

# Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion

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**Abstract.** Dispersal is one of the most important life-history traits affecting species persistence and evolution and is increasingly relevant for conservation biology as ecosystems become more fragmented. However, movement during different dispersal stages has been difficult to study and remains poorly understood. We analyzed movement metrics and patterns of autocorrelation from GPS data for 20 lions (*Panthera leo*) over a five-year period. We compared movement among different stages of natal dispersal (departure, transience, and settlement), in addition to that of territorial adults of both sexes. The movement of lions differed according to dispersal stage, sex, group size, and rainfall. As expected, during dispersal lions moved faster and further and in a more directional manner than pre- or post-dispersal. Transient movement was more directional than adult movement, but somewhat surprisingly, was slower with less net displacement than that of territorial males. Interestingly, the effect of group size on movement differed between transient males and territorial males; solitary dispersers moved faster and further than individuals in bigger groups, while territorial males had the opposite trend. Although our sample size is limited, our results suggest a transition from directional movement during transience to random or periodic use of a fixed territory after settlement. In addition, group size may affect the search and settlement strategies of dispersers while seeking a territory in which to settle.

**Key words:** African lion; animal tracking; dispersal; Hwange National Park, Zimbabwe; movement; *Panthera leo*; search strategies; seasonal variation; spatial autocorrelation.

## INTRODUCTION

Dispersal is one of the most important life-history traits involved in species persistence and evolution (Clobert et al. 2001). As ecosystems become more fragmented, dispersal is increasingly important as it is often the only mechanism by which organisms can move between populations and thus maintain genetically diverse meta-populations (Clobert et al. 2012). Despite its importance, little is known about dispersal movement or the search strategies employed by dispersing individuals as they move through novel environments. This is largely due to the practical difficulties associated with data collection of this often once-in-a-lifetime event. However, mortality rates, distances travelled, and selection of settlement sites largely depend on the search strategy of the disperser (Conradt et al. 2003, Doerr and Doerr 2004, Conradt and Roper 2006). The paucity of data on dispersal movement has resulted in most population and evolution models assuming that individuals move at random in heterogeneous environments

(for a review see Patterson et al. 2008); however, unrealistic representations of dispersal are likely to yield inaccurate predictions regarding dispersal behavior and processes (Bowler and Benton 2005). Furthermore, recent evidence suggests that dispersal movements are highly complex and may vary depending on the three stages of dispersal (departure, transience, settlement; Clobert et al. 2009, Delgado et al. 2009). A thorough assessment of the ecological and evolutionary implications of dispersal thus requires robust empirical studies that have been lacking and widely called for by recent reviews (Jacobson and Peres-Neto 2010, Clobert et al. 2012, Baguette et al. 2013). Such studies will inform conservation strategies (Macdonald and Rushton 2003) and improve the way dispersal is represented in simulation models (Zollner and Lima 2005) and connectivity studies (Schwartz et al. 2009).

Shifting between dispersal stages brings about changes in animal behavior (Gese 1998), particularly in territorial species where territory holders and dispersers show discernible ecological differences (Campioni et al. 2012). In addition to dispersers being relatively uninformed of key spatial and temporal characteristics of the new environment, dispersers and territory holders have different goals in that dispersers

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aim to establish a territory while avoiding conspecifics, whereas established individuals need to maintain their territory and defend access to mates (Campioni et al. 2010).

While research into movement patterns during dispersal is an emerging ecological field, the study of movement ecology is vast and advanced (for reviews see Holyoak et al. 2008, Schick et al. 2008) and can be integrated into dispersal studies. For example, Schick et al. (2008) argue that it is essential to understand the interaction between environmental conditions and the state of the organism to understand the drivers of biologically based transition processes. Various empirical studies on vertebrates have highlighted behavioral differences between the different dispersal phases in birds (Stutchbury 1991, Delgado and Penteriani 2008), reptiles (Aragón et al. 2006), and to a lesser extent, mammalian carnivores (Gese 1998); however, there is a lack of research linking these dispersal stages to characteristics of the external environment, which is imperative to understanding the drivers of movement (Schick et al. 2008). To our knowledge, there has been no research investigating seasonal movement patterns during dispersal compared with territorial adults of the same species and how movement varies depending on group size. Doing so provides a unique opportunity to evaluate the shifting search strategies of dispersers and to obtain insight into the drivers of movement. To this end, we studied the movement ecology of African lions (*Panthera leo*) in all three dispersal phases, in addition to territorial adults of both sexes.

Lions live in fission–fusion groups (Packer et al. 1990), and prides defend their territories. Adult males do not tolerate the presence of non-coalition members, with territorial encroachment usually resulting in conflict (Grinnell et al. 1995, Packer 2001). Dispersal in lions is sex biased, as subadult males always disperse, while females are usually philopatric (Pusey and Packer 1987). During “departure,” most individuals conduct prospecting searches outside their natal territory prior to eventual departure (N. B. Elliot, *unpublished data*). Little is known of the “transience” and “settlement” phases, but dispersing lions either settle in a vacant area or challenge resident males for territory. While many mammals, for example, the Eurasian badger (*Meles meles*), disperse seasonally and over short periods of time (Macdonald et al. 2008), lions may disperse throughout the year, and the number of transient months can be relatively prolonged, making it possible to gather substantial quantities of data during dispersal.

In this paper we investigate nine predictions (Table 1) relating to the hypothesis that individual needs vary in accordance with life stage, bringing about broad behavioral changes, such as shifting movement patterns and search strategies (Zollner and Lima 1999, Van Dyck and Baguette 2005, Zollner and Lima 2005, Stamps 2006, Schick et al. 2008, Penteriani et al. 2011). To

TABLE 1. Predictions of hypotheses relating to the movement of African lions (*Panthera leo*) in different demographic categories and how their movement is influenced by rainfall and group size.

Data set and predictions	Source
Comparing subadult dispersal stages	
1) <i>Transient lions move fastest and furthest</i>	1, 2
2) <b>Transient lions display most directional movement</b>	3, 4, 5
3) <b>Post-dispersal lions cease directional movements and display random and periodic movement</b>	7
Comparing transients and territorial adults	
4) <i>Transients move slowest and less far per night</i>	6
5) <b>Transient individuals display more directional movement</b>	3
6) <b>Territorial adults predominantly display periodic movements</b>	7
7) <i>Territorial adults respond to rainfall while dispersers do not</i>	8, 9, 10
8) <b>Transients in smaller groups move more per night compared to larger groups</b>	11, 12
9) <i>Territorial adults in bigger groups move further per night compared to smaller groups</i>	8

*Notes:* We analyzed two different data sets: The first consisted of pre-dispersal, transient, and post-dispersal lions; the second consisted of transients, territorial males, and territorial females. Type in boldface represents supported predictions, and type in italics indicates partially or weakly supported predictions. Predictions were based on hypotheses and findings from the following sources: 1, Delgado et al. 2009; 2, Campioni et al. 2012; 3, Zollner and Lima 1999; 4, Van Dyck and Baguette 2005; 5, Stamps 2006; 6, Zollner and Lima 2005; 7, Valeix et al. 2010; 8, Loveridge et al. 2009; 9, Campioni et al. 2010; 10, Vuilleumier and Perrin 2006; 11, Packer et al. 1988; and 12, Baguette and Van Dyck 2007.

achieve this, we used an extensive data set based on five years of fine-scale GPS data collected on 20 lions of varying status. We analyzed patterns of autocorrelation and classified movement as directional, periodic, or random, in addition to calculating various movement metrics. We then examine whether movement of lions differs depending on their demographic category (pre-dispersal, transient, post-dispersal, territorial adult), sex, group size, and rainfall.

## METHODS

### *Study area*

The study area (~7000 km<sup>2</sup>) was located in the northern section of Hwange National Park (HNP), Zimbabwe (19°00' S, 26°30' E). HNP covers ~15 000 km<sup>2</sup> of semiarid savannah. Vegetation consists primarily of woodland and bushland savannah (64%), and communities are dominated by *Baikiaea plurijuga*, *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., and *Terminalia sericea* (Rogers 1994). The long-term mean annual rainfall of 613 mm is highly variable (CV ≈ 26%) and generally falls between October and April. Surface water is available from seasonal waterholes, although only a few hold water in the dry season, during which time water is artificially supplied to some (~50) waterholes.

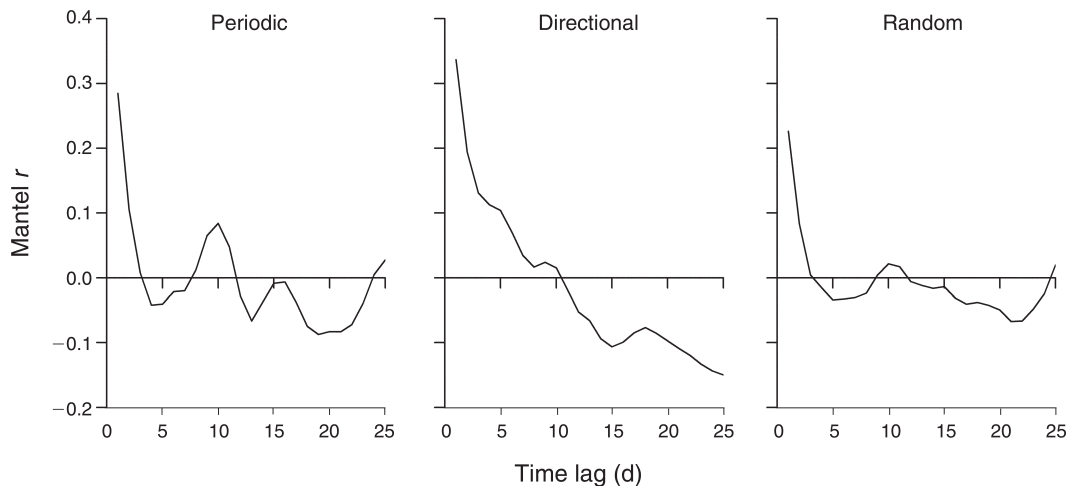


FIG. 1. Example Mantel correlograms that were visually classified by assessing the first half of the correlogram. These plots illustrate an individual that shifted from periodic to directional to random movement in three consecutive windows. See *Methods* and Appendix A for details on correlogram classification.

#### *Lion movement data*

Between 2007 and 2012, we obtained movement data from 20 lions in different social groups. Each was fitted with a GPS enabled radio-collar (see Loveridge et al. 2007 for details) pre-programmed to take hourly fixes when lions are active (18:00–07:00 hours).

#### *Data preparation*

To enhance accuracy, only fixes with a dilution of precision (DOP) < 10 were retained for analysis (Frair et al. 2010). This resulted in a data set of 40 669 locations for subadult males (93% DOP < 5), 72 030 locations for territorial males (96% DOP < 5), and 60 139 locations for territorial females (97% DOP < 5).

To reduce the effects of non-stationarity (Cushman et al. 2005), the study period was split into sequential, nonoverlapping temporal windows of 30-day intervals. In total we created 56 window periods, the first starting 1 October 2007 and the last on 22 May 2012. The data for each individual lion were split according to these windows, resulting in a total data set of 396 windows.

#### *Mantel correlograms*

Mantel correlograms reveal patterns of spatial and temporal autocorrelation that are highly informative in elucidating scales and patterns of ecological processes (Legendre 1993) and provide a detailed picture of movement variability (Cushman et al. 2005). To identify different movement patterns for each window and individual, we calculated two matrices (distance and time): The distance matrix was produced by calculating geographical distances between each pair of locations, and the time matrix was computed by calculating the difference in decimal days between each pair of locations. We used Mantel tests to assess the level of association between these two matrices (Mantel 1967). We computed Mantel correlograms (Oden and Sokal

1986) to assess the levels of spatial autocorrelation in lion movements across a range of lag times. We visually classified the correlogram “shape” for each window (for examples, see Fig. 1). Cushman (2010) simulated three path types under 18 different movement rules and showed that each path type had a characteristic autocorrelation structure and correlogram shape. Thus, correlogram shapes are diagnostic of broad movement patterns and provide an accurate and repeatable method to classify paths into categories such as directional, random, and periodic movement (Cushman et al. 2005, Cushman 2010). In the current study, we used the shape of the first half of each correlogram to classify the movement during that period into three “shape” categories: directional, periodic, or random movement. Directional movement, akin to a correlated random walk, is typified by a constant cline in the correlogram from positive to negative autocorrelation at increasing time lags, indicating a pattern of movement in which successive locations in time become farther apart in space. Periodic movement, resulting from central place random walks or periodic revisits to a collection of locations, is characterized by repeated cycles between strong positive and strong negative autocorrelation. Random movement within a fixed home range, akin to bounded correlated random walks, is typified by a rapid drop from positive to negative autocorrelation and subsequent fluctuation near zero autocorrelation (see Fig. 1 for sample correlograms; for full explanation of methods, see Appendix A, and Cushman et al. 2005, 2010).

#### *Movement metrics*

We calculated three movement metrics: speed, path length, and net displacement. Speed (m/h) was calculated by dividing the total distance travelled per night by the number of hours. Path length was the total

distance travelled each night, and net displacement was the distance between the first and last fix on a given night. Each parameter was then averaged per 30-day window.

### *Rainfall*

Daily rainfall was recorded at two weather stations within the study area, approximately 30 km apart. The figures were averaged to give a rainfall profile across the study area. We did not expect that rainfall in itself would impact lion movements, but rather, that the replenishment of water holes, vegetation growth, and subsequent prey dispersion would influence lion movement patterns. We therefore computed total rainfall for 60 days prior to the start of each window.

### *Demographic categories*

The data used in this study were from lions in three demographic categories: territorial males ( $n = 6$ ), territorial females ( $n = 5$ ), and subadult males ( $n = 9$ ). To assess changes in movement during dispersal, the subadult data were further split into the three phases of dispersal (Clobert et al. 2001): pre-dispersal ( $n = 4$ ), transient ( $n = 9$ ), and post-dispersal ( $n = 5$ ). Based on field observations, we classified the demographic categories as follows.

*Pre-dispersal.*—Four subadult males were collared while still with their natal pride. We were interested in investigating movements leading up to final departure and so only used data six months prior to dispersal (18 windows).

*Transience.*—The timing of dispersal was calculated as the midpoint between the last time a subadult was seen with its natal pride and the first time either was seen alone (mean time interval = one month;  $SD \pm 1.52$ ). Nine individuals made up the transient data set (58 windows).

*Post-dispersal.*—Establishment of a territory was deemed to have occurred when a transient subadult had been in a consistent home range for a minimum period of two months and continued to have a fixed home range thereafter. The onset of post-dispersal was then back-dated to the time at which the lion entered the new home range. We were interested in movements shortly after establishment and therefore discarded all data that extended beyond six months after settlement. Five transient males were deemed to establish territories (27 windows).

*Territorial adults.*—Lions in the study area have been closely monitored since 2002. All adults in this study were known to be territorial through direct observation and GPS data. In total we used 158 windows for territorial males and 135 for territorial females.

### *Group size*

All lions were closely monitored throughout the study period allowing for accurate recording of group size. Group size varied over the study period, being reduced

by deaths or increased by the addition of new members into a coalition or pride. For adult group size, we only included individuals over 36 months of age, while transient groups could be younger.

### *Statistical analyses*

The structure of our data necessitated different modeling approaches for Mantel correlogram shape (categorical response) and movement metrics (continuous response). Furthermore, we analyzed two different data sets that consisted of: (1) the subadult dispersal stages (pre-dispersal, transient, and post-dispersal); and (2) the transients, territorial males, and territorial females.

### *Movement analysis*

To assess the relationships between correlogram shape and demographic parameters and rainfall, we used generalized linear mixed models using combinations of two shape types per analysis (i.e., three sets of pairs). An example analysis consists of a response variable (e.g., periodic [0] or directional [1] movement), each of the fixed effects (demographic category, group size, and rainfall), their interaction terms and lion identity as a random intercept (see Appendix B for models and model selection statistics). These analyses were conducted in R 2.15.1 (R Development Core Team 2012), package lme4 v.0.9-0 (Bates et al. 2012) using a binomial error structure and logit-link function, with estimates provided on the logit scale.

To analyze the movement metrics, we fit mixed-effects linear models with a continuous response variable (either speed, path length, or net displacement), each of the fixed effects (demographic category, group size, and rainfall), their interaction terms and lion identity as a random intercept (see Appendix C for models and model selection statistics). We used R package nlme v.3.1 (Pinheiro et al. 2012).

### *Data sets*

First we compared the subadult data set during the three dispersal phases. Our primary interest in this data set was to assess change in movement depending on demographic category irrespective of group size or rainfall. Furthermore, our data set of pre- and post-dispersal was relatively small, necessitating simple models. For each movement metric and type, we constructed models with demographic category as the only explanatory variable (predictions 1–3 in Table 1).

Second we analyzed the data set comprising territorial males, females, and transient males (without the pre- and post-dispersal data). We assessed the relationship between movement and demographic category, group size, and rainfall. To investigate predictions 4–9 (Table 1), we created 12 a priori candidate models including each of the main effects and their interaction terms (Appendices B and C). The most complex model



TABLE 2. Estimated parameters and 95% confidence intervals (CI) from mixed models assessing variation in movement between transient, and pre- and post-dispersal lions in Hwange National Park, Zimbabwe.

Response variable and parameter	Estimate	SE	95% CI	
			Lower	Upper
Net displacement				
Transient	4336.2	304.6	3740.2	4932.3
Pre-dispersal	-1225.1	460.2	-2125.7	-324.4
Post-dispersal	-743.2	392.9	-1512.2	25.8
Path length				
Transient	5942.6	490.4	4982.9	6902.3
Pre-dispersal	-1239.8	586.8	-2388.2	-91.4
Post-dispersal	-298.6	498.2	-1273.5	676.3
Speed				
Transient	547.7	33.6	481.8	613.5
Pre-dispersal	-106.0	45.8	-195.7	-16.3
Post-dispersal	-47.4	39.0	-123.7	29.0
Directional vs. random				
Transient	0.8	0.3	0.1	1.5
Pre-dispersal	-1.6	0.8	-3.1	-0.1
Post-dispersal	-2.7	0.8	-4.4	-1.1
Directional vs. periodic				
Transient	0.3	0.3	-0.3	0.8
Pre-dispersal	-1.2	0.7	-2.7	0.2
Post-dispersal	-2.0	0.8	-3.6	-0.4
Random vs. periodic				
Transient	0.5	0.4	-0.2	1.2
Pre-dispersal	-0.8	0.5	-1.8	0.3
Post-dispersal	-0.4	0.6	-1.6	0.9

considered was: demographic  $\times$  group size + rainfall  $\times$  demographic. We used the same 12 a priori candidate models to analyze all three movement metrics and correlogram shapes. Model selection was used to identify the best model based on Akaike information criterion corrected for small sample size ( $AIC_c$ ). We decided a priori that if one model was clearly superior ( $w_i > 0.9$ ), this would be used, otherwise we would

average parameter estimates across models with  $AIC_c$  differences ( $\Delta i < 3$ ), correcting for model weights using R package AICcmodavg v.1.30 (Burnham and Anderson 2002, Mazerolle 2013). R syntax for all analyses and for computation of Mantel correlograms are provided in the Supplement.

## RESULTS

### Subadult male dispersal stages

Transient lions had higher net displacement and moved further and faster per night than either pre- or post-dispersal (prediction 1 in Table 1). This difference was largest between transient and pre-dispersal lions (Table 2, Fig. 2). Post-dispersal lions had the second highest values of these parameters, while pre-dispersers had the lowest.

Transient lions were more likely to use directional rather than random or periodic movement compared to pre- and post-dispersal lions (predictions 2–3 in Table 1; see Table 2 and Fig. 3 for comparisons).

### Transients and territorial adults

Lion movement varied depending on demographic category, rainfall, group size, or a combination of these. There was no top model ( $w_i < 0.9$ ) in our analyses of movement metrics (speed, path length, net displacement) or correlogram shape; thus, all reported parameter estimates were obtained by averaging across models with  $AIC_c$  differences  $< 3$  from the top model, correcting for model weights (see Appendices B and C for model selection statistics and model averaging procedure). The most supported candidate models for all movement metrics consisted of the interaction terms group size  $\times$  demographic and rainfall  $\times$  demographic, in addition to their main effects. The most supported candidate models in our analysis of correlogram shape contained only the main effects (demographic, rainfall, and group size).

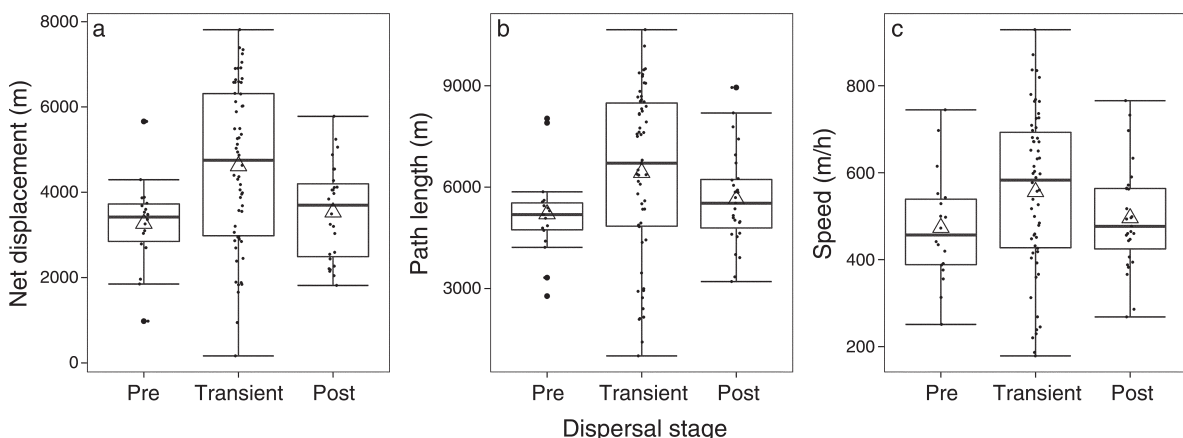


FIG. 2. Differences in movement patterns between pre-dispersal, transient, and post-dispersal African lions (*Panthera leo*) in Hwange National Park, Zimbabwe, in relation to (a) net displacement, (b) path length, and (c) speed. Boxes show medians, 25%, and 75% quartiles. Triangles indicate means. Whiskers indicate 10th and 90th percentiles. Dots represent the raw data.

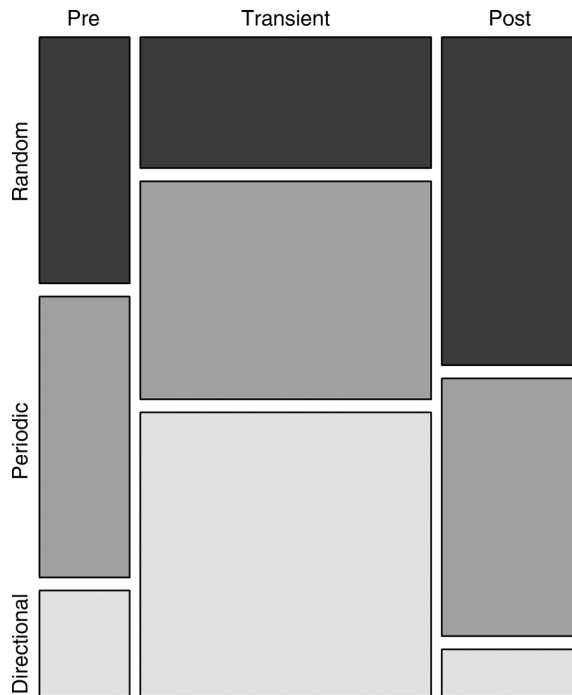


FIG. 3. Differences in correlogram shape in relation to pre-dispersal, transient, and post-dispersal lions in Hwange National Park. Correlograms were classified as long-range directional movement (directional), cyclical visits to focal areas (periodic), or random use within a home range (random). The width of segments is proportional to the amount of data for each dispersal stage. See Fig. 1 and Appendix A for further clarification.

#### Demographic categories

Compared to transient subadult males, territorial males moved faster (estimate  $\pm$  SE [all estimates shown with  $\pm$ SE] =  $164 \pm 49$ , 95% CI = 60–268) and further

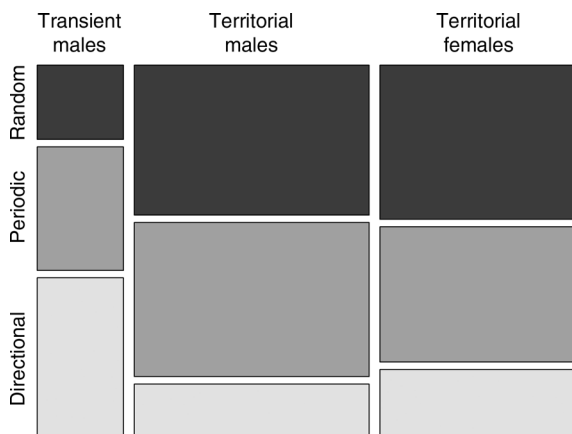


FIG. 4. Differences in correlogram shape according to lion demographics in Hwange National Park. Correlograms were classified as long-range directional movement (directional), cyclical visits to focal areas (periodic) or random use within a home range (random). The width of segments is proportional to the amount of data for each demographic. See Fig. 1 and Appendix A for further clarification.

(estimate =  $2307 \pm 634$ , 95% CI = 976–3637) per night, while females moved slower (estimate =  $-133 \pm 52$ , 95% CI =  $-242$  to  $-24$ ). Similarly, territorial males had higher net displacement (estimate =  $880 \pm 343$ , 95% CI = 160–1600), while females had lower net displacement (estimate =  $-1569 \pm 356$ , 95% CI =  $-2317$  to  $-821$ ) compared to transient subadult males (prediction 4 in Table 1).

Transient males were more likely to use directional rather than periodic movement (Fig. 4) compared to territorial males (estimate =  $-1.3 \pm 0.5$ , 95% CI =  $-2.3$  to  $-0.3$ ). Transient males were also more likely to use directional movement rather than random movement compared to territorial males (estimate =  $-1.9 \pm 0.6$ , CI =  $-3$  to  $-0.8$ ) and territorial females (estimate =  $-1.7 \pm 0.6$ , CI =  $-2.8$  to  $-0.5$ ; predictions 5 and 6 in Table 1). Although group size and rainfall were included in the top models (Appendix C), there was no clear trend (estimate and 95% CI included 0).

#### Rainfall

The way in which lions responded to rainfall depended on an interaction with demographic category. All demographic groups moved slower, less far, and with a lower net displacement with increasing rainfall, with the effects generally largest for territorial females (prediction 7 in Table 1; Table 3).

#### Group size

Group size ranged from one to four in adults and one to three in transient males. Movement metrics for territorial males, territorial females, and transient males differed depending on group size (Table 4, Fig. 5). Transient males in smaller groups moved faster, and had higher net displacement and higher path length than those in bigger groups (prediction 8 in Table 1). In contrast, territorial males displayed the opposite trend: Bigger groups moved faster, and had higher net displacement and a higher path length than smaller

TABLE 3. Model-averaged slope estimates from results of mixed-effects linear models investigating lion movement metrics (net displacement, path length, and speed) in relation to rainfall in Hwange National Park.

Response variable and interaction	Slope	SE	95% CI	
			Lower	Upper
Net displacement				
Rain $\times$ transient males	-0.28	1.12	-2.47	1.90
Rain $\times$ adult males	-0.09	0.86	-1.78	1.61
Rain $\times$ adult females	-1.51	0.98	-3.44	0.41
Path length				
Rain $\times$ transient males	-1.33	1.53	-4.33	1.68
Rain $\times$ adult males	-1.21	1.15	-3.47	1.05
Rain $\times$ adult females	-2.92	1.33	-5.52	-0.32
Speed				
Rain $\times$ transient males	-0.15	0.10	-0.35	0.04
Rain $\times$ adult males	-0.17	0.07	-0.30	-0.03
Rain $\times$ adult females	-0.21	0.08	-0.36	-0.05

TABLE 4. Model-averaged slope estimates from results of mixed-effects linear models investigating lion movement metrics (net displacement, path length, and speed) in relation to group size in Hwange National Park.

Response variable and interaction	Slope	SE	95% CI	
			Lower	Upper
Net displacement				
Group size $\times$ transient males	-1494	320	-2121	-867
Group size $\times$ adult males	405	121	168	642
Group size $\times$ adult females	-394	156	-701	-88
Path length				
Group size $\times$ transient males	-2085	482	-3029	-1140
Group size $\times$ adult males	674	171	339	1009
Group size $\times$ adult females	-130	226	-573	313
Speed				
Group size $\times$ transient males	-144	39	-220	-68
Group size $\times$ adult males	37	13	11	63
Group size $\times$ adult females	-11	18	-46	23

groups. Territorial females exhibited the same tendency as transient males, but increasing group size had a less marked effect as there was only substantial decrease in net displacement (prediction 9 in Table 1; Table 4).

#### DISCUSSION

Our findings show the extent to which lion movement is influenced by group size and rainfall and how this differs depending on demographic category. By incorporating an environmental variable in addition to the dispersal stages of the organism (Schick et al. 2008), we offer a unique insight into differential responses to shifting environmental conditions and group size depending on the life stage and sex of a species.

Transient lions exhibited directional movement, while adult movement was primarily a composite of random and periodic movements. Differences in movement are, to a certain extent, determined by an individual's ability

to perceive its surroundings and acquire knowledge (Vuilleumier and Perrin 2006). As such, dispersers moving through novel environments may move differently relative to territorial individuals that have learned to maximize the resources within that patch, as was reported with transient eagle owls (*Bubo bubo*; Delgado et al. 2009). The observed periodic movement in adults was expected, given that, in this ecosystem, waterholes are a key locus for lions; prey select areas close to waterholes (Valeix et al. 2009) and subsequently so do lions (Valeix et al. 2010), which appear to periodically rotate between waterholes (prediction 6 in Table 1; Valeix et al. 2011).

Pre-dispersal lions exhibited periodic and random movement patterns shifting to high levels of directional movement during dispersal (prediction 2 in Table 1). This accords with Zollner and Lima's (1999) simulated dispersal experiments and subsequent predictions: They found that straighter paths vastly improved the probability of survival and that this type of movement was the most effective search rule as straighter paths avoid redundant search and improve the likelihood of finding a vacant patch quickly (prediction 5 in Table 1). With territorial species such as lions, it is plausible that, unless a disperser is going to challenge for a territory, he will pass through in a directional manner, and minimize the chance of an aggressive encounter with the resident adult. Such directional movement suggests a sequential search strategy whereby individuals either accept or reject patches they encounter; if rejected, they continue the search in a directional manner, and do not revisit patches (comparative search strategies; Stamps et al. 2005, Stamps 2006). Consistent with this idea, the amount of directional movement declined dramatically once establishment occurred, replaced by random and periodic movements (prediction 3 in Table 1). In contrast, territorial adults displayed higher proportions

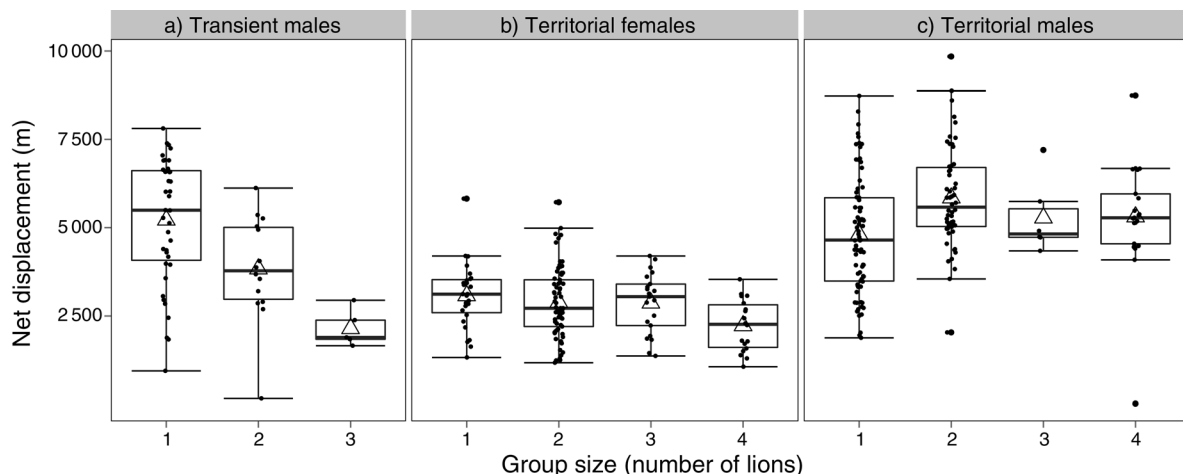


FIG. 5. Relationship between demographic category and group size in relation to net displacement of lions in Hwange National Park. There were no groups of four in transient lions. Boxes show medians, 25%, and 75% quartiles. Triangles indicate means. Whiskers indicate 10th and 90th percentiles. Dots represent the raw data.

of directional movement than did post-dispersal lions. We speculate that during establishment, a subadult lion consolidates a patch, around a waterhole for instance, leading to exaggerated patterns of periodic and bounded home range movements, and as it becomes familiar with and secure in its new territory, it switches to movement patterns similar to those of territorial adult males. Additional data on post-dispersal movements may confirm this.

Our findings concur with what Van Dyck and Baguette (2005) termed “special movements” in relation to directional dispersal movements designed for displacement (prediction 5 in Table 1). However, “special movements” are associated with high speed as reported for transient eagle owls that moved faster and straighter than established individuals (Delgado et al. 2009). In contrast, our results showed that transient males were slower and moved less than territorial males (prediction 4 in Table 1). One explanation is that by using directional movement at a decreased locomotory rate, transient males effectively search the area while limiting their detection probability. Zollner and Lima (2005) demonstrated that transient individuals can benefit from slower speeds due to more effective anti-predator behavior. More tortuous paths covering a larger area would entail leaving more scent, which would increase the likelihood of detection by territorial males. Indeed, increased activity has been shown to increase predation susceptibility (Ebenhard 1987) and predation rates (Norrdahl and Korpimäki 1998) in small mammals.

Depending on their demographic, group size influenced how individuals moved. When in small groups, transient lions moved faster and farther (prediction 8 in Table 1), as did territorial females, although the effect was less marked. In contrast, territorial males had the opposite trend (prediction 9 in Table 1). Fluctuations in lion home range size are strongly suggestive of expansionism (Kruuk and Macdonald 1985), as home range size increases with increasing pride biomass (Loveridge et al. 2009). Thus, with larger territories to defend, males in bigger groups have increased movement compared to smaller groups in smaller territories. On the other hand, females are not as active as males in patrolling their territories (Schaller 1972), and thus, while bigger groups of females have larger territories, their movements may reflect a strategy of food acquisition (which is concentrated around waterholes) and rearing of offspring. Lions in larger coalitions are more likely to gain residence in a pride (Bygott et al. 1979, Packer et al. 1988), and among transients it is plausible that a solitary disperser has little chance of displacing the resident males and would benefit from moving directly through an occupied territory. Thus, the decreased locomotion of transient individuals in bigger groups could reflect “boldness” as opposed to “shyness” (Baguette and Van Dyck 2007). While it has been reported that bold individuals

dispersed farther (Fraser et al. 2001) with larger and straighter movements (Delgado and Penteriani 2008), in our scenario the opposite could apply. Bigger groups may face fewer consequences if detected by resident males and can afford to remain within occupied territories for longer periods, thereby challenging for territory. Solitary individuals, on the other hand, represent the “shy” individuals and are frequently displaced from occupied territories causing them to move faster, with higher net displacement per night through the landscape while searching for a (often rare) vacant territory, and may be less inclined to challenge for one.

Lions showed differing response to rainfall in the preceding 60 days depending on their demographic (prediction 7 in Table 1). While the changing of seasons has no effect on lion home range size of either sex in HNP (Loveridge et al. 2009), we show that when using a more fluid approach to climatic data (i.e., rainfall as opposed to pre-defined seasons delineated by calendar months), variation in movement is detected. The slopes defining these relationships are shallow (Table 4), and our small sample size necessitates caution; however, these findings confirm our expectations. For instance, that females decreased their speed and path length with increased rainfall may be explained by the filling of waterholes and the addition of small cubs, which may constrain the movements of females. Cubs were more common in the wet season during this study. Indeed, cubs under six months of age were present in 49% of all female wet-season windows compared to 38% of dry-season windows.

In summary, our findings reveal that in territorial species such as lions, movement may be influenced by the sex and dispersal stage of an individual. This variation may be further explained by incorporating group size and environmental variables. Our results indicate a transition from directional exploratory strategies during dispersal to restricted random and periodic movement during settlement, followed by more expansive movement after establishment. As ecosystems become increasingly fragmented, it is crucial to elucidate the patterns and processes of movement during the different stages of dispersal to better understand the associated shifting behaviors. This will improve our understanding of how species may persist in fragmented landscapes and how fencing, for example, may curtail and alter the movements described in this paper. Our results provide the first investigation of seasonal movement patterns during dispersal in conjunction with territorial adults and how this varies depending on group size. There has been wide recognition of the importance of empirical studies on dispersal movements, and we hope that our results will improve the way dispersal is represented in simulation models (e.g., Zollner and Lima 2005) and connectivity studies (e.g., Schwartz et al. 2009).



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## SUPPLEMENTAL MATERIAL

### Appendix A

A detailed description for classifying correlogram “shape” into directional, periodic, or random movements, also including background information on the method and a simulation to further illustrate it ([Ecological Archives E095-247-A1](#)).

### Appendix B

Model selection statistics for generalized linear mixed models investigating correlogram shape (directional, periodic, and random movements) of lion movement paths in Hwange National Park ([Ecological Archives E095-247-A2](#)).

### Appendix C

Model selection statistics for mixed-effects linear models investigating lion movement parameters (net displacement, path length, and speed) in Hwange National Park ([Ecological Archives E095-247-A3](#)).

### Supplement

Sample R code of all analyses in the manuscript in addition to R code and instructions for computing mantel correlograms ([Ecological Archives E095-247-S1](#)).