

## Can prey behaviour induce spatially synchronic aggregation of solitary predators?

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Spatio-temporal patterns of predator aggregations within their settlement areas (i.e. temporary settling zones used during dispersal or, more generally, foraging patches) were studied. By integrating the main behavioural rules of juveniles of Spanish imperial eagles *Aquila adalberti* during dispersal with the temporal availability of the eagles' main prey, we have developed several individual-based models under different simulation scenarios. The results suggest that the spatial synchrony of the aggregation patterns that we observed were derived from a combination of behavioural responses of the prey and the distances between available settlement areas. These results are discussed in the context of predator–prey relationships, optimal foraging and self-organizing processes.

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The questions surrounding pattern formation are considered to be some of the most challenging in many fields of science, with the causes of heterogeneity in the spatial distribution of system components still being obscure (Petrovskii and Malchow 1999). Animals display a wide range of coordinated behaviours, as for example when foraging. Relationships between predators (for better hunting) and prey (for better predator deterrence) represent typical examples (Rosenzweig et al. 1997, Bahr and Bekoff 1999, Brown et al. 2001). In this context, the results suggest that predators may influence the behaviour and spatial patterns of preys (Lagos et al. 1995, Brown and Kotler 2004, Yunker 2004). When this occurs, what are the consequences to the behaviour and spatial arrangement of predators? Most studies of

predator–prey interactions have focused on prey behaviour (Abramsky et al. 1996, Lima 2002, Nelson et al. 2004), leading to an incomplete view of possible behavioural and ecological interactions. In addition, there is a lack of knowledge about the way in which a prey's response to predation pressure may in turn affect the behaviour of the predator.

The study of the relationships between predators and prey, as well as patch and prey models, is one of the most active fields of behavioural ecology. Over the past decade, the study of animal foraging has been guided by the awareness that simple models are often inadequate to provide useful predictions. Stochastic dynamic modelling and individual-based models were identified as useful tools to approach complex, real-life situations

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(Perry and Pianka 1997; but see Bart 1995). In the past, attempts to reconcile empiricists' and theoreticians' approaches to animal foraging have been largely unsuccessful (Kareiva 1989). To obtain a better understanding of behavioural, ecological and evolutionary components of animal foraging it is necessary to combine both observational and theoretical work. In the past, predator–prey simulations have generally neglected the incorporation of prey behaviour under predation pressure (Giraldeau and Caraco 2000) and only recently some changes have occurred in the treatment of this subject (Lima 2002). Therefore, it is crucial to understand how predator aggregations are influenced by variations in the spatial scale under which the system evolves. Especially when aggregations are not determined by social interactions and foraging in groups per se does not increase individual foraging efficiency (Valone 1989, Beauchamp 1998). In fact, group foraging behaviour was mainly analysed in the context of social influences on foraging (Giraldeau and Beauchamp 1999, Galef and Giraldeau 2001, Dubois and Giraldeau 2003) and the effect of group size on the efficiency of resource exploitation (Bélisle 1998, Rita and Ranta 1999, Coolen 2002).

The present simulation study made use of several individual-based models built on well-studied aspects of the behaviour of radio-tagged juveniles of Spanish imperial eagles *Aquila adalberti* (Ferrer 1993a, 1993b, 2001). Our results leads us to propose that observed spatio-temporal patterns of eagle aggregations within settlement areas (i.e. temporary settling zones used during dispersal or, more generally, foraging patches used during dispersal) are induced by behavioural modifications of the eagles' main prey, the rabbit *Oryctolagus cuniculus*, as well as distances between available settlement areas. Under spatial constraints due to the evolution of the system in which they act, originally solitary foragers exploit foraging patches similarly to social species, but with no awareness of the emergent aggregation patterns to which they contribute.

## Methods

### Field inspiration and background

A long-term study of the Spanish imperial eagle population of Doñana (southwestern Spain) inspired the approach used here. The information available on this bird of prey represents one of the most extensive sets of data on a vertebrate species available today (data collection started in 1890). Furthermore, from 1986 to 2000, 30 first-year juveniles of this population were radiotagged to study dispersal dynamics and space use within settlement areas (Ferrer 1993a, 1993b, 2001).

### The eagle-rabbit behavioural interactions

Within dispersal areas exists a complex relationship between eagles, rabbits and the time eagles spend in a settlement area (for more details see eagle-rabbit game in Penteriani et al. 2005a, 2005b). The main factor influencing spatio-temporal occupancy of a foraging patch is the time (approx 12 days) that the rabbit population takes to change its behaviour (i.e. activity timetable and use of space) under predation pressure. The continuous and predictable presence of this large predator in a small area (approx 450 ha) forces rabbits to temporarily modify their behaviour (they switch from diurnal to nocturnal activity), consequently decreasing the availability of prey in the patch (Ferrer 1993a, 1993b). One of the consequences of this “nonlethal” predator effect on rabbits (i.e. trait-mediated indirect interaction; Abrams 1995) is that eagles use different temporary settling areas in rotation (Ferrer 1993a). When eagles are unsuccessful in hunting (rabbits are few or not available at all), despite increased effort, individuals change food patches and move to another settlement area to avoid starvation. This usually occurs after approx. 12 days. This dynamic process of successive area exploitation, as a function of rabbit availability, causes contemporaneous aggregations of several solitary eagles (in one or few areas), as well as the simultaneous disappearance of them from other areas (Ferrer 2001, Penteriani et al. 2005a). This predator–prey interaction is based on the behavioural response of the prey to predation pressure, rather than on predator density. Evidence does exist to show that foraging predators may affect prey availability and, consequently, capture success (Neill and Cullen 1974, Parrish 1992, Loggerwell and Hargreaves 1996, Ainley et al. 2003).

Non-social individuals often select the same foraging patches simultaneously but the change in the behaviour of the rabbit seems to be unaffected by the number of eagles contemporaneously in residence (Ferrer 2001). This is probably due to the fact that all the individuals sharing the same hunting territories (during dispersal they do not display territorial behaviour, nor do they show any social behaviour during predation) hunt at approx the same time, e.g. when diurnal thermals occur. Because the thermal occurrence depends on several factors (e.g. temperature, weather condition, season), eagles predation is not predictable by rabbits and, as a result, there are not fixed diurnal hours where rabbits are both protected from eagles and free from nocturnal predators. When diurnal predation pressure decreases (and nocturnal predation increase, e.g. mortality increase because of owls and mammals predation at night), rabbits become diurnal again and, consequently, available to the eagles. Because information on dynamics of nocturnal predation were not available, we considered that rabbits became available for eagles after a time equal to the time that rabbits required to shift to nocturnal activity (i.e. 12 days).

## Simulation models

### *General premises of a simple model*

Our simulation provided a parsimonious explanation, consistent with the known facts, of the apparently complex phenomenon of “synchronized” spatial aggregations of solitary predators.

We built several individual-based models simulating the movements of eagles among several foraging patches, distributed randomly on a regular  $50 \times 50$  grid (with wraparound boundaries), to explore if: (a) the prey’s behavioural response to predator presence could explain individual aggregations, and whether the aggregations differ from patterns exhibited by individuals moving randomly (model A); and (b) inter-area distances could influence individual aggregation, that is the likelihood of patch occupancy decreased exponentially with distance (model B). To do this, we added to the model A a probability of area occupancy negatively related to the area distances. Random movement outputs were generated by random models, one for each of the models described above. In these random models: (a) individuals can stay in the same patch or move randomly to another foraging patch with the same probability; and (b) preys do not show behavioural response to predation.

Both the change in the rabbit behaviour and the consequent random movements among patches indicate that our model differed from ideal free distribution models, in which individuals are free to settle everywhere and have a complete knowledge about the quality of each habitat (Cressman et al. 2004). That is, eagles are not foragers having memory of the rabbit profitability within available patches. Moreover, no social interactions (e.g. conspecific attraction) are included to explain individual grouping (e.g. group foragers search for others that have found food and join them; Beauchamp et al. 1997, Giraldeau and Beauchamp 1999, Coolen 2002).

Finally, to understand if aggregations patterns are a property of small systems, large systems (e.g. spontaneous aggregations only emerge when high numbers of individuals are involved), or both, we ran two versions of the model A with different numbers of both individuals and patches, i.e. 5 areas: 10 individuals and 50 areas: 100 individuals. Changing such a ratio of areas: individuals did not qualitatively change the results presented here.

### *Model A (rabbit behavioural changes)*

Each foraging patch was characterised by a value indicating the diurnal activity of rabbits and ranging from 1 (totally diurnal rabbits, i.e. the resource is entirely available) to 0 (totally nocturnal rabbits, i.e. the resource is not available at all). At the beginning of the simulation several eagles were randomly distributed among patches. When a settlement area was occupied by at least one individual, the rabbit profitability of each site started to linearly decrease in a way proportional to the number of

time-steps an individual exploited that patch (as estimated from empirical data, M. Ferrer, unpubl.). The decrease in the diurnal activity of rabbit population was independent of the number of individuals simultaneously exploiting that patch and only the first individual to reach an empty patch started the decrease of rabbit activity. When the rabbit diurnal activity in a patch decreased below a given threshold (50% of rabbit diurnal behaviour recovery, as suggested by field information), all the eagles in the area moved randomly to one of the other available areas. As individuals left a site, the abandoned patch started to recover a fraction of rabbit diurnal activity in each successive simulation time-step. Area recovery was of a quantity equal to the one it lost when the eagle went beyond it. Changing the time-steps needed to reduce the rabbit diurnal activity below a given threshold (and, consequently, to make an area available for eagles again) did not qualitatively change the results presented here.

### *Model B (rabbit behavioural changes + inter-patch distances)*

This model is identical to the 5: 10 model A, except for the addition of the influence of the distance factor. In fact, in the model B, after predators leave an area due to low rabbit availability, their probability to occupy a new patch depends on the distances between patches, with the nearest area having the highest probability of being occupied. Such a probability decreased exponentially with distances.

## Aggregation index and statistical analyses

Individual grouping within foraging patches (recorded during 10 000 iterations after the simulation began) was calculated using the following aggregation index:

$$\frac{1}{N^2} \sum_{i=1}^A n_i^2$$

where  $A$  = total number of foraging patches,  $N$  = total number of eagles and  $n_i$  = number of eagles in the patch  $i$ . The index ranges from 0.2 (no aggregation, 2 eagles in each area) and 1 (all the individuals assembled in one area) in the 5: 10 case, and between 0.02 and 1 in the 50: 100 case.

The nature and amount of departure of the frequency distributions of aggregation from normality was represented by asymmetry (Sokal and Rohlf 1981). High positive values of skewness indicate that the displacement of the curve tail is tilted to the right of the distribution, that is towards the highest level of aggregation. Comparisons between aggregation distributions were made by the nonparametric Kolmogorov-Smirnov two-sample test, particularly sensible to differences in samples distribution (e.g. skewness).

## Results

Spontaneous emergence of aggregations occurred at significantly higher level when the movements of predators were affected by both prey behaviour and inter-area distances than when they moved randomly (Table 1, Fig. 1a–c, 2). In fact, both model A and B showed the highest frequencies of individual grouping (i.e. aggregation index = 1, that is all the individuals assembled in one area only). All aggregation distributions varied significantly from a random distribution (Table 1), suggesting that the aggregations did not occur haphazardly. Moreover, it is unlikely that rabbit availability alone caused the emergence of spontaneous aggregations of individuals because, when we introduced the patch occupation probability as a function of the distance among areas into the simulation (model B), the highest levels of aggregation became significantly more frequent (Fig. 1d, Table 1). In fact, starting from the value of the aggregation index  $\cong 0.32$ , more eagles occupied a patch simultaneously in model B than in model A (Fig. 1d).

Figure 2 shows an example of the dynamic patterns of individual aggregation for model A (ratio 5: 10), as well as how model A's pattern differs from the corresponding random model. We observed the appearance of periods of all lengths during which eagles aggregated in only a few areas (the highest values of the aggregation index) which were followed by returns to low activity (the intermittent bursts exhibited by the curve), which

corresponded to a random and scattered distribution of the individuals.

## Discussion

The simulation outputs, based on the most parsimonious assumption (i.e. rabbit availability), were able to reproduce the patterns of eagle aggregations that were observed in the field (Ferrer 1993a, 1993b). Initially, solitary wandering individuals aggregated spontaneously within settlement areas and they then moved synchronously among them. Groups of predators were most likely to form in patches in close proximity to those areas that they had just left due to low prey availability. Such a result is particularly interesting when we consider the absence of any kind of social interactions (e.g. conspecific attraction and public information; Sergio and Penteriani 2005) in our simulations to explain individual grouping within feeding patches. That is, we were able to reproduce the patterns of aggregations observed in the field without make use of conspecific attraction as a mechanism that allows animals (with imperfect knowledge of the environment in which they move) to locate high quality habitats by the presence of conspecifics (Stamps 1988, Reed and Dobson 1993, Beauchamp et al. 1997). As an end result, we showed that the behaviour of preys can determine the aggregation of predators even in

Table 1. Spontaneous patterns of predator aggregation within foraging patches when individual movements ( $n = 10\,000$ ) were either random (random model), depend on the behavioural changes of preys (model A) or on the effects of prey availability combined to a negative correlation between area distance and occupancy rate (model B). Model A was tested for both the ratios of 5 areas: 10 predators and 50 areas: 100 predators, whereas model B was only built for the ratio 5 areas: 10 predators (see text for additional information on the simulations). Kolmogorov-Smirnov two-sample test was used to compare the aggregation outputs of the different models.

		<u>Model A (5: 10)</u>	
		Random movements	Rabbit behavioural changes
$\bar{x} \pm SD$		$0.28 \pm 0.05$	$0.33 \pm 0.09$
Range		0.20–0.68	0.20–1.00
Asymmetry		1.40	1.62
Z = 18.06, P = 0.0001			
		<u>Model A (50: 100)</u>	
		Random movements	Rabbit behavioural changes
$\bar{x} \pm SD$		$0.030 \pm 0.002$	$0.034 \pm 0.004$
Range		0.024–0.040	0.025 – 0.070
Asymmetry		0.52	1.31
Z = 38.04, P = 0.0001			
		<u>Model B (5: 10)</u>	
		Random movements	Rabbit behavioural changes + distance
$\bar{x} \pm SD$		$0.28 \pm 0.06$	$0.38 \pm 0.11$
Range		0.20–0.82	0.20–1.00
Asymmetry		1.49	1.23
Z = 33.32, P = 0.0001			
		<u>Model A vs model B (5: 10)</u>	
Z = 17.26, P = 0.0001			

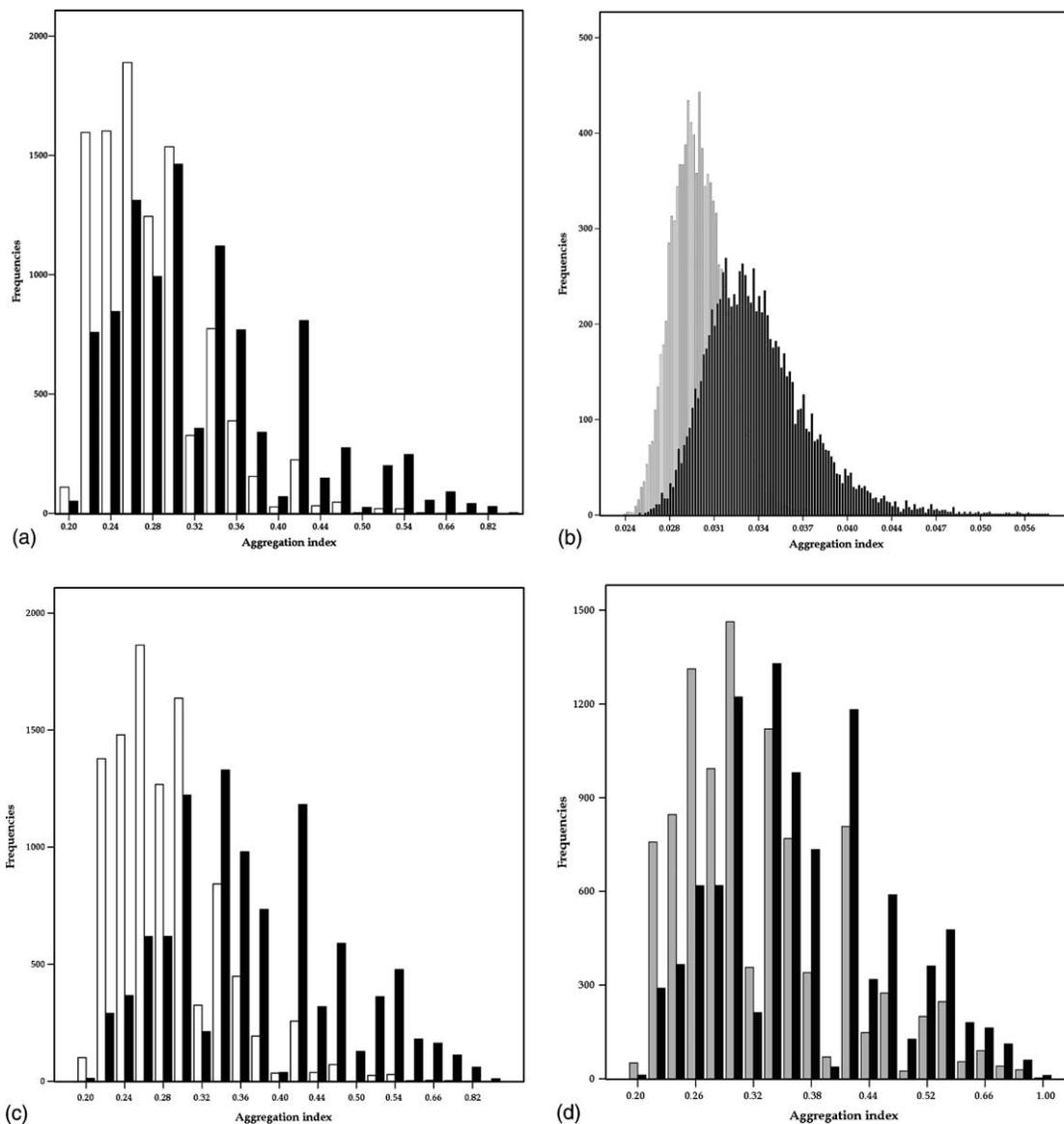


Fig. 1. The level of individual aggregation increases (for both 5: 10 and 50: 100 ratios of areas: individuals) when random movements are compared to a situation in which individual movements are constrained by rabbit availability (a) = 5: 10; (b) = 50: 100 or by the double effect of rabbit availability and inter-area distances (c). Compared to the effect of rabbit behavioural modifications only, the introduction in the model of an additional movement-constraining effect (i.e. inter-area distances) increases the individual grouping starting from the value of the aggregation index  $\cong 0.32$  (d). In (a–c): white bars = random model output; black bars = A and B models. In (d): grey bars = model A; black bars = model B.

absence of social interactions or facilitating factors on the foraging success.

In biological systems, aggregations due to local instability (represented here by the modification of the rabbit behaviour) are a known mechanism (Kelso et al. 1988). The aggregation of eagles in foraging patches can be viewed as the emergence of a spontaneous spatial pattern that permits individuals to best exploit the patches available for settling through a self-reinforcing dynamic (Perry 1995). Especially for systems character-

ized by distance-dependent movements, the more time eagles spend hunting, the lower the rabbit availability and therefore the greater the emergence of eagle grouping. This serves to avoid the simultaneous overfeeding of all areas and death due to starvation. As expressed by Perry (1995), this is "... a dynamic that literally feeds on itself".

Several types of animal aggregations can be explained by the evolutionary assumption that joining a group increases the survival or reproductive success of the

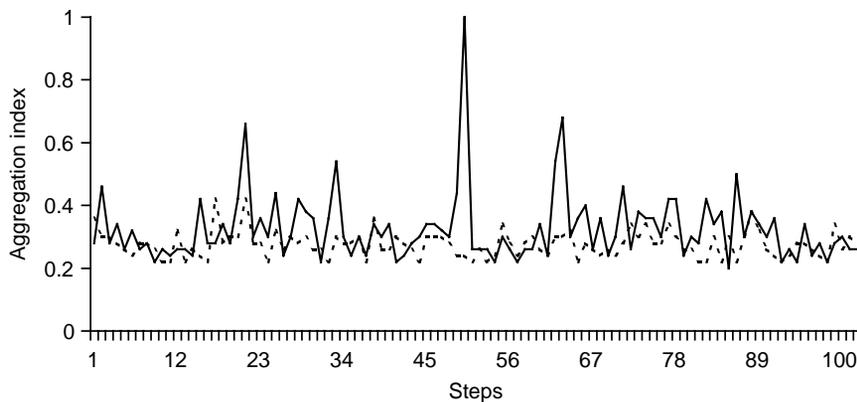


Fig. 2. Detail of 100 representative steps for the simulation output of the model A (behavioural changes of prey, bold line) and its correspondent random model (broken line), both for 5 areas and 10 eagles. Emergence of individual aggregation from predator–prey behavioural interactions is higher than in the case of the model simulating random spatial occupancy. We observe “periods of peak stasis”, during which all individuals are concentrated in the same area (higher values of the aggregation index), prior to the

return of activity representing random distributions of individuals. This curve behaviour, characterized by periods of stasis interrupted by intermittent bursts, is representative of a punctuated equilibrium, a typical behaviour of decentralised systems (Discussion).

group members (Parrish and Hamner 1997, Parrish and Edelman-Keshet 1999, Bonabeau et al. 1999). For examples, in foraging groups, food search are more successful, compared to the efforts of a lone individual, due to the greater amount of information that a group can gather and analyse. Despite this fact, and given the knowledge that inanimate objects can aggregate themselves and create impressive emergent patterns, it is hard to argue that all animal aggregations must have a functional purpose arising from an individual decision. Starting from a situation of full prey availability, predators are frequently alone in their foraging patches, and prey behaviour determines low aggregations. However, as the number of available areas decreases due to the behavioural response of the prey, there tends to be a few patches that are occupied by groups of individuals. In the end, it is common to find that all the predators have unconsciously aggregate in only 1–2 patches. Co-evolution is an integral part of predator–prey communities, illustrating the mutual evolution of predator and prey strategies: predators respond strategically to prey behaviour and vice versa. Such a reciprocal influence is crucial in attempting to understand behavioural predator–prey interactions (Lima 2002). For example, co-evolution has frequently been invoked for benefits and costs of aggregations for hunting predators (Lett et al. 2003). The system that we explored is interesting because it is part functional aggregation (due to the fact that groups of eagles can better exploit the rabbit resource within a foraging patch) and part simple, spontaneous pattern (the individuals have no awareness of the pattern that they create). In addition, the pattern of patch use that emerged fits well with models of optimal patch exploitation that form the core of classical foraging theory (Giraldeau and Caraco 2000). Non-social aggregations of solitary predators in a limited number of the spatially available areas allow the recuperation of the rabbit population of the remaining ones, forming a perfect example of optimal patch

exploitation. Anyway, because we presented the simplest scenario that could be responsible of the observed predator–prey patterns (e.g. we did not assume in our model migration/immigration rates, reproduction, prey population reduction by predation pressure), future works are needed to explore the possible influence of the intrinsic dynamics of both predator and prey populations on the emergence of such aggregations.

As emphasized by Lima (2002), when approaching predator–prey interactions from the behaviour of predators, new emergent behaviour might change the way in which we think about such interactions. For example, predator–prey systems have already shown the possibility of exhibiting self-organization capable of producing stabilizing heterogeneities in prey spatial distributions (Hassel et al. 1991, Jansen 1995, de Roos et al. 1998, Gurney et al. 1998, van de Koppel 2005) and hierarchical structures (Sakaguchi 2003), due to the dynamic instability of the non-linear mutual interactions between predators and prey. Above all, such spatial patterns may facilitate persistence of unstable prey-predator interactions and increase stability over large spatial scales (van de Koppel 2005).

The study of self-organization, despite the large amount literature on the topic, is a relatively new field, especially when considering the emergence of decentralized patterns in ecological systems (reviewed by Camazine et al. 2001). We consider it appropriate to define self-organization as the emergence of complex patterns at the global level of a system due to simple, local interactions between individuals (or between individuals and their immediate environment – biotic or abiotic) that have no awareness of the overall picture to which they contribute.

In the past, self-organization was assumed to be a phenomenon mainly linked to large numbers, i.e. thousands, hundreds of thousands or million of agents, elements or events involved (Nicolis and Prigogine 1977, Deneubourg et al. 1986). Furthermore, social

species have been the most investigated group of animals (Deneubourg and Goss 1989, Camazine et al. 2001), especially in the context of aggregation (Parrish and Hamner 1997, Parrish and Edelstein-Keshet 1999) and foraging (Seeley 1987, Portha et al. 2002). However, evidence has shown that self-organized patterns can also arise from small numbers of individual interactions with an absence of sociality and cooperative behaviour (Rivault et al. 1999, Ferrer and Penteriani 2003).

It is possible that spontaneous aggregations of eagles represent an example of a self-organized pattern? Without attempting a comprehensive explanation, let us spell out some essential features of our pattern formation that coincide with those typical of decentralized phenomena. The pattern of aggregations we reproduced resulted from: (a) internal constraints of the system (Kelso et al. 1988, Camazine et al. 1990), represented by prey availability and inter-area distances (i.e. local cues of our system); (b) simple interactions (Seeley 1987) between a predator and its main prey; (c) changes of prey behaviour, giving the foraging patches an unstable and fluctuating environment, capable of developing temporary decentralized structures (Nicolis and Prigogine 1977); (d) behavioural changes of predators due to the information (i.e. prey availability) given by area conditions (i.e. stigmergy, Kelso et al. 1988); and (e) feedback loops (Seeley 1987, Kelso et al. 1988) represented by the fact that not only individual interactions shape the overall pattern of the system (i.e. prey behaviour), but that the conditions within the system (i.e. prey availability) also determine the behavioural responses of predators. In addition, the self-grouping of predators determined: (a) the emergence of new properties (Bonabeau et al. 1995), such as individual aggregations and coordinated movements among areas; (b) an overall pattern of aggregation and movements that could not be predicted by the behavioural rules of the parts of the system (i.e. nonlinearity of the properties, Kelso et al. 1988, Bonabeau et al. 1995); (c) criticality (Kelso et al. 1988, Bak and Paczuski 1995), illustrated by a shift toward a self-organized configuration when approaching the critical threshold of the system (i.e. prey diurnal availability), which evolves into a critical nonequilibrium state (Fig. 2); and (d) a punctuated equilibrium behaviour (Bak and Paczuski 1995), i.e. as a consequence of criticality, the system exhibits periods of stasis interrupted by intermittent bursts of activity (Fig. 2).

When invoking self-organization as a possible explanation of predator aggregations, we also consider it important to stress that: (a) Gurney and Veitch (2000) provided evidence that self-organization is a component of some types of cyclic predator–prey relationships, in which prey can recover when its density falls below a threshold as a consequence of the reduction in local predator density; and (b) a common mechanism underlying spontaneous pattern emergence in most of the

published predator–prey models is a strong interaction between predator and prey (van de Koppel 2005), as in our eagle–rabbit model.

If self-organization can explain eagle aggregation, this could be the first time, to our knowledge, that self-organization has emerged as a regulating element of small systems (i.e. our model testing aggregation for 5 areas and 10 individuals). This may be due to the fact that we were using a non-social species whereas the preferred models to study the emergence of decentralized patterns in animal aggregations have been social species, for which small numbers of individuals do not allow the emergence of self-organization (Deneubourg et al. 1986). In the end, one of the most fascinating aspects of decentralised systems is their ability to create complexity from simplicity, merely reflecting simple individual interactions with their surrounding environment and not individual complexity. However, the question of how spontaneous patterns and evolution interact still remains unanswered in the study of biological systems.

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