t), a_{i3}(t), a_{i4}(t), b_{i1}(t), b_{i2}(t), b_{i3}(t), b_{i4}(t)) \quad (3)$$

In simple terms, the vector considers the positional differences of one sheep to each of the other four sheep and to each of the four deer, with the order depending on who is nearer at time t . Since we are working with two dimensional positions, the embedding vector consists of 16 variables. Following the same reasoning, the deer embedding is likewise composed of positional differences to the other animals:

$$w_i(t) = (c_{i1}(t), c_{i2}(t), c_{i3}(t), -b_{1i}(t), -b_{2i}(t), -b_{3i}(t), -b_{4i}(t), -b_{5i}(t)) \quad (4)$$

The negative signs in equation 4 are used to simply switch the reference species, using the previously defined convention of vector $b_{ij}(t)$ for interspecies positional difference. By considering this modeling scheme, we are aiming to construct a model that takes into account the influence of neighbors, depending on who is closer, i.e. the movement behavior of a sheep could be more strongly affected by the nearest sheep than the second nearest sheep, regardless of who the actual animal is.

Since we want to emphasize the relationship between animals in our models, i.e. their relative separations, the absolute navigational directions in the input data are not important. Nonetheless, this can affect the models quite significantly, e.g. if the data includes segments of sheep moving northeast constantly, the model might capture absolute northeast movement as important instead of what could be movement directed away from the deer. The complete removal of this navigational bias is impossible when working with experimental data, but by rotating the directions of movement and separations randomly we hope to attenuate it. To

maintain relative separation distances intact, for every sheep data sample we keep position $s_i(t)$ fixed and then rotate the change in position $\Delta s_i(t+1)$ and each difference vector in $z_i(t)$ by a random angle selected from a uniform distribution in the interval $[0, 2\pi]$. The same methodology follows for the deer sampling. By doing this, we expect the navigational biases of the models to not be significant when important interactions are happening between the animals, i.e. when the system is not in a steady state.

Model retrieval and verification

Due to the anticipated complex dynamics in the experimental data, we decided to run our modeling algorithm several times in order to obtain a set of models and from these, average their statistics, since we don't expect a single model to capture all the relationships that could be within the data. We retrieved five different models for each species from the full dataset, this gave us a total of 25 different model combinations to run simulations from, by taking each possible pairing of each of the 5 models per species.

As specified in aim (i) of the Introduction, we wish to verify how well our models follow the data. For this, we do not take the conventional approach of using a different verification dataset to calculate the error between its positional values and those of the model simulations. Since we are attempting to model the collective dynamics of their interactions, i.e. how an animal moves based on the positions of the other animals, and not attempting to predict the absolute trajectories of the animals, we argue that a direct comparison of positions is not a useful way of testing if a model is adequate. Instead, we consider the Euclidean separations between animals at a time interval as the measure to compare between the input data and the model

simulations. For this, we define the separation between two sheep i and j , at a time interval t as $\xi_{ij}(t) = \|s_i(t) - s_j(t)\|$, the separation between a sheep i and a deer j as $\delta_{ij}(t) = \|s_i(t) - d_j(t)\|$, and then finally deer separations as $\eta_{ij}(t) = \|d_i(t) - d_j(t)\|$. We argue that the separations between animals over time are a good measure of how their change of position depends on the others.

We used the same initial conditions and the same number of time intervals from each continuous data segment (see Input data), to carry out simulations that can be comparable to the input data. By comparing occurrence distributions of the separation measures $\xi_{ij}(t)$, $\delta_{ij}(t)$ and $\eta_{ij}(t)$ between the input data and the models, we attempt to verify if the models can follow the separation dynamics adequately. In addition to a rough qualitative comparison of the distributions, we use the cross entropy:

$$H(p, q) = - \sum_x p(x) \log q(x) \quad (5)$$

between the normalized occurrence distribution of the source data $p(x)$, and the distribution of a model simulation $q(x)$, with x representing the occurrence space. The cross entropy is a measure of how distant a hypothesized distribution is from the "true distribution", and for our case the former and the latter correspond to the model and the input data respectively. It is quantified in number of bits, and therefore a larger number of bits symbolizes more complexity in the cross-distributions. If we equate $p(x) = q(x)$ then we have the original definition of entropy, and we can use it to calculate a self-entropy for the input data. Models with close cross entropies to the self-entropy of the input data should be considered "good models" because they are close to the "true distribution", which in this case is the input data. By comparing the entropy of the input data

distribution to the cross entropies, we can verify quantitatively if the model simulations are a good representation of the collective dynamics of the input data. In order to carry out a fair comparison, the separations at the initial conditions are not considered in the distributions, since these same values were used to initialize the model simulations.

Quantitative description of the dynamics

In accordance to aim (ii) in the introduction, we average separation statistics from a wide range of simulations in order to estimate the aggregation and separation behaviors that our models captured from the data. We considered around 25 random instances of 200 different initial condition parameters for each combination of models, which gives us a total of 5000 different simulations for each of the 25 model combinations. In order to vary densities in our simulations, the parameter that was changed for each of the 200 initial condition scenarios was the radius of the circle in which the individuals were randomly placed (r_c), mixing sheep and deer indiscriminately. By spanning from circles with a radius of 5 m all the way to 2 km, we attempt to cover a wide range of separation scenarios for the sheep and deer, and thus are able to average how their separations change over time due to their interactions. As defined in aim (iii) of the introduction, we wish to explain how the attraction or repulsion of a single animal towards others is more closely related to clusters of animals than to a single individual, e.g. a sheep could avoid a group of deer with more intensity than a single deer. Because of this, we propose the usage of cluster interactions in the analysis in order to better visualize how groups of animals have a greater impact on the dynamics.

We therefore calculate averaged changes in separation of an animal to a cluster of animals. To do this we first define the separation of a sheep i to a group of M sheep at a time interval t :

$$\xi_i(t) = \|s_i(t) - \langle s_j(t) \rangle_M\| \quad (6)$$

This measure tells us how close a sheep is to the center of mass of its M nearest sheep neighbors.

We use the same approach to define cluster separations for the other interactions:

$$\delta_i(t) = \|s_i(t) - \langle d_j(t) \rangle_L\| \text{ for separations between a single sheep and a group of } L \text{ deer,}$$

$$\bar{\delta}_i(t) = \|d_i(t) - \langle s_j(t) \rangle_M\| \text{ for separations between one deer and } M \text{ sheep, and finally}$$

$$\eta_i(t) = \|d_i(t) - \langle d_j(t) \rangle_L\| \text{ for separations between a single deer and a group of } L \text{ deer. In order to}$$

quantify attraction and repulsion between animals, we consider the change in separation between time intervals, i.e. the dynamic increase or decrease of separation. For this, we define a difference operator, which for the case of sheep - sheep dynamics is:

$$\Delta \xi_i(t) = \xi_i(t) - \xi_i(t-1) \quad (7)$$

From this measure, a negative value of $\Delta \xi_i(t)$ symbolizes attraction because the separation at t is less than the one at $t-1$, and conversely a positive value stands for repulsion because the separation at t has increased. The same Δ operator will be extended to the other separation measures, e.g. $\Delta \delta_i(t)$, $\Delta \bar{\delta}_i(t)$, and $\Delta \eta_i(t)$, in order to have a general picture of all the interactions in the system. It is also evident that our attraction and repulsion measures are largely dependent on how far the neighbors are to the individual, and for this we calculate them at different radius and plot curves for different values of M or L , e.g. a $\Delta \eta_i(t)$ at a radius of 50 m for $M = 2$, symbolizes the attraction of one deer to its two nearest deer neighbors when both of them are within a 50 m radius. In addition, we consider the 60% confidence interval of all the

$M = 1$ curves, which was calculated by removing the five upper and lower values of each model combination for each curve, i.e. from 25 combinations, removing the 10 extrema gives us a $15/25 = 60\%$ CI.

Modelling and graphs were carried out using Matlab Language of Technical Computing (Matlab 2006). Programming code is available from the authors (Michael Small) on request.

Results

In this section, we describe our results in two parts. First, in accordance to aim (i) we verify our models by showing how they offer an adequate representation of the intra and inter species dynamics of the experimental data, by running simulations using the same initial conditions and comparing separation distributions. Second, we consider a wide range of animal density scenarios to compute more definite statistics about the dynamics of the system and therefore be able to have more quantifiable conclusions about (ii) the attraction/repulsion properties between species and which species drives the movement of the other, and (iii) the effect of distance and clusters of animals in the interactions between species. For basic examples of some of the behaviors that were consistently observed in individual simulations, we provide some videos as supplementary material and their descriptions in the Appendix.

Fig. 1 shows the frequency distribution for intraspecies separations of the input data and an averaged distribution from simulations of all the models. Both distributions are followed reasonably well by the models, with the only significant difference at short separations of sheep

(between 0 and 10 m). These short separations are within the margin of error of the GPS measurements (14 m), and possibly caused by noise in the system. While the experimental data has few instances at short separations of sheep, the models have a high frequency of occurrences within these separations, and thus have a considerable deviation in this region. In other words, the models capture a strong attraction component between sheep from the input data, but do not retrieve a short-range repulsion interaction.

In Fig. 2 we can see the frequency distributions for separations between sheep and deer, with considerable resemblance between the distributions and a cross entropy that differs by less than a tenth of a bit to the original entropy. From these comparisons we conclude that our models can adequately represent the separation dynamics of the input data, with the only considerable difference happening with the movement of sheep at close distances. Regardless of this divergence, the models follow the interspecies dynamics very well, and thus we can expect them to be a good representation of the interactions between species.

The minimum and maximum cross entropies for each model combination (5 sheep and 5 deer models give 25 combinations) are shown in Table 1. All the cross entropies are very close, with the maximum deviation being of only 0.35 bits (around 4% of the self-entropy), between the model with minimum deer-deer cross entropy and the input data ($8.88 - 8.53 = 0.35$) (Figs. 1 and 2, Table 1). Of special note is that all of the models had a lower number of bits for deer-deer separations compared to the input data (Table 1), and from this we can infer that the models offer a more compact representation of deer-deer interactions than the actual data.

Starting with the intraspecies relationships, we can see in Figure 3a how for $\Delta\xi_i(t)$ the $M = 2$ curve exhibits the most negative value from 0 to about 100 meters. This means that within this range, sheep are more attracted towards the average position of their two nearest neighbors. Within this range, after $M = 2$, the $M = 1$, $M = 3$, and $M = 4$ curves follow respectively in order of more attraction. After reaching minima (i.e. strongest attraction) at approximately at 100 m, all curves except $M = 1$ decrease their attraction. The continuous decrease of $\Delta\xi_i(t)$ at higher radii for $M = 1$ indicates that for longer separations, the sheep are strongly attracted to their single nearest neighbor. This is natural, since the communication among neighbors that are further away is affected by that distance. For deer interactions, the attraction is weaker and more linear. All three curves ($L = 1$, $L = 2$, and $L = 3$) follow a roughly linear decrease from 0 to 250 m, with strongest attraction to the nearest neighbor, following the expected order of weakest attraction to the whole cluster of 3 neighbors ($L = 3$). These results are consistent with the fact that animals of the same species tend to group together, and so they move towards their nearest neighbors and slow down once they are within around 50 m of each other. We also note that for smaller radii the attraction is lower, since it implies that the animals are already close. As mentioned in the previous subsection, we find that sheep tend to group more strongly than deer, and this confirms our hypothesis H2.

Now we consider the interspecies separation dynamics. In Fig. 4, we show the dynamics from 5 to 50 m, and exclude shorter separations because of the limited amount of measured data that was available for short separations of different species. This is consistent with the observation that sheep and deer do not like to be close to each other. By comparing Fig 4a and Fig 4b we can see how, in general, one sheep is more strongly repulsed from deer compared to

how one deer moves away from sheep, i.e. higher positive values of $\Delta\delta_i(t)$ when compared to $\Delta\bar{\delta}_i(t)$. This suggests that a single sheep without its group appears more vulnerable and timid, and thus tries to move strongly away from the deer and join its group. While deer also move away from sheep, they are more independent and this can be clearly visualized in Fig. 4b by observing their relatively weak repulsions. In general, for both cases of interspecies dynamics, a single animal tends to be more proactive to distance itself from the whole group of the other species than to a single animal. This can be neatly seen in Fig. 4, where $\Delta\delta_i(t)$ and $\Delta\bar{\delta}_i(t)$ increase as the cluster of neighbors increases.

In order to analyze how distance can affect the interspecies interactions, as outlined in aim (iii), we consider a wider metric range at longer separations. The interspecies dynamics can give us more information about the system coupling, i.e. which species depends on which and who shows more independence, which actually addresses aim (ii). In Fig. 5, we show these separation dynamics at radii longer than 100 m. In Fig. 5a we can see an optimal distance ($\Delta\delta_i(t) = 0$) at around 180 m and how at greater separations a single sheep is attracted towards the deer regardless of the number of neighbors within the radius (L), with strong attraction at longer separations. Nevertheless, the 60% confidence interval is quite wide for the $L = 1$ case, hence the behavior could vary considerably at longer distances, very likely depending on whether or not the sheep are grouped together. In Fig. 5b we get more definite conclusions and a tighter confidence interval. Essentially, a single deer could be attracted or repulsed towards the sheep, and it depends on the number of sheep within its radius. We can see this in Fig. 5b, e.g. at around 800 m a deer will be repulsed when only 1 or 2 sheep are within the radius ($M = 1$ and $M = 2$), but attracted for a higher number of sheep ($M = 3$, $M = 4$ and $M = 5$). Once again, this

confirms that sheep show stronger grouping tendencies than deer, and that the species are coupled especially when the sheep are together, i.e. sheep and deer show more attraction between them when the sheep have formed a group, and they tend to follow the deer with a distance approximately equal to the optimal 180 m which occurs at $\Delta\delta_i(t) = 0$. This confirms hypothesis H3, as the larger more independent deer drive the movement of the smaller sheep. Our results from both interspecies analyses support hypothesis H1.

Discussion

In the analysis of our models, we found that sheep showed strong grouping tendencies (hypothesis H2), but were coupled to the movement of deer, with a repulsion between species at shorter separations (H1). The method we used considered some useful changes to the original one used in the modeling of homing pigeon flights (Dieck Kattas et al. 2011). Firstly, two different models types are built, one for each species. Both models depend on each other to produce simulations, since the sheep movement depends on the deer and vice versa, thereby increasing the complexity of the global system. Secondly, the embedding scheme changed significantly. While the previous study used velocity information, i.e. positional data from two time intervals, we did not consider it here due to the slow sampling of the data (30 minute intervals). Additionally, the positional difference vectors of the embedding (such as those in equations 3 and 4) were considered individually for the M neighbors in this study, while the previous one used a single averaged vector from the M nearest neighbors. Basically, we separated these difference variables in order to analyze the effect of each neighbor. This consideration was useful to successfully find how the interaction strength between neighbors

changes significantly depending on the number of neighbors within a certain distance. Both approaches have advantages and disadvantages, i.e. considering each neighbor individually might give more information of the interactions but results in a more complex model, while using an averaged vector of neighbors could drastically simplify a model for larger groups or when more variables are considered. We believe that this choice should be based on the actual system in question, and which variables are hypothesized to affect it, so that the model can capture the essential information without being too big.

Our methodology of building models of collective behavior from experimental data and then analyzing them with measures based on separation statistics to quantify attraction/repulsion, has been shown to be efficient in capturing the significant behavioral patterns that drive the collective behavior of sheep and deer spatial movement. Even when using a different dataset which considered two species and a much slower sampling rate than with pigeon flocks, the method was effective and thus gives support to its generality and flexibility. Additionally, our models showed how changing the number of interacting neighbors considerably affects the attraction and repulsion properties of the system, which indicates the importance of the topological range in the spatial movement behavior of mammals as it has been confirmed for birds (Ballerini et al. 2008). The topological distance model basically considers that animals interact with a fixed number of nearest neighbors regardless of their distance, contrasting to the more traditional models which use interactions to all neighbors within a limited radius (Vicsek et al. 1995; Couzin et al. 2002). While the distance clearly affects the interactions, i.e. the separations affect the strength of attraction/repulsion, and there is a radius delimiting the sensory

range an animal has to detect its neighbors, within these boundaries an individual will only pay attention to a limited number of neighbors.

Our results showed that animals of the same species tend to group together (H1), with the sheep having stronger attraction tendencies than the deer, and this is consistent with observations in other studies and our predictions (Bon and Campan 1996; Price 1999; Pérez-Barbería et al. 2005). This could be explained by the selection of aggregation as a trait favored in domestication of animal stock species (Price 1999), because breaking the group when fleeing makes shepherding difficult. Furthermore, we inferred a tendency for the species to move away from each other, with greater strength when a single sheep is near a group of deer, which is in accordance to a previous modeling study that found that in ungulates (Perez-Barberia and Yearsley 2010) and as we hypothesized (H3). When firmly grouped together as a single group, the sheep move away from the deer with less urgency, in order to maintain their intraspecies grouping bonds (Bon and Campan 1996; Price 1999; Pérez-Barbería et al. 2005). The deer, while not showing strong herding tendencies, still try to be together at weaker rates, and tend to cross the same terrain as the sheep, and vice versa, at different time intervals; implying that sheep and deer make a similar use of the space, probably food and shelter, and thus they have an interspecies attraction at longer separations between the groups. From this we conclude that the system is coupled: even with strong repulsions at short separations, a group of sheep is attracted to the deer and follows them at longer distances. This might happen because of the facilitating grazing effect of deer on sheep, by reducing the sward height and making it more suitable to the bite depth of sheep (Bell 1970; Farnsworth et al. 2002), and thus both species use the same areas at different time intervals.

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Figure captions

Figure 1. Frequency distribution of intraspecies separations in the input data and an averaged distribution of simulations from all the models. The entropy of the former and cross entropy of the latter are displayed.

Figure 2. Frequency distribution of interspecies separations in the input data and an averaged distribution of simulations from all the models. The entropy of the former and cross entropy of the latter are displayed.

Figure 3. (a) Averaged change of separation of one sheep to the nearest M sheep and (b) of one deer to the nearest L deer, within a fixed radius: attraction(-)/repulsion(+), between animals of the same species

Figure 4. (a) Averaged change of separation of one sheep to the nearest L deer and (b) of one deer to the nearest M sheep, within a fixed radius: attraction(-)/repulsion(+), between animals of a different species

Figure 5. (a) At larger distances, averaged change of separation of one sheep to the nearest L deer and (b) of one deer to the nearest M sheep, within a fixed radius: attraction(-)/repulsion(+), between animals of a different species.

Table 1. Cross entropies of models and data (cross entropy is the actual entropy of the system). Minimum and maximum cross entropies from all the 25 model combinations and averaged distribution from all the models.

Cross entropy (bits)	minimum	maximum	averaged [†]	Input data
sheep-sheep	8.39	8.60	8.56	8.29
sheep-deer	10.09	10.16	10.12	10.06
deer-deer	8.53	8.71	9.05	8.88

[†] The averaged cross entropy is not an average of the cross entropies of the 25 models but an averaged distribution of separations from the 25 models (hence we have a higher value for the averaged distribution of deer-deer separations that is outside the range of entropies from the individual models).

Fig. 1a

Fig. 1b

Fig. 2

Fig. 3a

Fig. 3b

Fig. 4a

Fig. 4b

Fig. 5a

Fig. 5b

Appendix

Qualitative description of the simulated dynamics

We now present as supplementary material, videos of simulations which mimic some of the most basic observed behaviors in order to visualize the dynamics. Each iteration of our models corresponds to 30 minutes in the data, following the sampling time of the input data as described in section 2. The variety between our 25 model combinations gave a wide range of interesting behaviors. We will summarize three essential scenarios which we observed repeatedly throughout our simulations, and these give a basic picture of how the interactions between sheep and deer affect their movement throughout time. All our simulations were performed by randomly placing the 5 sheep and 4 deer within a circle of radius r_c meters and therefore a low value of r_c implies high density conditions because the animals are very close together, and a high r_c corresponds to low density with the animals further apart.

The first basic scenario consists of each species aggregating on their own and then later moving in the same direction or maintaining a distance between them. This was especially observed for cases of high density, with the sheep and deer initially separating, clustering within their own species, and finally the sheep following the deer with some distance. The latter was visualized after the groups of sheep and deer are formed initially in the simulation, producing afterwards a stable coupled movement where the sheep group trails the deer group indefinitely, or it tries to maintain a stable separation with the more independent moving sheep. Video high.mp4 shows snapshots of a simulation where this happens, the animals are initially close together at $t = 0$ and later the two

species move away from each other, but finally move in the same direction. The coupled global direction in the final stable state implies that sheep and deer like to move in the same areas.

Another interesting situation that we encountered in some simulations is the deer forming two groups around the sheep. This happens more regularly in cases of intermediate density values.

Video med.mp4 shows a scenario where the sheep group together and start moving, but the deer settle into two different groups without forming a single cluster because doing so would involve getting closer to the sheep. Essentially we can see here that the deer are more independent and do not prioritize grouping. Even a single independent deer can still be the head of the combined group sheep and deer, without being clustered to anybody else. Sheep being separated by deer does not commonly happen at these density levels, implying that the sheep have a stronger tendency to group together.

Finally, for cases of lower densities, the behaviors are quite varied depending on the models and the placement of the individuals. Sometimes the two situations described previously would also appear with low density initial conditions, but with an obvious larger transient time which required the individuals to cluster and then move together from higher separations. Nevertheless a very interesting scenario occurs if the sheep start separated by long distances and with deer in-between them. The sheep form two distinct groups with their nearest neighbors, but they do not fully aggregate because the deer block their path. Video low.mp4 shows a simulation of this case. Even the deer do not totally unify into a single group, with three of them near the top sheep group, and one approaching the bottom group. After a long transient, the system shows this loose equilibrium with the sheep unable to have a unified group or moving direction.

Video high.mp4 (click on the file name below to activate the video display)

High.mp4

Video med.mp4 (click on the file name below to activate the video display)

Med.mp4

Video low.mp4 (click on the file name below to activate the video display)

Low.mp4

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