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Original Article

Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality

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Group territoriality is exhibited in a diverse range of species and is associated with complex behaviors such as cooperation and altruism. Current hypotheses for the evolutionary transition from solitary to group territoriality consider resource dispersion and population density as the primary drivers. We developed a spatially explicit, agent-based simulation model based on African lions (*Panthera leo*) to explore the evolution of group territoriality across a range of landscape heterogeneities and population densities. We also examined, within these differing landscapes, how 3 potential behavioral advantages to group territoriality (cooperative defense, increase in territory size, and territorial inheritance) influence the evolution of this trait. Simulation results demonstrate that group territoriality may be an emergent property, which evolves due to synergistic interactions of landscape structure, population density, and behavior. Social individuals were significantly more likely to dominate in both resource-poor and resource-rich, heterogeneous landscapes where individuals exhibit all 3 behavioral traits. Similar environment–behavior interactions may have shaped the evolution of sociality from solitary territoriality across a broad range of taxa.

Key words: **emergence, group territoriality, landscape heterogeneity, *Panthera leo*, resource dispersion hypothesis.**

INTRODUCTION

Group territoriality has arisen independently across insects (Adams 1990), birds (Brown 1970; Woolfenden and Fitzpatrick 1984), fish (Clifton 1990), and mammals (Waser 1981; Packer et al. 1990; Wilson and Wrangham 2003; Bowles 2009). Although widespread, group territoriality is comparatively rare, suggesting that this form of sociality can only evolve under a restricted set of conditions. Group-territorial species commonly exhibit a range of highly complex traits, including numerical assessment (McComb et al. 1994), adaptive lethal aggression (Manson and Wrangham 1991), and diverse forms of altruism (Olendorf et al. 2004; Bowles 2008).

Past work has focused on ecological drivers as potential hypotheses for the evolution of group territoriality, so we developed an agent-based simulation model that explores how both landscape heterogeneity and population density may have influenced the evolution of group territoriality in African lions (*P. leo*). Detailed study points to group territoriality as the foundation of lion sociality (Packer et al. 1990; Mosser and Packer 2009). Though occasionally gregarious, all other felids maintain individual territories, whereas lions are highly dependent on their pride-mates for survival and reproduction (Packer et al. 2001). Also unlike other *Panthera* species, lions are found almost exclusively in savanna habitat, a landscape characterized by heterogeneity (Pickett et al. 2003; Boulain et al. 2007; Levick and Rogers 2008) and high levels of primary productivity (Sinclair 1979). Accordingly, lion sociality is commonly viewed as an adaptation to savanna habitat (Kleiman and Eisenberg 1973; Packer 1986; Mattern and McLennan 2000).

Group territoriality has been considered to be more advantageous in species that rely on heterogeneous resources, and the resource dispersion hypothesis (RDH), proposed by Macdonald (1983), formalized the long-standing recognition of a relationship between resource distribution and patterns of sociality (Crook 1964; Wilson 1975; Bradbury and Vehrencamp 1976; Kruuk 1978; Von Schantz 1984). The RDH states that landscape heterogeneity facilitates the formation of social groups because the economics of territory defense in a patchy landscape yields territories that not only support an individual or breeding pair, but that may also support additional individuals at low cost to the territory owner. Macdonald (1983) termed these passive aggregations "spatial groups." Criticism of RDH (Revilla 2003a, 2003b) has prompted the clarification that resource dispersion alone is an unlikely causal mechanism for the evolution of sociality, but, when paired with a

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behavioral advantage to grouping (such as cooperative territorial defense), spatial groups could pave the way to sociality as an adaptive behavioral strategy (Johnson and Macdonald 2003).

Group-territorial individuals benefit from a range of behavioral traits. Empirical work confirms the advantages of cooperative defense: larger groups win intergroup contests (Carlson 1986; Cheney 1987; Grinnell et al. 1995; Adams 2001; Wilson and Wrangham 2003) and have higher quality territories (Woolfenden and Fitzpatrick 1984; Kauffman et al. 2007; Mosser and Packer 2009). Groups can also share the energetic costs of territorial maintenance (Davies and Houston 1981; Clifton 1990), allowing for territorial expansion (Kruuk and Macdonald 1985). Individuals in group-territorial systems further benefit from natal philopatry and territorial inheritance (Woolfenden and Fitzpatrick 1978; Lindstrom 1986), particularly in heterogeneous landscapes (Stacey and Ligon 1987). The benefits of these behavioral patterns may only be realized at high population densities (Gaston 1978; Packer 1986; Koenig et al. 1992; Emlen 1994; Horiuchi 2007), thus the advantages of group territoriality are expected to interact with the overall resource availability of the landscape. We explore the significance of these traits and examine how this might vary in the context of different landscape patterns.

We created a model to explore the individual fitness benefits of solitary versus social territoriality given different patterns of landscape structure and individual behaviors. We capture different patterns of landscape heterogeneity by varying the distribution of resources on the landscape (evenly spread to highly clumped). Population density was altered by varying the average overall resource availability of the landscapes. Three behavioral traits—cooperative territorial defense, territorial expansion, and territorial inheritance—were each entirely present or absent in different simulations. The individual lions formed "groups" that contained 1 or more individuals. Groups attempted to maximize the value of their territories within the constraints of the economics of territorial defense (Davies and Houston 1984; Adams 2001) and depending on the outcome of competitive territorial interactions. We tested for the persistence of alternative genotypes in mixed populations: *solitary* individuals that always remained alone and *social* individuals that formed groups with related individuals whenever possible. Different simulation scenarios tested the hypothesis that the evolution of group territoriality requires a heterogeneous landscape with high population density, as well as individuals that express behavioral traits that allow them to realize the benefits of group-territory formation.

MATERIALS AND METHODS

Our agent-based, spatially explicit, stochastic model simulates a population of female lions through time. The model structure and parameters are based up on existing empirical data on African lions, with much of this derived from the long-term study population of the Serengeti National Park, Tanzania. This lion population has been studied continuously since 1966 (Schaller 1972; Bertram 1973; Hanby and Bygott 1979; Packer et al. 2005), providing detailed individual-based demographic and spatial information on more than 1100 adult female lions residing in 45 lion prides. The 2700-km^2 study area is located at the center of the Serengeti ecosystem and encompasses the landscape heterogeneity characteristic of a savanna landscape.

Each simulated lion population is modeled as residing on a finite 2-dimensional lattice of cells. The model progresses in time steps, each of which represents a year; individual lions follow the life-history pattern of Serengeti lions (Supplementary Tables A1 and A2) and form groups of 1 or more individuals, depending on genotype (solitary vs. social). Each simulation runs for 500 time steps (years) with 20 replicates for each scenario. The models reached equilibrium well before 500 time steps, and outcomes differed little for the same set of parameters, thus 20 replicates were sufficient to capture any stochastic variation. Each time step progresses as follows: 1) lions age or die, 2) lions reaching maturity disperse or join their parent's group, 3) adult lions reproduce and can do so every year, 4) groups assess their territories, and 5) groups compete with neighbors for territory. We ran scenarios that varied resource dispersion and availability, and the presence or absence of cooperative territory defense, territorial expansion, and territorial inheritance. An animation of 1 simulation is presented in the Supplementary Video Online.

Landscapes

Analysis of female lion reproductive success shows that individual fitness is dependent on access to river confluences (the point at which tributaries meet), which provide food, water, and shelter in a single location (Mosser et al. 2009); an earlier analysis showed that hunting success in these same lions was associated with proximity to confluences (Hopcraft et al. 2005). River confluences represent the sort of high-quality patches envisioned in the RDH (Macdonald 1983), so we created heterogeneous landscapes with "hot spots" analogous to river confluences. We consider 2 landscape-level configurations of hot spots (Figure 1A): a random distribution and a clustered pattern derived directly from the map of river confluences in the Serengeti lion project study area, which follows a power-law distribution (Supplementary Figure A1). Power-law relationships are common in nature (Scanlon et al. 2007) and not unexpected for a fractal drainage network (Turcotte 2007).

The model runs on a 60 × 40 cell lattice "landscape," in which each cell represents 1 km^2 of land. This lattice is similar in size and scale to the Serengeti lion study area. Each lattice cell has an associated resource value. All cells have the same value in homogenous landscapes. In heterogeneous landscapes (Figure 1B), "hot spots" are assigned a maximum resource value, and the remaining cell values decrease with the distance of the cell from the nearest hot spot. Hotspot "peakedness," the rate of cell value decline with distance, varies according to an exponent, P; a value of $P = 1$ indicates a linear decline of value with distance from the nearest hot spot, whereas larger values of P indicate a faster decrease in cell value with distance (see Supplementary Appendix A, Equation 1). Landscapes with sharp declines in quality are realistic for lions as territorial defense prevents free movement across the landscape (McComb et al. 1994; Grinnell and McComb 2001); prides monopolize hot spots within their territories (Supplementary Figure A2).

Resource availability is modeled as the overall "landscape value," which refers to the mean value of all cells on the landscape. Minimum cell values are fixed across all landscapes, so landscapes with the same mean value, vary only in the maximum value (V_{max}) across the landscape and with P (as described above). Landscapes with higher values of P thus have higher V_{max} as well. Figure 1B shows 2 landscapes of equal value (mean value = 160, minimum cell value = 140); the top one has a low peakedness ($P = 4$, $V_{max} = 171$), whereas the bottom one has high peakedness ($P = 64$, $V_{max} = 330$).

We examine a range of landscape values. In general, population density is expected to increase with higher landscape values. In the lowest value landscapes, the mean and minimum resource values are set such that homogeneous landscapes can only support solitary

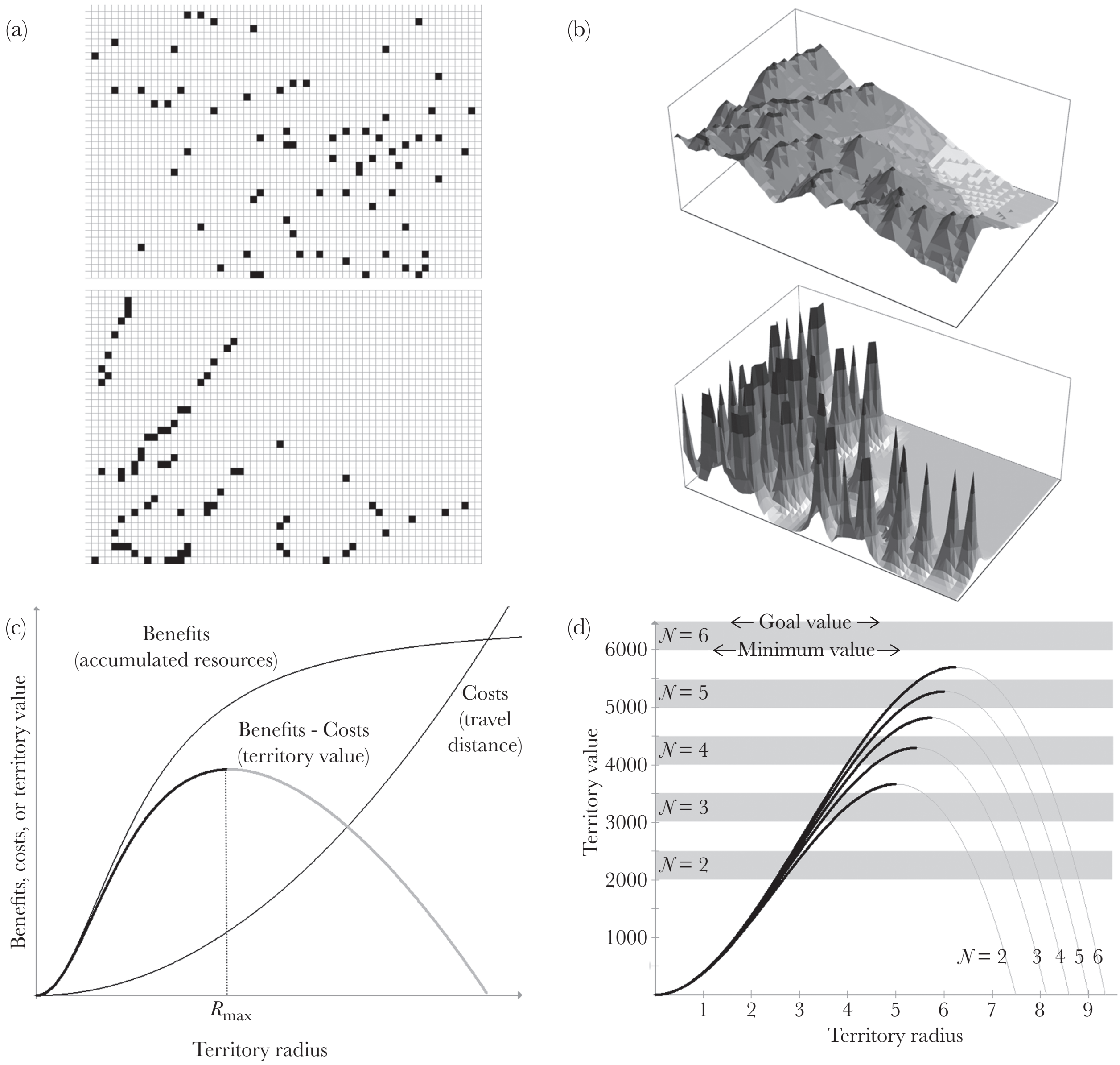

Figure 1

(a) Randomly located hot spots (top) and a clustered hot-spot landscape (bottom). (b) Clustered hot-spot landscapes (mean value = 160, minimum cell value = 140) of low peakedness (top, $P = 4$, $V_{max} = 171$) and high peakedness (bottom, $P = 64$, $V_{max} = 330$). (c) Territories increase in size, accumulating asymptotic benefits while defense costs accelerate. Territory size and value are maximized where (benefits−costs) is maximized, at R_{max}. (d) Landscape resource values set a limit on group size. In this example, the mean landscape value is 140, and groups of 2–4 can reach both the minimum territory value and goal territory value; groups of 5 can reach the minimum territory value but not the goal territory value and thus reproduce at a rate less than the maximum; groups of 6 cannot reach the minimum territory value and cannot survive in this landscape.

lions, whereas heterogeneous landscapes cannot support any lions in areas of minimum cell value. In the highest value landscapes, the mean and minimum resource values are set so that homogeneous landscapes can support groups of multiple lions, as can all areas in heterogeneous landscapes.

Territories

A "territory" is the collection of cells defended by a group of 1 or more lions. Each territory has a central point, much like an object's center of mass, which is calculated as the mean of the locations of all territory cells, weighted by each cell's resource value (Supplementary Appendix A, Equation 2). The realized value of each territory cell to its owner is a combination of the cell's absolute value and its distance from the central point (Supplementary Appendix A, Equation 3); this discounted value reflects the travel cost to outer regions of a territory (Getty 1981; Mitchell and Powell 2004). The total value of the territory to its owner is the sum of these adjusted cell values. As individuals seek to maximize territory value, a territory will not expand beyond the radius (as described below), where cell values would be negative due to travel costs.

The maximum territory radius for a solitary individual (a group of 1) is set to 4 cells, corresponding to the 4-km mean territory radius of solitary females in the Serengeti National Park (Mosser and Packer 2009). If the behavioral trait of territorial expansion is present, then the maximum territory radius increases with group size (Supplementary Appendix A, Equation 4), as observed in a number of group-territorial species (Macdonald 1983). If the trait of territorial expansion is turned off, then the maximum radius of a territory simply remains at 4 cells.

When cells are added to or removed from a territory, the territory is adjusted to maximize the value of the territory to its owners. First, the territory central point is recalculated based on the new set of territory cells. Next, the value of each cell to the territory owners based on this new central point is calculated. Any cells with a value of 0 or less are removed from the territory; the territory central point and territory value are then recalculated.

Groups

Each individual belongs to a group that contains 1 or more individuals. Each group may have a territory. To maintain the territory, the territory must meet a minimum value for that group. To maximize fitness, groups attempt to manage their territories such that the territory value reaches a "goal" value, above which no additional benefits accrue (Figure 1D). Requirements for the minimum and goal territory values increase linearly with each additional adult in the group. The goal territory value for a group of size N is set to less than the minimum territory value for a group of size $N + 1$, so that adding an additional member to a group requires an increase in territory value—an assumption that is tested in the sensitivity analyses (see below).

A group without a territory attempts to gain one by finding a vacant area that meets the group's minimum requirement. For a territory-holding group, minimum and goal territory values are recalculated each time step according to current group membership. Territories shift, grow, or shrink as groups attempt to meet the goal values (see Supplementary Information for details). If the group's territory value is below the minimum, the group abandons the territory, all 2- to 3-year-olds disperse, and all younger offspring die (Packer et al. 1990).

Solitary and social lions

All individuals possess a genotype of either "solitary" or "social." Each simulation begins with a population of purely solitary individuals. Offspring are assigned their parent's genotype (assuming asexual reproduction) with probability 0.99 and the other genotype with a mutation probability of 0.01. This mutation rate is commonly used in simulation modeling (see as an example, Nowak et al. 2004) and is high enough to ensure competition between genotypes in a reasonable amount of time, but not so high that random walks dominate model dynamics. Solitary individuals always leave their natal group at maturity and live alone. Social individuals may or may not remain in their natal group, depending on the ability of the natal territory to support them as adults; if they leave their natal group, they always remain together with other members of their natal cohort (VanderWaal et al. 2009). Social groups are always composed of related individuals, thus kin selection is an implicit component of our model. We vary territorial inheritance by either requiring social offspring to leave their natal group with their cohort at maturity (no inheritance) or allowing social offspring to remain in the natal group (inheritance).

Demography

Territorial adults incur stochastic age-specific background mortality; those without a territory have a 50% chance of dying per time step (see Supplementary Tables A1 and A2). Dependent offspring die if the territory value is below the minimum or if the territory is lost, and dependent offspring with a dead parent have a 75% chance of dying per time step (Packer et al. 1988).

Lion females mature at age 3 (Packer et al. 1988), and many disperse from their natal groups (VanderWaal et al. 2009). A dispersing cohort group (of 1 or more 3-year-old lions) attempts to establish a territory in the nearest open area that meets its minimum territory value requirements (VanderWaal et al. 2009), but it will continue to survive (albeit with a higher mortality) without a territory if no suitable area is available.

All territory-holders ≥4 years of age may reproduce, if they have no dependent offspring age 3 or younger. To simplify our system, we assume that individuals reproduce asexually and model only females. The probability of reproduction depends on the value of the territory relative to the goal and minimum territory values (Mosser et al. 2009). The reproductive rate is 100% at the goal value and declines linearly to a rate of 0% at the minimum value. The number of offspring produced by an individual per reproductive event ranges stochastically from 1 to 3 (Packer and Pusey 1995).

Intergroup competition

At each time step, each group is allowed to contest a fraction of each neighboring group's territory, provided that the cells would increase the value of its own territory. Neighbors are considered in random order, and desirable cells are identified within neighboring territories. A group can contest up to 25% of the average territory size on the landscape, which is the average degree of territory overlap in Serengeti lions (Mosser 2008). Willingness to attack or defend a territory depends on relative group size (Supplementary Appendix A, Equation 5; McComb et al. 1994). For simplicity, we assume equal fighting ability of all individuals. A group will invade a neighbor's territory if its probability of winning is ≥55% and will defend against invasion if its probability of winning is ≥45%, representing a weak advantage of prior ownership, which is common for territorial species (Maynard Smith and Parker 1976) and consistent with lion behavior (Mosser and Packer 2009 and see Supplementary Appendix A, Figure A3).

Fights occur when both groups engage in the contest and are associated with a 5% probability of 1 individual dying in each group (Grinnell et al. 1995). The winner of the contest is determined stochastically, with the probability of the attacking group winning being directly proportional to group size (Supplementary Appendix A, Figure A3), if the behavioral trait of cooperative defense is turned on. If cooperative defense is absent each group has a 50% chance of winning the contest. If an attacking group is successful, the contested cells are incorporated into the attacking group's territory and the 2 territories are subsequently reconfigured to maximize resource value and density.

Hypothesis testing

To assess the success of social versus nonsocial strategies, we calculated the proportion of lions with the social genotype in the population at the last time step of each simulation and present the mean across the 20 replicates. Equal proportions of solitary and social lions represent equality of the 2 strategies, thus proportions of social individuals <0.5 indicate an advantage to a solitary strategy, whereas proportions >0.5 suggest an advantage to a social strategy.

Total landscape value is varied between 80 and 180, which alters population density from low to high. The influence of landscape heterogeneity (resource dispersion) is tested by varying the hot-spot peakedness (*P*), where a value of 0 refers to a homogenous landscape and 64 represents the most heterogeneous landscapes. The effect of landscape structure is further tested with landscapes of random- versus power-law-distributed hot spots. The benefits of the 3 behavioral traits are assessed by turning on or off each trait for all individuals in the population. In different simulation runs, we run 1 set of the possible combinations of the presence or absence of these traits. When cooperative territorial defense is absent, group size has no impact on intergroup competition, and thus larger groups have no advantage in intergroup contests. In the absence of territorial expansion, the maximum territory radius remains at 4 cells regardless of group size. When territorial inheritance is absent, all cohorts are forced to disperse at maturity, though social cohorts remain together in sibling groups. We expect that the social genotype, or group territoriality, will be more common in more heterogeneous landscapes (those with higher values of *P*) and in higher values landscape (those that support higher population densities). We also predict that at least 1 behavioral advantage will be required to allow for the social gene to thrive, and that the presence of multiple behavioral traits will add to the success of the social strategy.

In addition, uncertain values and key parameters were included in sensitivity analyses to assess the robustness of our conclusions (see Supplementary Information).

RESULTS

Landscape value and population density

Group territoriality is more likely to be the favored strategy (>50% of the final population) as total landscape value increases, depending on landscape structure (Figure 2). The effect of landscape value is nearly absent in homogenous landscapes, where the social genotype is never favored. In landscapes with randomly distributed hot spots (Figure 2A), increasing landscape values and increasingly heterogeneous landscapes consistently predict a higher proportion of social individuals. Where hot spots are clustered (Figure 2B), the effect of landscape value interacts with landscape heterogeneity. These patterns are consistent throughout the sensitivity analyses (Supplementary Table A3). Although the simulations consistently showed that a high landscape value supports high lion population density (see Supplementary Figure A4), population density alone did not determine the prevalence of social individuals.

In heterogeneous landscapes (with hot-spot peakedness, *P*, of 16–64) with clustered hot spots, the social genotype is most advantageous at low and high population densities, but lower at moderate densities (Figure 2B). The bimodal effect of landscape value, illustrated in Figure 3, demonstrates the relative success of the opposing strategies in different portions of a variable landscape. The social genotype is particularly advantageous when low value areas are uninhabitable by either genotype (Figure 3A). Although

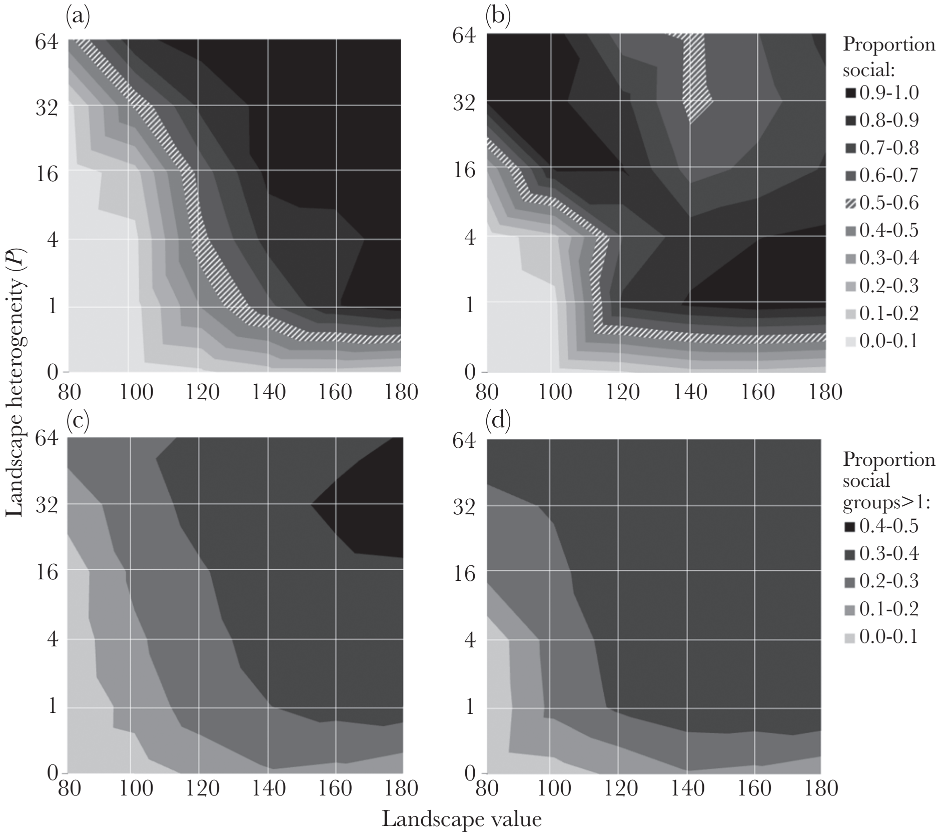

Figure 2

The effect of landscape value and landscape heterogeneity on sociality. Landscape heterogeneity is determined by peakedness, *P*, where $P = 0$ denotes a homogeneous landscape. Top: High landscape heterogeneity and high landscape value favor the social genotype. Percent of agents in the final population that carry the social gene, where <50% indicates an advantage to the solitary strategy and >50% indicates an advantage to the social strategy, for (a) random and (b) clustered hot spot distributions. Bottom: Percent of "social" groups in the final population that contained more than a single adult agent for (c) random and (d) clustered distributions.

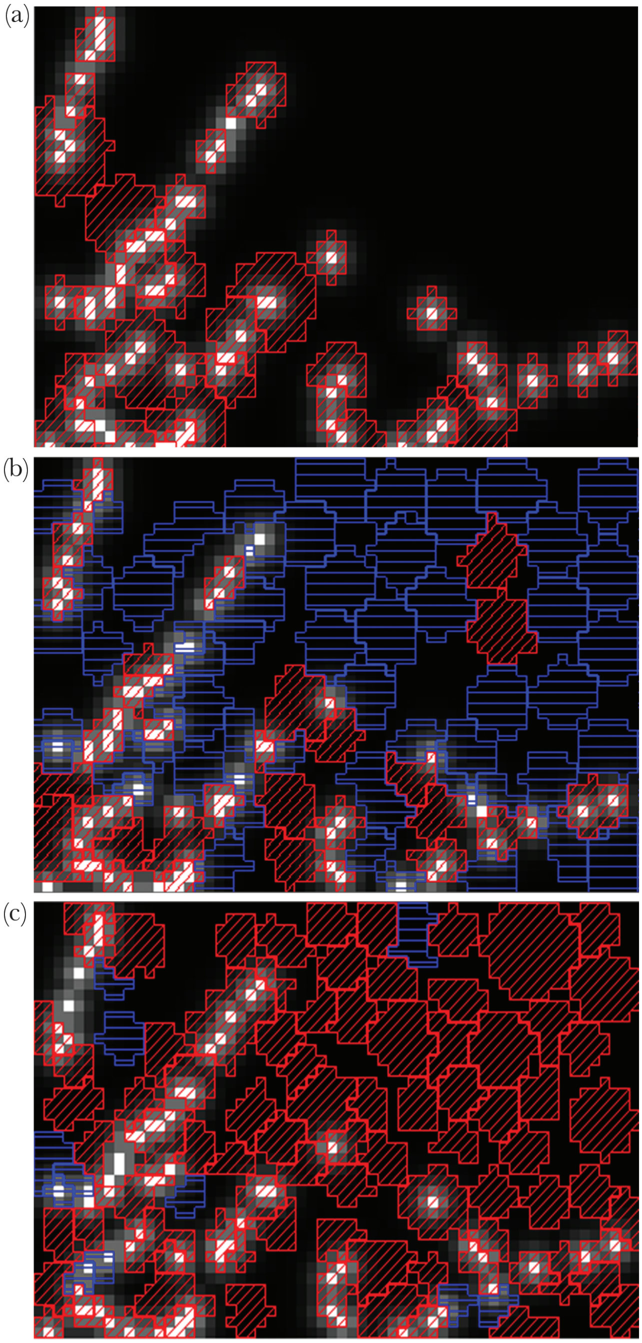

Figure 3
Example spatial distribution for territories with solitary (blue) and social (red) genotypes in highly heterogeneous (P = 64) clustered hot-spot landscapes. Landscape values are shown in gray scale with white cells indicating high value and black cells indicating low value. (a) Low mean landscape value (80), where social groups monopolize the rare best areas in a poor-quality habitat. (b) Middle mean landscape value (140), where solitary groups are more successful than social groups outside the hot-spot clusters. (c) High mean landscape value (180), where social groups can thrive in any part of a high population density (high-quality) landscape.

overall population density is low, the fine-scale population density actually experienced by each agent is quite high because only a portion of the landscape is inhabitable. At moderate landscape values (Figure 3B), social groups continue to dominate the high-quality hot spots, whereas solitary individuals thrive in the remaining areas. At highest landscape values (Figure 3C), sociality is favored across the entire landscape as social groups can also dominate the lower value areas. These results highlight how landscape value and population density interact with landscape structure to influence patterns of group territoriality. Individual fitness is affected by the local environment, which fundamentally depends on the way resources are distributed across a landscape.

Landscape structure

Resource heterogeneity appears to be necessary for the evolution of group territoriality in lions. Sociality increases with increasing landscape heterogeneity (Figure 2A), but the effect of high heterogeneity is most striking at lower landscape values, where social groups can exclude solitary agents from clustered hot spots and solitaries cannot survive in poor-quality habitat (Figure 3A). These effects are consistent across all sensitivity analyses (Supplementary Table A3).

Figure 2C,D show that the social genotype is often unexpressed (i.e., social "groups" of 1 adult), even in landscapes where it is highly favored. Because heterogeneous habitats can only support a limited number of multilion groups, the majority of dispersing social offspring must live alone in poor-quality habitat.

Behavioral advantages

Ecological factors are insufficient for the evolution of group territoriality. The social genotype is never favored if social individuals have none or just one of the 3 possible behavioral advantages (cooperative defense, territorial expansion, or territory inheritance; Figure 4). In some landscapes, the social genotype is favored when cooperative defense is paired with territorial inheritance. In particular, high landscape heterogeneity is required for the social genotype to be favored in the absence of territorial expansion. In most cases, however, all 3 behavioral traits are necessary for the social genotype to spread and the behavioral advantages of group formation are highly synergistic (Figure 4). For example, cooperative defense plus territorial inheritance lead to a higher proportion of social individuals (~0.92) than would be expected based on the effects of either factor in isolation (only ~0.07 and 0.08, respectively). The co-occurrence of all 3 factors in combination with some degree of landscape heterogeneity leads to sociality far more often than expected if the combined impact of each factor was either additive or multiplicative, as indicated by the stars in Figure 4. The sensitivity analyses revealed only minor variations in these results (see Supplementary Appendix A for these details).

DISCUSSION

Lions are one of the best-studied mammalian species, and many components of our model were parameterized with empirical data, whereas the remaining variables relied on qualitative assessments that were subjected to rigorous sensitivity analyses (see Supplementary Appendix A). We simplified the model by only considering interactions among females, thus ignoring the impacts of males, whose infanticidal behavior promotes the formation of "nursery groups" that collectively defend vulnerable young against outside threats (Packer et al. 1988); males are also known to kill females from neighboring groups to enhance the reproductive success of females in their own group (Mosser and Packer 2009; also see Wilson and Wrangham 2003). In addition, many of our modeling decisions were conservative, so as to prevent the social strategy from inevitably causing the evolution of group territoriality.

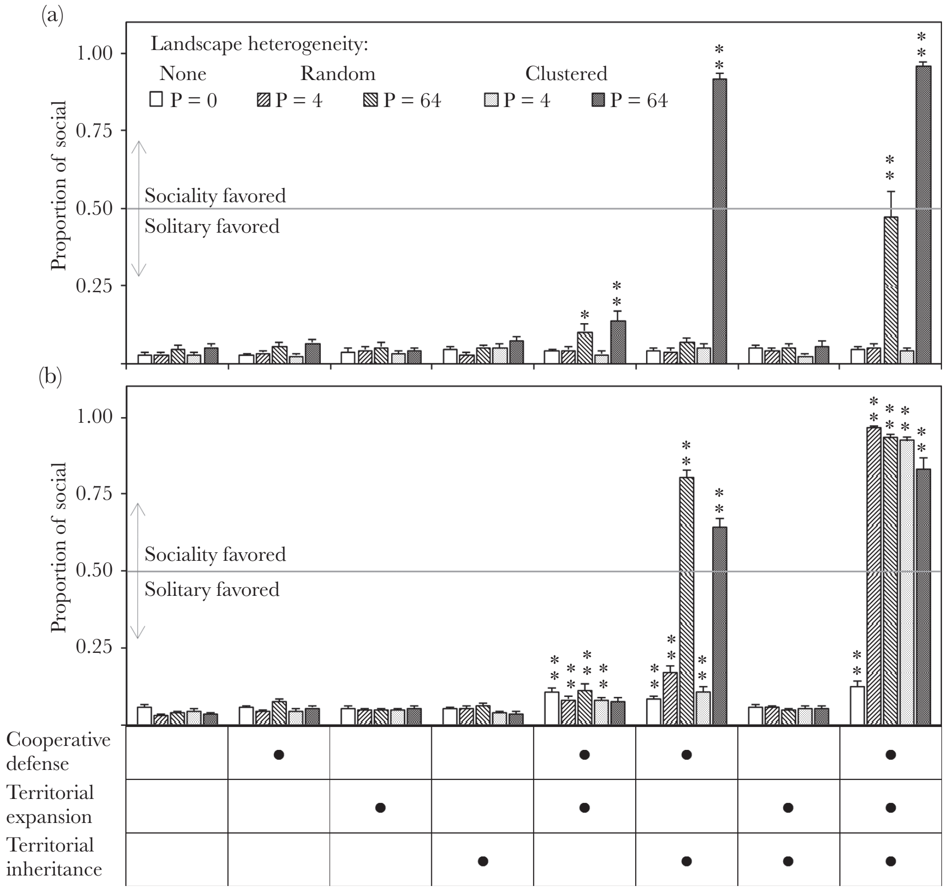

Figure 4

Proportion of social individuals at the end of each simulation. Success of the social genotype emerges from the interaction between behavioral and landscape traits. Scenarios are grouped by behavioral traits (boxes at bottom). Scenarios are shaded according to landscape type (homogenous, random hot spots, and clustered hot spots) and landscape heterogeneity (none: $P = 0$, low: $P = 4$, high: $P = 64$). (a) Low population density and landscape value. (b) High population density and landscape value. Error bars indicate standard errors across 20 replicates. We have indicated where interactions produce synergistic effects that are greater than statistical predictions, suggesting patterns of emergence: *Additive synergy (the whole is greater than the sum of the parts), **Multiplicative synergy (the whole is greater than the product of the parts).

Nevertheless, our model outputs mimic observed patterns of spatial distribution: like real prides (Supplementary Figure A2), simulated prides were centered on discrete hot spots, and low-quality areas remained unoccupied (Figure 3A).

Our results indicate that a combination of landscape value, landscape heterogeneity, and multiple behaviors are necessary to explain the rise of group territoriality in African lions and that the trait demonstrates many of the hallmarks of an emergent property (Corning 2002). Lion sociality likely arose from the more typical felid pattern of solitary territoriality when a specific set of conditions converged: the environment must have been productive and heterogeneous at the appropriate scale, sustaining a suitable population density and containing sufficiently high-quality patches, and individuals must have possessed a behavioral predisposition towards cooperative territorial defense, in particular, with territorial expansion and inheritance further bolstering the advantages of group formation.

Our results indicate that cooperative territorial defense is necessary for the evolution of group territoriality. In group-territorial species, there is often strong selective pressure for numerical superiority and effective cooperative defense: larger groups are known to control higher quality territories (Kauffman et al. 2007; Mosser and Packer 2009) and intergroup aggression is often directed at altering the balance of power (Wrangham 2006). Although we find that territorial expansion and inheritance are also important, both are a natural component of group formation in territorial species. The advantages of territorial expansion are often dictated by the distribution of resources (Kruuk and Macdonald 1985) and sex-biased natal philopatry is ubiquitous in terrestrial animals (Pusey and Packer 1987).

Although newly introduced lions to reserves in South Africa are more likely to live as solitaries at extremely low population densities (Miller S, personal communication), our models predicted that nearly half of lion groups should be comprised of solitaries (Figure 2C,D), whereas lone females only account for ~16% of lion prides in the Serengeti and Ngorongoro Crater, Tanzania. This discrepancy may arise because of our assumption that solitary agents would rarely engage in territorial contests and thus do not suffer the associated mortality risk. In reality, solitaries suffer far higher mortality than group-living females (Packer et al. 1988). This result may, however, reflect the more flexible sociality seen in a range of species. Group-territorial animals often show fission–fusion grouping patterns (Aureli et al. 2008), where individual group members spend considerable time alone, whereas for others species, social grouping only arises only occasionally (Davies and Houston 1981; Waser and Waser 1985; Kruuk 1989; Caro 1994). Our model required that all group members remain together at all times, thus flexible social systems could only be mimicked by generating a high proportion of solitaries.

Among felids, it is somewhat puzzling that leopards, one of the lions' closest living relatives (Weredelin et al. 2010), are so consistently solitary despite occupying the same savanna habitats as lions. However, leopards are mesopredators that suffer significant interference competition from lions (Balme et al. 2009, 2013; Packer et al. 2009), and any "group" of leopards that tried to occupy the same hot spots as sympatric lions would be subject to considerable disruption. It is thus noteworthy that lions only came to dominate African savannas with the disappearance of the even larger saber-toothed cats >5 million years ago (Weredelin et al. 2010)—and these earlier species may themselves have been group living (Carbone et al. 2009; Christiansen and Harris 2012). So, even proto-lions could not have developed sociality until they were able to dominate the landscape in the same manner as in our model.

Although we developed the model to understand the evolution of sociality in African lions, our conclusions should also apply to other species that have followed a similar evolutionary trajectory from solitary territoriality, such as wolves *Canis lupus* (MacNulty et al. 2011; Tallents et al. 2012), European badgers *Meles meles* (Kruuk 1989), Australian magpies *Gymnorhina tibicen* (Veltman 1989), Chowchillas *Orthonyx spaldingii* (Jansen 1999), and *Egernia* genus lizards (Chapple 2003). Evidence from these and other species suggests that the selective pressures associated with territoriality may provide a context in which group formation is advantageous. This approach, however, may not explain the transition to group territoriality for species that are initially gregarious due to other underlying factors such as predation or limited nesting sites. Nevertheless, any species that is both social and territorial has the potential to be subject to the same selective pressures that govern the dynamics of group-territorial competition. Many gregarious territorial species, which may be social primarily for other reasons, are also affected by the potential advantages of cooperative defense (e.g., Adams 1990; Pope 2000), territorial inheritance (e.g., Woolfenden and Fitzpatrick 1978; Russell and Rowley 1993), and territorial expansion (e.g., Langen and Vehrencamp 1998). Our model may therefore not only helps to explain the evolution of sociality in African lions but also provides insight into the complex dynamics of a broad range of group-territorial species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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