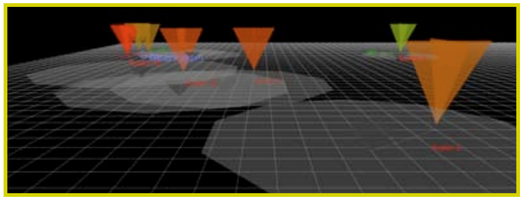

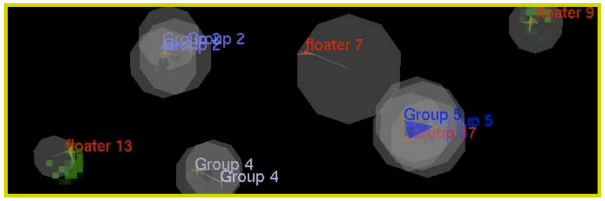

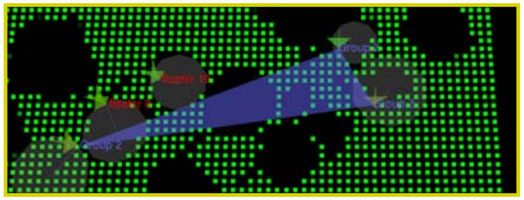

Virtual prairie dogs weigh in on the *Resource Dispersion Hypothesis*

Christopher X J. Jensen, Dylan Moore, and Jennifer L. Verdolin

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Goals of the project

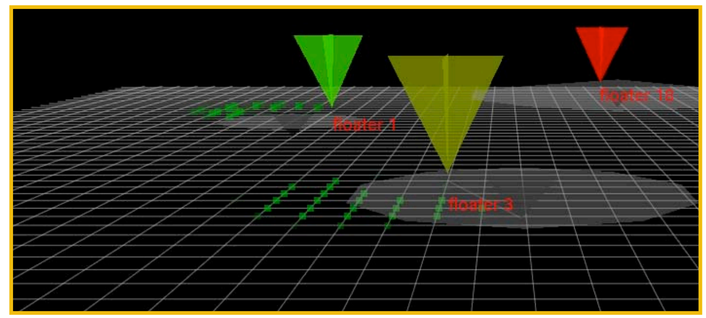
- Create a realistic simulation of social group formation in relation to resource availability
- Understand what kinds of behavioral rules make it possible to form social groups based on group defense of resources
- Test the ***Resource Dispersion Hypothesis*** using the resulting model

fieldTest

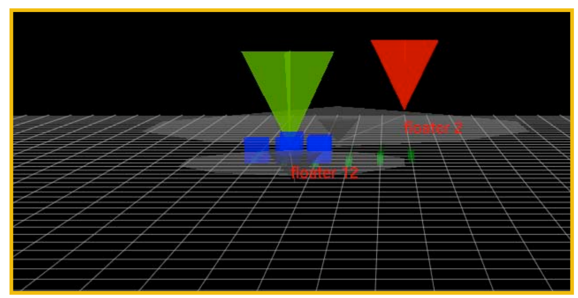
How *fieldTest* works: Scope

- Inspired by prairie dogs, but works for any organism that displays group defense of territory based on food availability

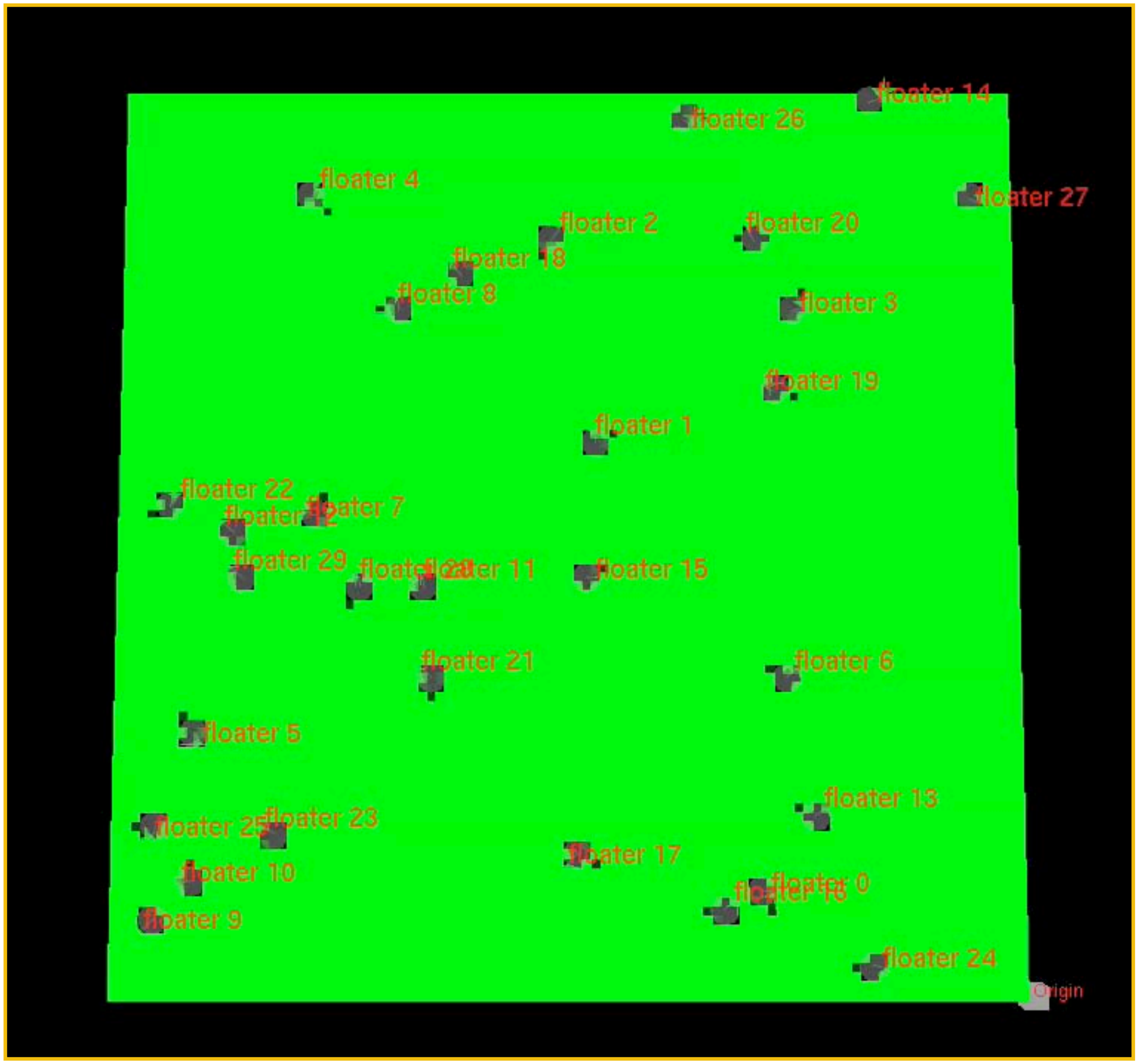
- Food located on two-dimensional, bounded grid



- Assumes resource acquisition is the primary motivator of behavior



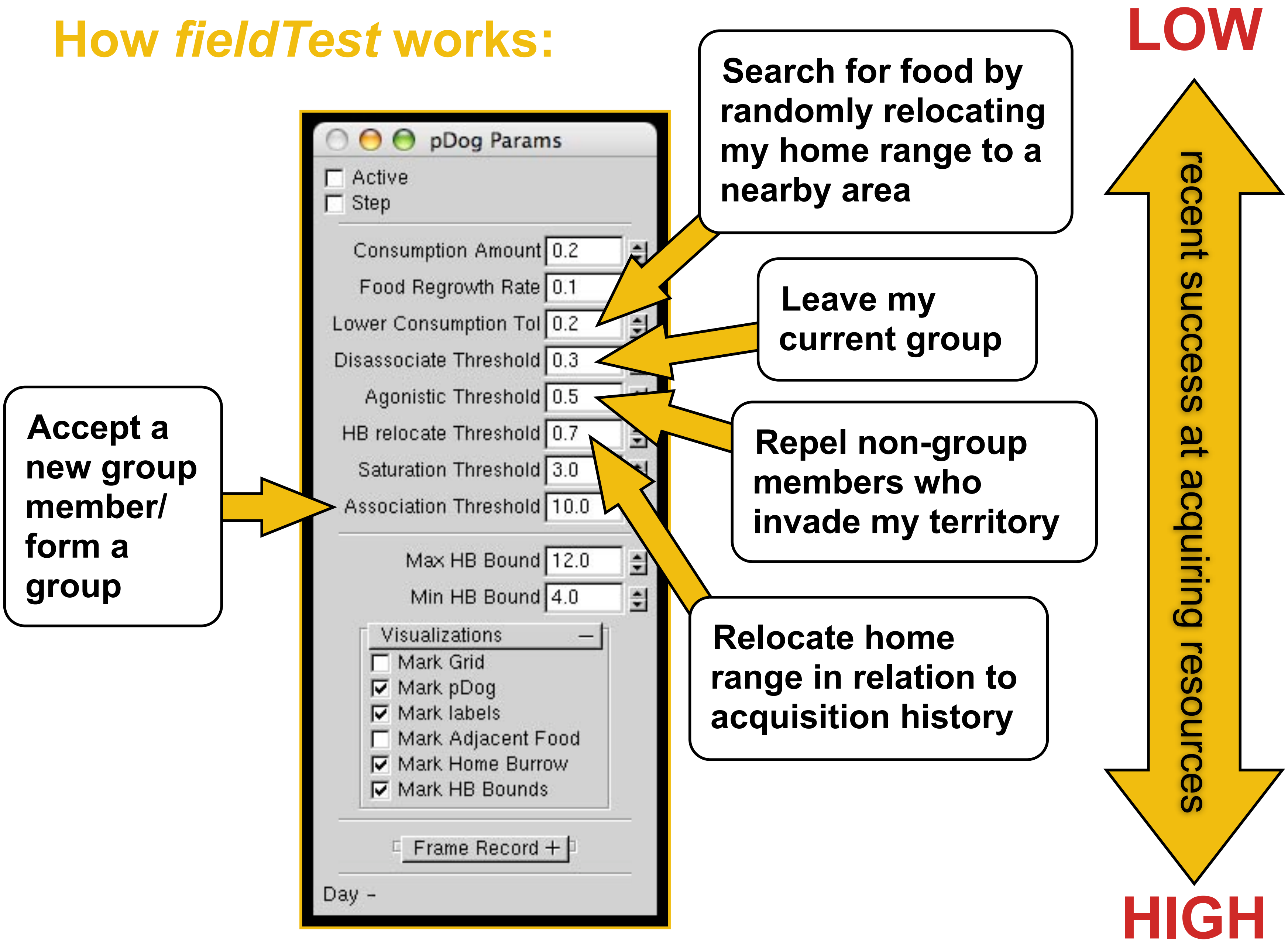
How *fieldTest* works:



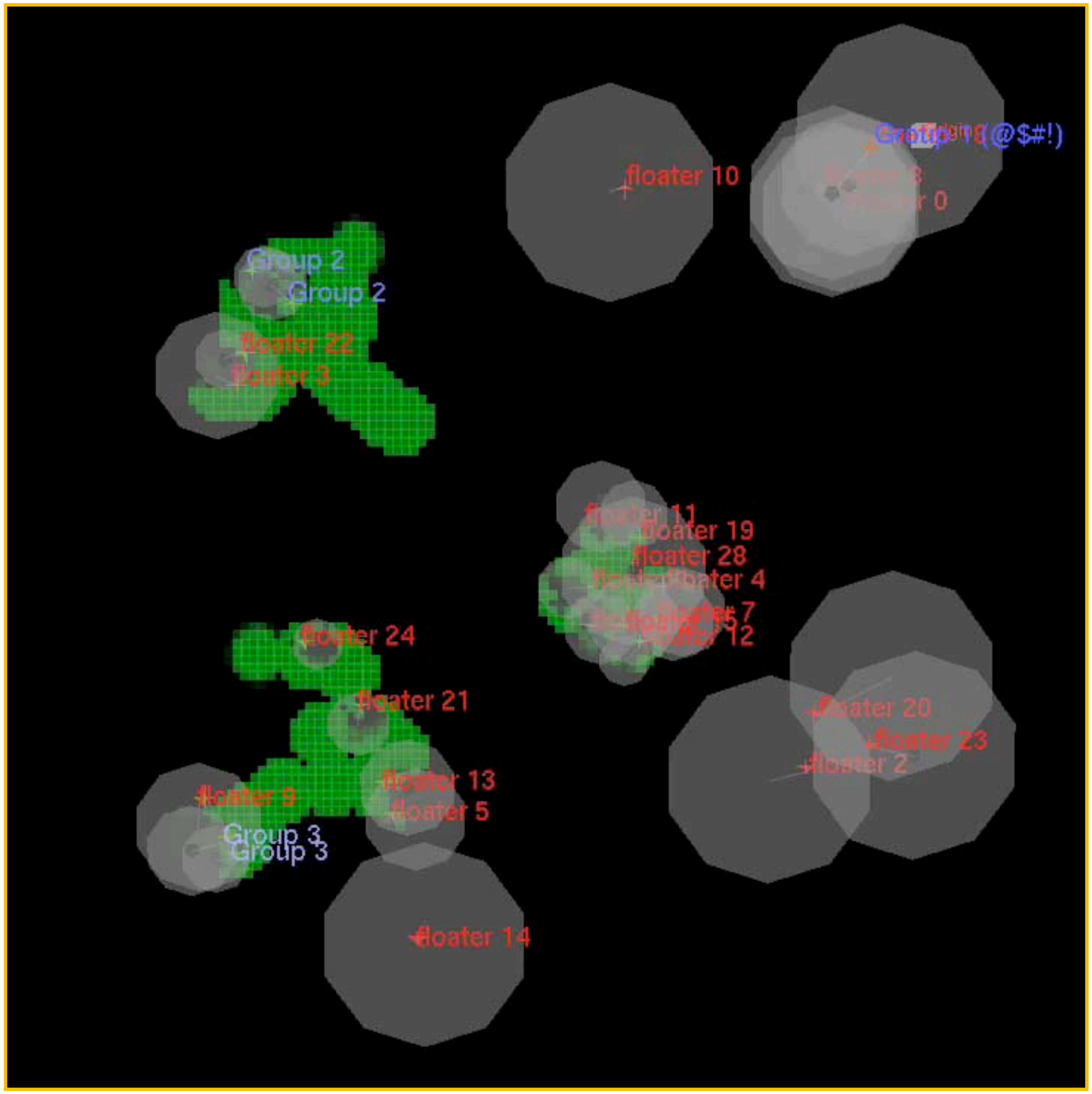
Spatially explicit, individual-based

Food regrows at specified rate

How *fieldTest* works:



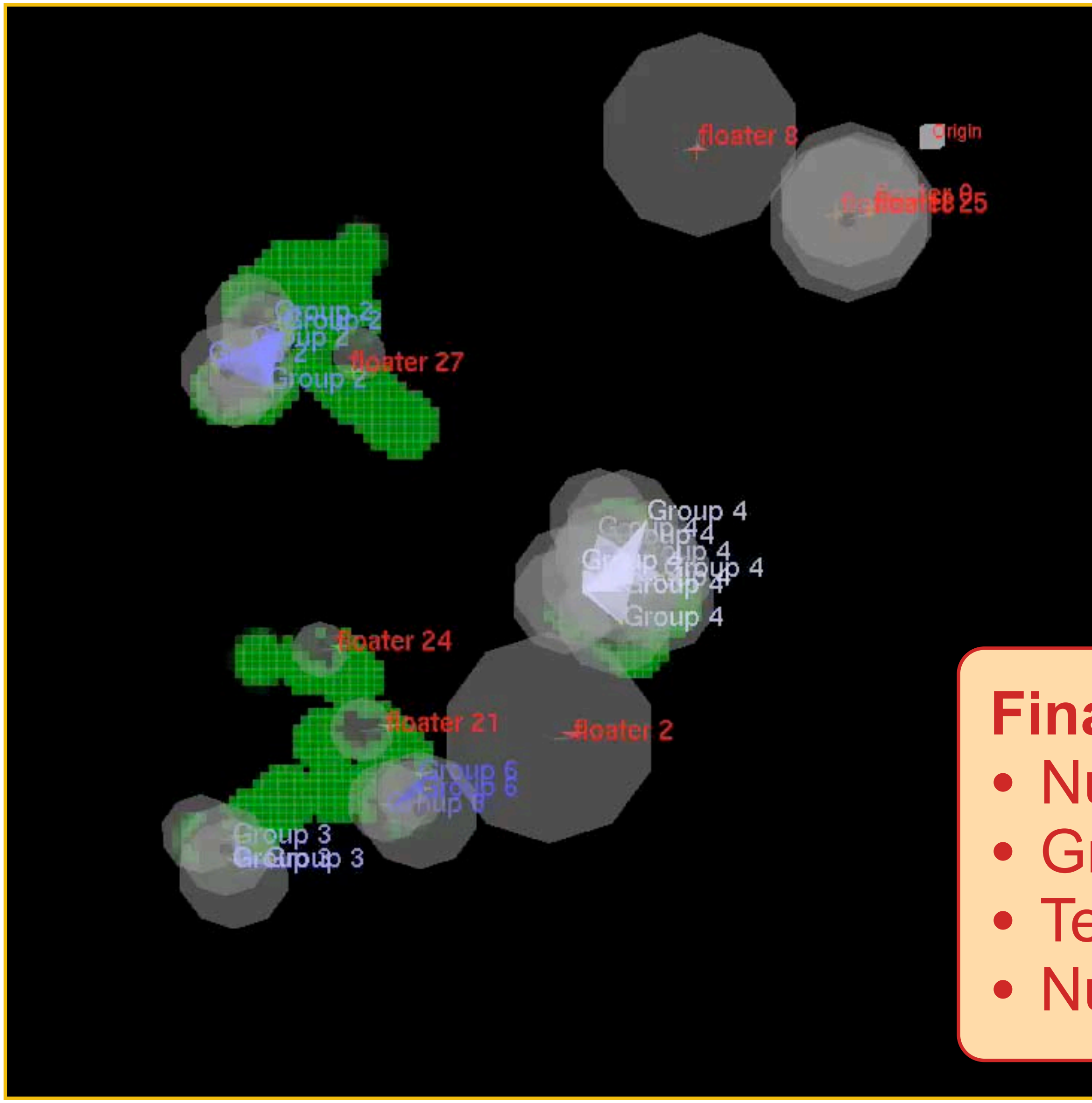
How *fieldTest* works:



Individuals reorient their territory based on where food is found

Groups form based on prolonged sharing of territory

How *fieldTest* works:



Groups form and will defend against invading "floater" individuals

Final Output:

- Number of groups
- Group sizes
- Territory Sizes
- Number of floaters

Predictions of the *RDH*:

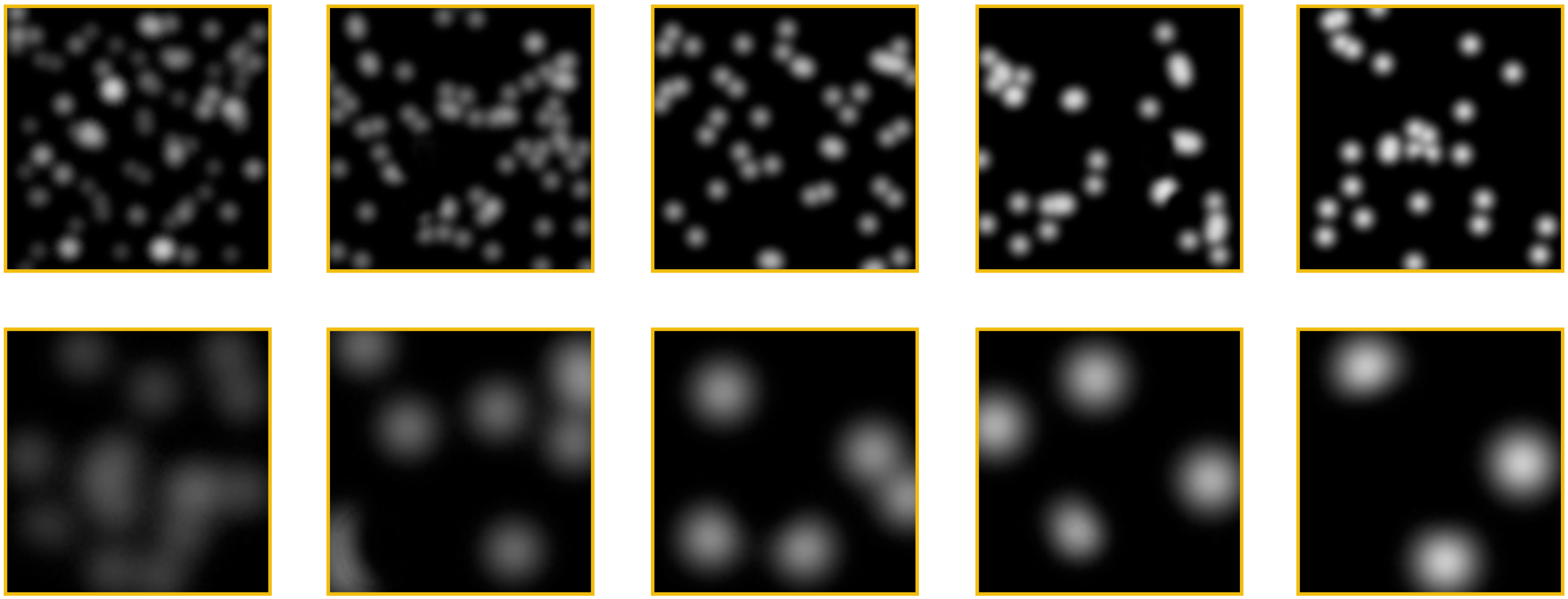
1. Group size and territory size are independent.
2. The more heterogeneous the resource distribution, the larger the territory size of each group.
3. The more heterogeneous the resource distribution, the larger the group size.
4. The greater the abundance of resources, the larger the group size supported.

Comparing the *RDH* with *fieldTest*:

	Resource Dispersion Hypothesis	***fieldTest***
Nature of information available to individuals	Global, complete	Local, incomplete
Nature of space	All heterogeneity assumed identical	Heterogeneity specific to particular landscape
Nature of outcomes	Deterministic	Probabilistic

Testing the *RDH* with *fieldTest*:

100x100 grids **Patch Scale = 11**



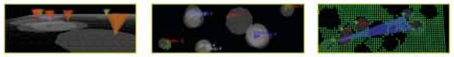
100 grids tested **Patch Scale = 33**

Three different food abundances:

Food regrowth rates of 5%, 10%, 15%

How *fieldTest* works:

Want to know more?



Virtual prairie dogs weigh in on the *Resource Dispersion Hypothesis*

Christopher X J. Jensen, Dylan Moore, and Jennifer L. Verdolin

How the simulation program *fieldTest* works

Space:
The simulation is performed on a two-dimensional grid that is bounded on all four edges. The user can specify the height and width of this grid.

Time:
The simulation occurs over a series of days, each of which is broken into a specified number of time steps.

During each **time step**, these events *sometimes* occur:

1. Individuals may move to an adjacent location.
2. Individuals may consume food.
3. Individuals may repel another individual who is not a member of their group.
4. Individuals may form or join a group.
5. Individuals may leave a group.

At the end of each **day**, these events *sometimes* occur:

1. Individuals may relocate their home burrow (HB).
2. Individuals may resize their territory.

At the end of each **day**, these *always* occur:

1. Wherever food has been eaten below its maximum, food regrows.
2. Each individual returns to the HB.

Distribution of Food:
The landscape of the simulation is specified by providing an image file with grayscale patterning. Purely black areas are interpreted to contain 0.0 units of food, while purely white areas are interpreted to contain 1.0 units of food (the maximum allowed). Intermediate shades of gray are interpreted to contain between 0.0 and 1.0 units of food, in increments of 0.00390625 (grayscale images have 256 shades from black to white). The amount of food at each location specified by the image represents the maximum amount of food that can exist at that location. At the outset of the simulation, all locations are assumed to contain the maximum possible density of food.

Regrowth of Food:
Food regrows at the end of each day based on the specified food regrowth rate (FRR) parameter, which ranges from 0 to 1. Regrowth occurs as a percentage of the maximum amount of food in each location. For example, if FRR=0.5, a location with a maximum food density of 0.7 will grow back at a rate of 0.35 per day. Food can only grow back to the maximum amount originally specified by the landscape image file.

Movement of individuals:
At the beginning of the simulation, individuals are randomly placed somewhere on the grid. During each time step, individuals move one at a time until all individuals have moved. The order of movement is randomized, such that individuals move in a different order during each time step.

At the beginning of each day, individuals emerge from their HB. During each time step, individuals may move one step away to any of eight adjacent locations; the individual may also stay in the current location. Movement is biased: individuals can detect the amount of food in the adjacent locations and the chance of movement to a particular location is probabilistically weighted by the relative amount of food in that location. Once individuals have landed on a location with food, they will remain on that location until all of the food is consumed.

Individual behaviors:
Eating: As long as an individual is not threatened (see *Agonism* below), she will consume all food at her current location at the prescribed rate per time step. If there is no food at the current location, the individual will attempt to move towards an adjacent space containing food. Once an individual has reached the maximum daily consumption potential for a given day she will stop eating until the next day.

Consumption memory: Each individual has a "memory" of its daily average food consumption and the average location of that food over a prescribed number of days. Daily average food consumption is scaled to the maximum daily consumption potential and determines the behavior of the individual.

Home burrow relocation: If the daily average amount of food consumed is less than a prescribed percentage of the maximum daily consumption potential, that individual will either relocate its home burrow to the location closest to the center of its food memory (higher consumption success threshold) or to a random nearby location outside of its current territory (lower consumption success threshold).

Group Formation: If the daily average amount of food consumed is greater than a prescribed percentage of the maximum daily consumption potential, that individual will tolerate other individuals who enter her territory. After a prescribed cumulative number of days of tolerance, adjacent individuals will form a group. Further additions to the group are also mediated by the prescribed cumulative tolerance period.

Agonism: If the daily average amount of food consumed was less than a prescribed percentage of the maximum daily consumption potential, that individual becomes agonistic, refusing to form new groups and repelling any floaters who enter her territory. Non-group members are actively repelled by the agonistic individual, who will approach and force away outsiders. The agonistic individual always prevails.

Group Abandonment: If the daily average amount of food consumed is less than a prescribed percentage of the maximum daily consumption potential, individuals with group membership dissociate from their group, becoming a floater.

Group behaviors:
Maintaining group cohesion: Every group member must have a territory that overlaps with at least one other member of the group. When an individual's territory does not overlap, the group enters a mode in which all members of the group move with bias toward the center of the group.

Melding of groups: Just as individuals can form a group based on a prescribed number of days of tolerance, two adjacent groups can similarly combine to form a single group once members have tolerated each other for the specified number of days.

Simulation run procedure:
Simulations can be run for any prescribed maximum number of days. The user can also specify a number of "stable days" sufficient to cause the simulation to terminate. Stable days are consecutive days where all groups have not changed (no additions or subtractions to group membership).

Data output:
The food distribution of each entered landscape is analyzed to output the variance-to-mean ratio at two scales: per grid cell and per quadrat, where the edge length of the quadrat is specified by the user and must evenly divide the landscape length and width. During the simulation, data is logged for the number of groups, average group size, variance in group size, average group territory size, variance in group territory size, and the number of floaters in each day. The program outputs this data for a specified number of days, always pulled from the end of the simulation.

Methods used for the simulations presented

Creating food fields for testing:
Each landscape was designed to provide the same average density of food. To determine what this baseline density should be, we assumed that each of the 50 individuals would be satisfied by consuming 50% of their maximum daily consumption potential of 3.0 food units, translating to a total of 75 units of food required per day. At a daily food regrowth rate of 10%, that requires that 750 units of food be available in the entire 100x100 landscape, for an average food density of 0.075.

Landscapes to be fed into fieldTest were created in Adobe Photoshop. Each landscape was initiated as a 100 x 100 pixel image file with a pure black background, representing a landscape with no food on it. A brush tool of varying diameter and density was used to lay down food semi-randomly. The goal was not to be perfectly random, but rather to create a diversity of landscapes with varying heterogeneities. Half (50) of the landscapes were made using a brush with diameter 11. The other half (50) were made with a brush with diameter 33. For each brush size, five different densities were used (expressed as "flow" in the photoshop brush tool): 15%, 30%, 45%, 60%, and 75%. Two brush sizes and five densities provided ten combinations, and ten replicate landscapes were constructed for each combination, yielding a total of 100 landscapes. For each of the 100 different landscapes, circular "patches" of food were created with the brush tool set to pure white. Image files are capable of representing 256 shades of gray, which means they range in gray value from 0 (pure black) to 255 (pure white). To determine the correct amount of food based on this range of gray, our target average food density based on a maximum of one food unit (0.075) was scaled to a maximum of 255, yielding a target mean gray value of 19.125. Photoshop's analysis tools were used to measure the mean gray value and calibrate each to a value of 19.125 ± .02. Where subtraction of some food was necessary, a brush of identical diameter and density set to pure black was used to prune until the target mean gray value was achieved. Each landscape was saved as a 32-bit TARGA file.

Simulation runs:
The landscapes described above are modeled after 100 meter by 100 meter plots used in previous prairie dog studies performed by Verdolin. Each simulation was run for a maximum of 500 days, with early termination of the simulations if group membership was stable for a period of 50 days. Each day was divided into twenty-four time steps, designed to represent fifteen-minute intervals of activity over a total of six hours of foraging.

A total of fifty individuals were included in each simulation. These individuals were configured to consume 0.2 units of food per time step with a maximum daily consumption potential of 3.0 food units. Individual territories were set to range from a minimum radius of four meters to a maximum radius of twelve meters from the home burrow. Each individual remembered the location and daily average amount of food consumed over the past five days. Home burrow relocation to the remembered consumption center was triggered below 70% of the maximum daily consumption potential. Home burrow relocation to a random nearby location outside of its current territory was triggered below 20% of the maximum daily consumption potential.

Individuals with a daily average consumption rate greater than 50% of the maximum daily consumption potential tolerated other individuals who entered her territory. The tolerance period for group formation and addition was ten days. Agonistic behavior was triggered below 50% of the maximum daily consumption potential. Below 30% of the maximum daily consumption potential, individuals with group membership were set to dissociate from their group, becoming a floater.

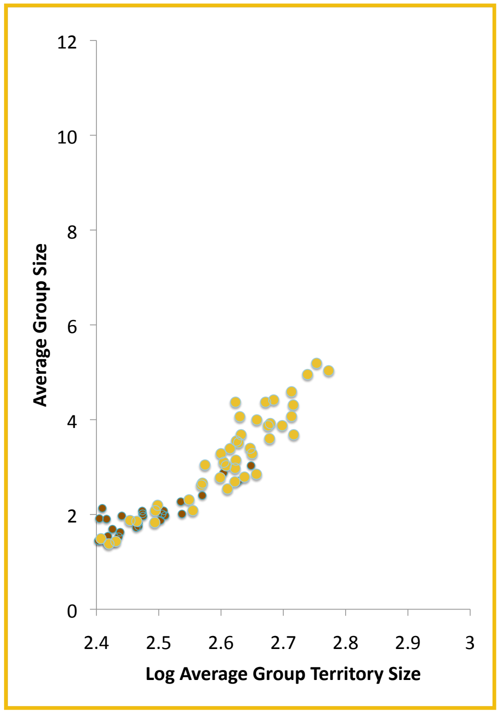
To test the effect of differing abundances of food, the food regrowth rate was varied. In addition to the baseline value of 0.10, sensitivity analysis was performed at ± 50% of this baseline value (0.05 and 0.15). Each of the one hundred food fields was run at all three of these food abundances, resulting in a total of three hundred simulations.

Data collection and organization:
Variance-to-mean ratios were calculated for each food landscape at two scales: 1x1 and 10x10. The number of groups, average group size, variance in group size, average group territory size, variance in group territory size, and the number of floaters were outputted for each of the last fifty days of each simulation. This output was used to generate figures which plot variance-to-mean ratio versus the various fifty-day average characteristics listed above for each simulation run.

ESA Annual Meeting 2009, contact Chris Jensen at cjensen@pratt.edu or 718-636-3572, http://pratt.edu/~cjensen

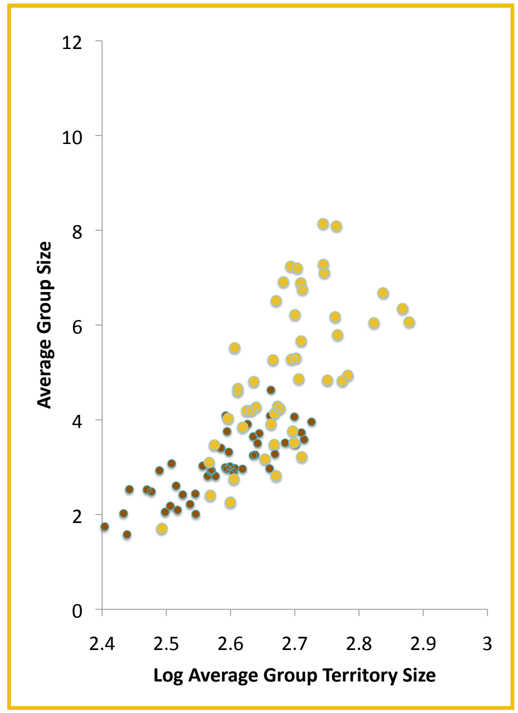
RDH: Group size and territory size are independent.

$R^2 = 0.75, P < 0.001$



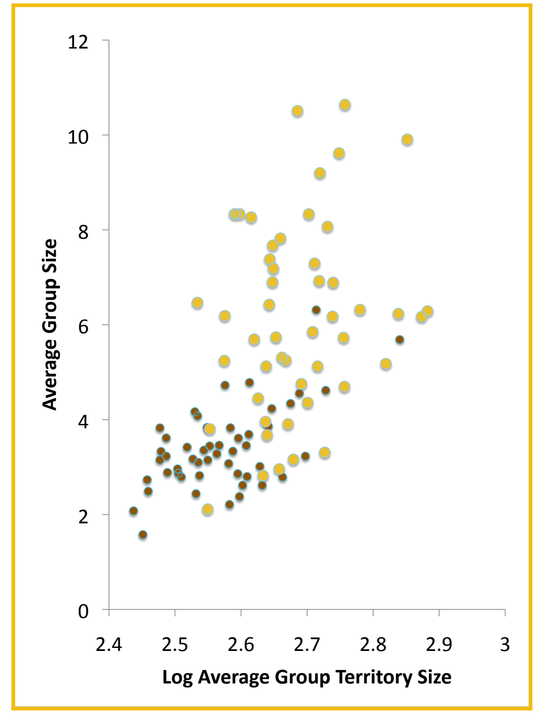
Regrowth = 5%

$R^2 = 0.60, P < 0.001$



Regrowth = 10%

$R^2 = 0.32, P < 0.001$

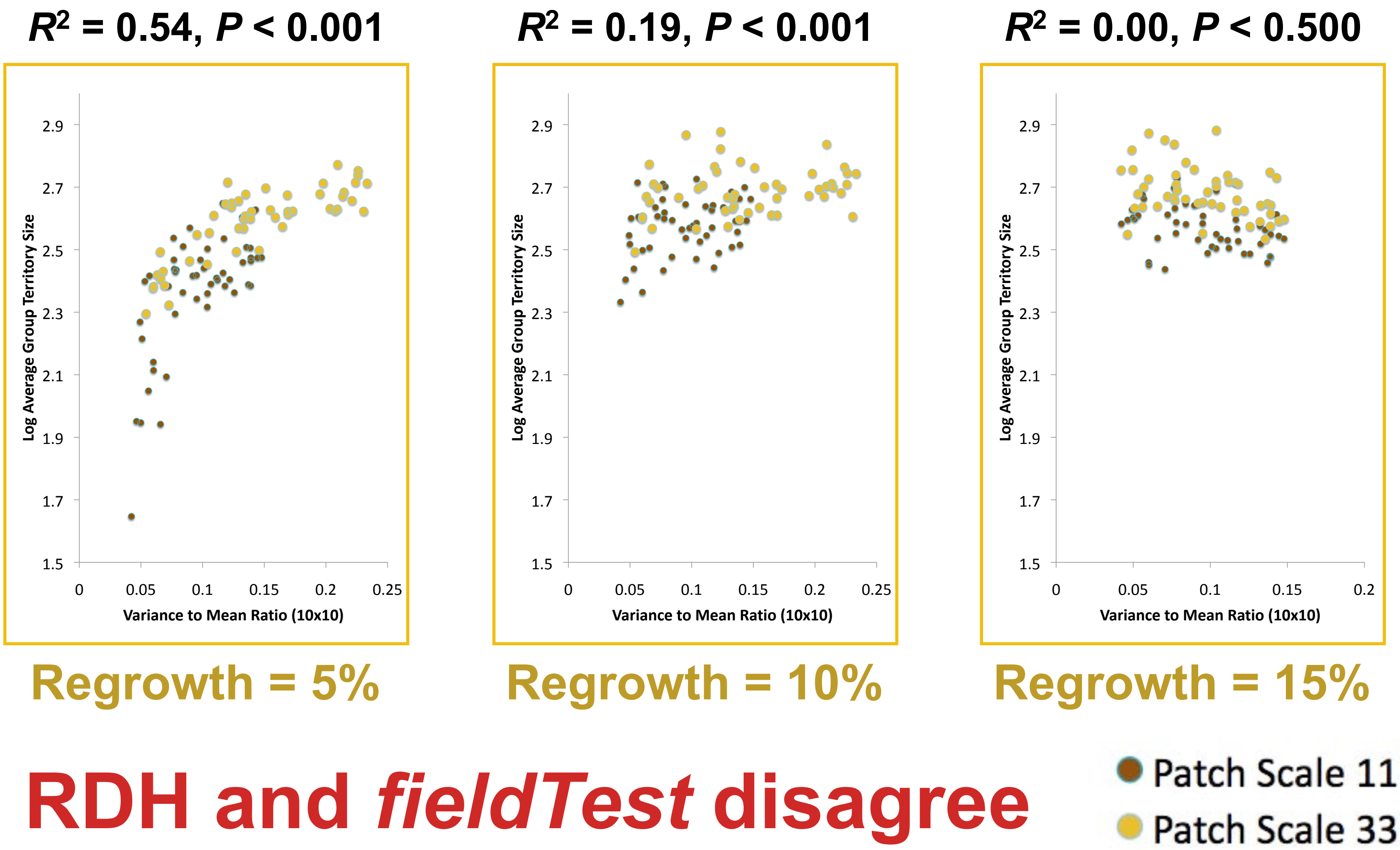


Regrowth = 15%

RDH and *fieldTest* disagree

Patch Scale 11
Patch Scale 33

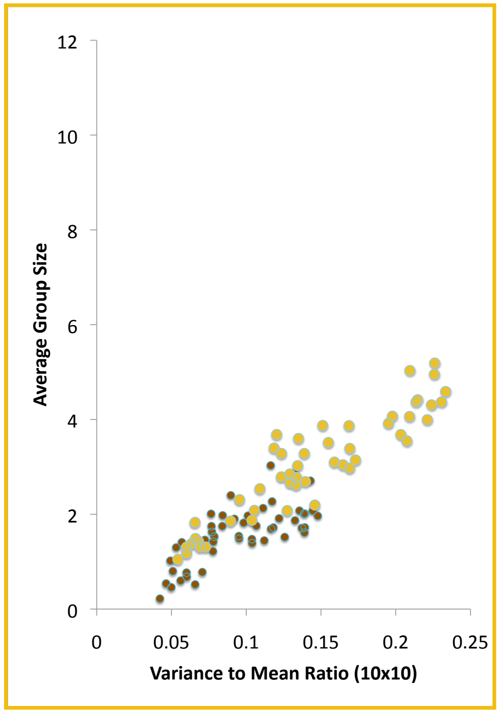
RDH: The more heterogeneous the resource distribution, the larger the territory size of each group.



RDH and *fieldTest* disagree

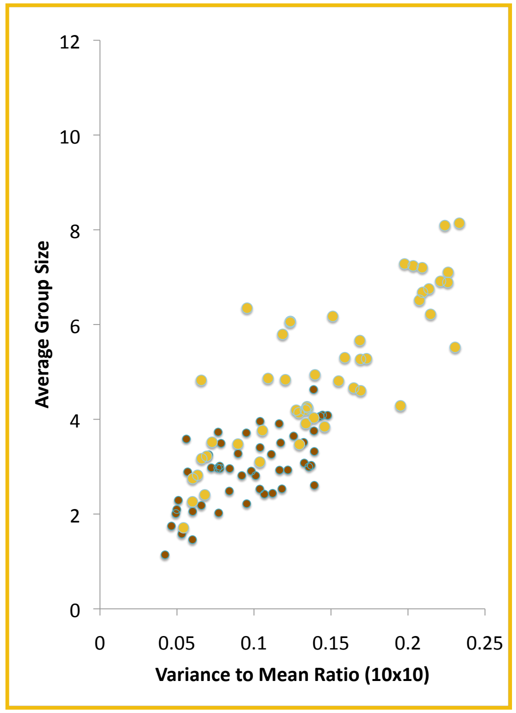
RDH: The more heterogeneous the resource distribution, the larger the group size.

R^2 = 0.81, P < 0.001



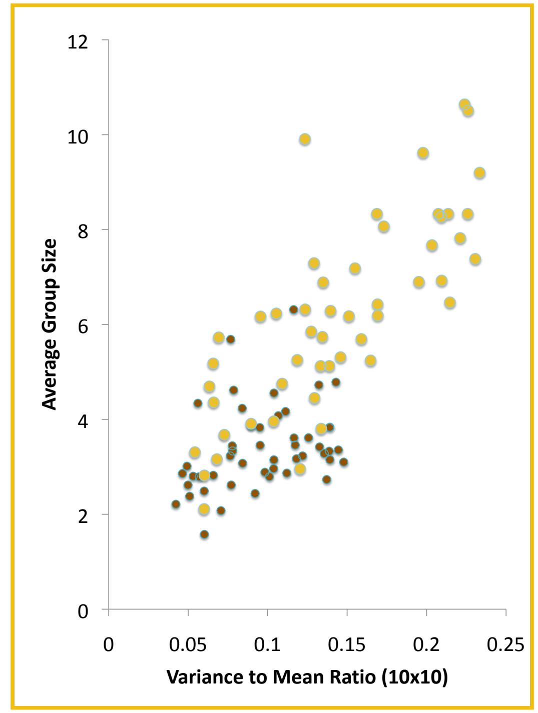
Regrowth = 5%

R^2 = 0.69, P < 0.001



Regrowth = 10%

R^2 = 0.59, P < 0.001

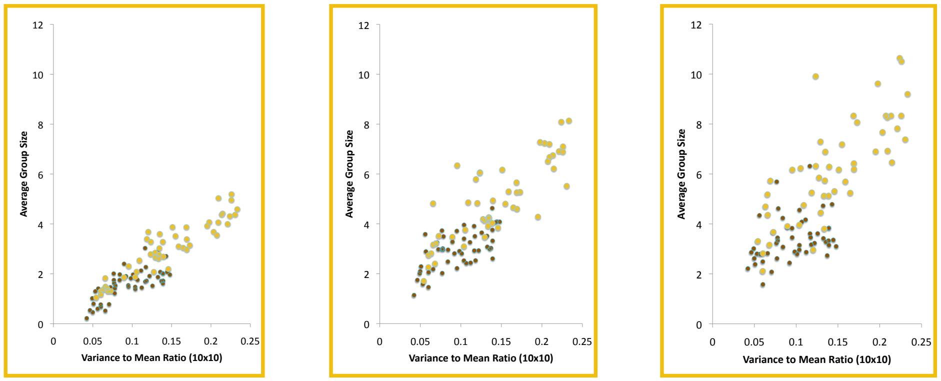


Regrowth = 15%

RDH and *fieldTest* agree

- Patch Scale 11
- Patch Scale 33

RDH: The greater the abundance of resources, the larger the group size supported.



RDH and *fieldTest* agree

	Slope	Intercept	R^2
5% regrowth	20.5	-0.16	0.81
10% regrowth	26.4	0.76	0.69
15% regrowth	32.1	0.92	0.59

In vivo tests of the *RDH*:

Resources, not Kinship, Determine Social Patterning in the Territorial Gunnison's prairie Dog (*Cynomys gunnisoni*)

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Abstract

In this study, we describe patterns of relatedness in Gunnison's prairie dog (*Cynomys gunnisoni*) social groups. Kin selection is often cited as a mechanism for the evolution and maintenance of social groups, and Gunnison's prairie dog females are occasionally described as being strongly philopatric. Overall, randomization tests revealed that females within territorial groups were not more closely related to each other than expected at random. A similar pattern was found among males and between males and females, indicating that there was no sex-biased dispersal occurring in these populations. Ecological variables measured in this study, such as food abundance and food dispersion, were not correlated with relatedness. In addition, territory size and density/m^2 did not correlate significantly with relatedness. Although there was variability in the spatial overlap among individuals within groups, there was no indication that relatedness explained this variation. These results suggest that kin selection is not maintaining social groups in these populations, but that competition for access to resources required by both males and females may explain dispersal and social group patterns in these populations.

Introduction

A central theme of behavioral ecology lies in understanding the evolution and maintenance of animal grouping patterns and cooperation. Because living in groups can carry significant reproductive costs (e.g., reduced resource acquisition, increased infanticide, and reproductive suppression), individuals living in groups must experience fitness benefits that exceed the actual fitness costs of sociality (Alexander 1974; Betram 1978; Wasser & Barash 1983; Wrangham & Rubenstein 1986; Janson 1992; Emlen 1997; Solomon & French 1997; Armitage 2003).

Kinship structure can have a profound influence on the degree and nature of social interactions by affecting the level of cooperation (Hamilton 1964a,b), dispersal, inbreeding avoidance (Shields 1982) and the degree of reproductive skew (Vehrencamp 1983). Although genetic relatedness is not a prerequisite for social groups, kinship may influence the degree of aggression during periods of environmental stress and membership status in a group (Giraldeau & Caraco 2000). Though there is some evidence that as relatedness increases aggression decreases, both within the group and with neighboring related groups (Brown & Brown 1993; Reeve & Nonacs 1997), more recent empirical investigations suggest that increased competition and aggression among relatives may reduce or eliminate kin-selected benefits (West et al. 2001; Griffin & West 2002). Kin-related groups may also determine when and which other individuals join a group, thereby regulating group size (Giraldeau & Caraco 2000).

The connection between cooperation and kinship was first proposed by Hamilton (1964a,b). Hamilton proposed that the costs and benefits of social

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ORIGINAL PAPER

Gunnison's prairie dog (*Cynomys gunnisoni*): testing the resource dispersion hypothesis

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Abstract Few studies have experimentally tested the resource dispersion hypothesis (RDH). In this study, I tested whether space use and social organization of Gunnison's prairie dog responded to changes in the dispersion and abundance of resources. Food manipulations were carried out during the reproductive and nonreproductive seasons across 2 years. Gunnison's prairie dog adults responded to the experiments by decreasing territory size as food became patchier in space and time. Both males and females modified their home ranges, with no detectable difference between sexes, either prior to or during the experiments. As food became patchier in space and time, the spatial overlap of adults increased, whereas it decreased as food became more evenly dispersed. The average size of a group, defined as those individuals occupying the same territory, did not change significantly as a result of the experiments. Where changes in the composition and size of groups did occur, there was no indication that such changes were sex specific. Results from this study support critical components of the RDH and strongly suggest that patterns of space use and social structure in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution.

Keywords *Cynomys gunnisoni* · Resource dispersion · Social structure · Group living

Communicated by P. Banks

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Introduction

A general principle, first described by Crook (1965), is that individuals in a population tend to aggregate more as the dispersion of their food becomes more clumped (patchy) in space. This broad correlation has been verified in an extensive array of organisms (birds: Myers et al. 1981; Stouffer et al. 1988; Gunnison's prairie dogs, *Cynomys gunnisoni*: Slobodchikoff 1984; Travis and Slobodchikoff 1993; European badgers, *Meles meles*: Kruuk and Parish 1982, 1987; brown hyenas, *Hyaena brunnea*: Owens and Owens 1996; primates: Yamagiwa and Hill 1998; see Lott 1991 for review). Many of these correlations are likely due to the costs associated with competition among group members for resources balanced against the benefit of exploiting a clumped resource (Waser 1977, 1988; Bradbury and Vehrencamp 1976; Janson 1992; van Schaik and Janson 2000).

An extension of this general pattern, the "resource dispersion hypothesis" (RDH) states that the abundance and distribution pattern of critical resources may provide a distinct underlying mechanism for the evolution of groups (Macdonald 1983, 1984; Slobodchikoff 1984; Carr and Macdonald 1986; Slobodchikoff and Schultz 1988; Bacon et al. 1991a, b; da Silva et al. 1993; Woodroffe and Macdonald 2000). The RDH differs from Crook's hypothesis in that it is limited to territorial animals, while Crook suggested that territoriality could act as an impediment to sociality (Crook 1965). Although the RDH is also similar to Brown's (1982) model of optimal group size, two unique assumptions differentiate the RDH from this and other models. First, the RDH assumes shared territorial defense as the primary benefit to group living. Second, no other benefits or external forces are assumed necessary to explain group formation and maintenance, though the model does not preclude other benefits from existing.

Conclusions

- In contrast to the *RDH*, *fieldTest* predicts that group size and territory size should covary.
- In contrast to the *RDH*, *fieldTest* predicts that territory size has a complex relationship to resource heterogeneity that depends of the relative food abundance.
- In agreement with the *RDH*, *fieldTest* predicts that group size increases with resource heterogeneity.
- In agreement with the *RDH*, *fieldTest* predicts that group size increases with resource abundance.
- Particular landscapes may contain spatial idiosyncrasies that produce social grouping patterns at odds with *RDH predictions.*

Pratt

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