Recursive movement patterns: review and synthesis across species

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Abstract. Recursive movement—returns to previously visited areas—is a widespread phenomenon exhibited by a large range of species from bees and birds to primates and large felines, at different spatial scales. Nevertheless, the wide scope and generality of this phenomenon remain underestimated by the scientific community. This limited appreciation for the pervasiveness of recursive movement can be attributed to its study by parallel lines of research, with different methodologies and nomenclature, and almost no cross referencing among them. Among these lines of studies are traplining behavior in foraging ecology, path recursions in movement ecology and the ecology of fear in predator–prey studies. We synthesize these three lines of research, to underline the mechanisms driving these patterns and create a conceptual model for recursive movement behavior across species and spatio-temporal scales. The emergence and complexity of recursive movement patterns are determined by the rate of resource recovery, environmental heterogeneity, the predictability of resource recovery, and the animal’s cognitive capabilities. Our synthesis can be used to generate predictions within and among systems, as well as to promote the sharing of knowledge and methodologies gained in each sub-field. Such sharing can greatly advance our understanding of behavioral and ecological processes and provide novel opportunities for future research.

Key words: bumblebees; circular path; conceptual model; foraging; periodicity; predator–prey interactions; route optimization; shell games; spatial memory; traplining.

INTRODUCTION

Movement is an elementary property of almost all organisms on earth, and as such, it is a crucial component of almost any evolutionary and ecological process with direct impacts on the dynamics of life on all scales—from individual fitness through persistence of populations to ecosystem health (Kokko and Lopez-Sepulcre 2006, Nathan 2008). Scientists increasingly recognize the need to understand and predict movement patterns of organisms at all spatial levels, making the question “what drives animal movement?” a fundamental question in ecology (Nathan 2008, Morales et al. 2010, Hastings et al. 2011). Recently, Nathan et al. (2008) proposed a conceptual framework for movement ecology in which an organism’s internal state, its motion
and navigation capacities, and external factors all interact to generate movement. This movement ecology paradigm identifies the fundamental principles producing movement paths and facilitates further investigations into specific movement patterns.

Recursive movement pattern, i.e., returns to previously visited areas, is a widespread phenomenon in the animal kingdom, theoretically explored using a variety of models (e.g., Ohashi and Thomson 2005, Berger-Tal and Avgar 2012, Riotte-Lambert et al. 2013) and empirically shown for a large range of species from different trophic levels and at different spatial scales. These include bees (Thomson et al. 1997, Williams and Thomson 1998), birds (Gill 1988, Garrison and Gass 1999), bats (Lemke 1984), primates (Watts 1998), ungulates (Edwards et al. 1996, Bar-David et al. 2009), large felines (Laundre 2010), and elephants (English et al. 2014). Nevertheless, the wide scope and generality of this phenomenon may be still considerably underestimated by the scientific community. This is because recursive movement behavior has been studied in several different lines of research which have been developed in parallel, using different methodologies and terms to analyze and describe the same phenomenon, with almost no cross referencing among them.

The goal of this paper is to review and synthesize three lines of research dealing with recursive movement patterns across different species and spatio-temporal scales in order to identify the underlying mechanisms driving these patterns. We propose that the differences among these lines of research are mostly the result of historical and methodological reasons, and that consequently, each line of research puts emphasis on different aspects of the same phenomenon. We use our synthesis to create a conceptual model of the main factors controlling the emergence and complexity of recursive movement which can serve as a basis for generating predictions within specific systems and for comparing among different systems.

LINES OF RESEARCH STUDYING RECURSIVE MOVEMENT PATTERNS

We define recursive movement as repeated visitations to the same particular locations in a systematic manner. In this synthesis, we chose to focus on three major lines of research—trapline foraging, path recursion, and ecology of fear studies, each investigating recursive movements from a very different perspective, thus ensuring that our synthesis remains focused while still covering a very wide scope of ecological studies.

One of the most extensive lines of research on recursive movements is the study of traplining behavior, within the foraging ecology sub-field. Trapline foraging is defined as repeated visitation to a series of resource points or patches in a predictable order (Ohashi and Thomson 2005). Traplining has been reported in a large variety of species, and is always associated with foraging from renewable resources (e.g., nectar, insects, fruits, foliage). A more recent line of research involves studies of path recursion (Bar-David et al. 2009). Empirically, path recursion studies focus on the large-scale movement of medium to large social herbivores, which track patches of high quality foraging, returning to these patches in a regular manner. The third line of research comes from the study of the ecology of fear, within the study of predator–prey systems (Brown et al. 1999, Mitchell 2009). While not studying recursive movement directly, this line of research reveals that predators may move between patches containing potential prey in a recursive, systematic manner. In the following sections we expand on and identify the mechanisms which underlie each line of research (summarized in Table 1).

Trapline foraging

Studies of recursive movement behavior in bees go back to Darwin (reviewed by Freeman 1968) and Manning (1956) who produced detailed accounts of this behavior. About 40 years ago, D. H. Janzen gave this phenomenon a name and coined the term traplining to describe Euglossine bees visiting flowers in a regularly repeated fashion (Heinrich 1979, Thomson et al. 1997). The name comes from an analogy to human trappers checking their traps on a regular basis (Thomson et al. 1997). Early studies of traplining provided only descriptive accounts to define it, and as such, different criteria have been used to conclude that animals are exhibiting traplining behavior. These include noting regular appearances of individuals at fixed resource sites.
Traplining behavior is always associated with foraging from renewable resources patchily distributed in space. Such resources include nectar (e.g., Gill 1988, Dreisig 2000), seeds (e.g., Cody 1971), insects (Davies and Houston 1981), fruits (Janson 1998), and foliage (Watts 1998). Anderson (1983) offered the first mechanistic explanation for traplining behavior and suggested that traplining occurs as a natural consequence of animals attempting to minimize travel distance between renewable resources. However, several studies have since shown that traplining animals do not necessarily choose the shortest route available as this route is not necessarily the most profitable one (Janzen 1971, Ohashi and Thomson 2005). Later studies have shown that by systematically returning to renewable resource patches animals can improve their foraging efficiency in three ways. First, when the resources renew in a decelerating manner, foragers can increase the mean reward from each foraging trip by returning to patches before the renewing rate diminishes too much (Possingham 1989). Second, foragers can deter competitors by reducing the mean reward yield encountered by other foraging individuals (“defense by exploitation”; Paton and Carpenter 1984, Garrison and Gass 1999). Third, foragers can reduce the variance of the reward encountered, making the outcome of a visit to a resource patch more predictable. This is a beneficial foraging strategy for risk-averse foragers who prefer to forage in constant and predictable resource patches (Possingham 1989). These benefits were shown to apply for animals foraging alone as well as for animals foraging in competitive environments (Ohashi and Thomson 2005). Furthermore, traplining foraging has been shown to improve foraging performance by improving the forager’s experience, thus increasing its competitive advantage over random foragers (Ohashi et al. 2008), as well as to increase the forager’s ability to detect and adjust to changes in the environment such as fluctuation in competition intensity (Ohashi et al. 2013).

To summarize, the main driver of recursive movement in traplining is the rate of resource recovery (Possingham 1989, Ohashi et al. 2008, Ohashi and Thomson 2009)—the time required...
for the resource to recover following local exploitation—which has direct implications on resource availability, profitability and on the forager’s competitive capabilities.

**Path recursion**

It is well established that large herbivores exhibit nonrandom movements, track areas of highest quality foraging, and repeatedly return to these high-quality foraging locations (Sinclair 1977, Fryxell et al. 1988, 2005, Hewitson et al. 2005, Owen-Smith et al. 2010). This has been shown to be a useful strategy, enabling the herbivores to consume regrowing vegetation in its high primary productivity stage (McNaughton 1985, Prins 1996, Owen-Smith et al. 2010). Path recursion analyses are part of the recent and rapidly expanding ecological literature that follows the latest advances in telemetry technology. These advances allow researchers to accurately sample animals’ movement at a very high frequency and for long periods of time using GPS tags or collars (Cagnacci et al. 2010). The vast quantities of movement locations data that became available to ecologists offers numerous new insights into animals’ decision making processes and behavior, but also calls for novel and rigorous statistical tools in order for these insight to be correctly inferred from the data. Bar-David et al. (2009) used GPS locations data from African buffalos, Syncerus caffer, to analyze recursive movement behavior among resource sites. Using a simple simulation model they have found that it is resource recovery rate that may control the recursion movement pattern exhibited by large herbivores, and that it may lead them to move in circular paths.

This study was followed by a series of papers developing the topic of path recursion (e.g., Lethbridge et al. 2010, Benhamou and RIotte-Lambert 2012, Li et al. 2012, RIotte-Lambert et al. 2013). Most of these studies offer further developments to the statistical methods, aimed at improving the detection of recursion and circular patterns using high resolution movement data, as well as our understanding of the factors that are influencing movement recursions. These statistical tools are usually verified using GPS locations data sets from medium to large herbivores equipped with GPS collars (e.g., buffalo, Benhamou and RIotte-Lambert 2012; impala, RIotte-Lambert et al. 2013).

Summarizing the path recursion literature, recursive movement behavior is mainly suggested to be driven by the recovery of renewable resources patches. This hypothesis has been supported by several theoretical models, but so far it has never been experimentally tested.

**The ecology of fear**

While not directly studying recursive patterns, this line of research includes increasing theoretical and empirical evidence regarding predators’ recursive movement behaviors. Predator–prey interactions are behaviorally sophisticated games in which both prey and their predators try to optimize their risk management strategies (Brown and Kotler 2004, Berger-Tal et al. 2010). Brown et al. (1999) suggested that in addition to the killing of prey, predators can deplete food patches by frightening prey, causing them to move away from the patch or to become vigilant to the point where catching additional prey individuals becomes extremely difficult. Therefore, predators may improve their chances of catching prey by moving away from a patch when the prey reaches a certain vigilance threshold (making them harder to catch), and not returning to the patch until the prey’s vigilance is greatly decreased. Similar dynamics were proposed by Mitchell (2009) where he introduced the concept of “ratcheting” prey vigilance that increases after an encounter with a predator, and then decays over time until the next encounter. As a response, predators should optimally delay their follow-up visits to patches in periods in which prey exhibits increased vigilance (Laundre 2010), and only return to a patch when vigilance is reduced again. In other words, prey complacency (which translates into prey catchability) can be viewed as a recoverable behavioral resource which predators should try and maximize by leaving areas when it is low, and returning when it has renewed sufficiently. The rate of complacency recovery is determined by various factors such as the size of the area, the density of the prey and the attack mode of the predator.

Empirical studies show that predators’ reactions to the vigilance behavior of their prey can lead to two different movement strategies. Predators may move randomly between food...
patches in order to make their revisits to the patches unpredictable (e.g., sharp-shinned hawks preying on birds; Roth and Lima 2007). Alternatively, predators may move in a systematic manner in a way that will allow for enough time to pass for the vigilance behavior of the prey in a given patch to be sufficiently reduced before returning to it, as suggested above (e.g., pumas preying on mule deer, Laundre 2010; little egrets preying on fish, Katz et al. 2013). It is important to note that unlike traplining or path recursions, the ecology of fear is a game between two species, and while predators try to manage the prey’s behavior, prey may be selected to make their behavior less predictable. The more unpredictable the behavior of the prey will be, the less stable recursive movement behavior of the predator will become.

To summarize, the movement of predators between patches containing behaviorally reactive prey may be controlled by the recovery rate of the prey behavior.

**SYNTHESIS**

We have briefly reviewed three lines of ecological research, each developing in its own separate sub-discipline with virtually no cross references among them. Research on trapline foraging was developed as part of the foraging ecology sub-field; research on path recursion is part of the growing movement ecology sub-field, and the ecology of fear line of research is a central part in the study of predator–prey interactions. There are notable differences among these lines of research, e.g., the systems investigated, the spatial scales, the species and their behavioral patterns. Yet, remarkably, the different behaviors seem to produce the same recursive space-use patterns, where an individual returns to previously visited locations in a systematic manner (Fig. 1).

One of the main differences between the lines of research presented here is the spatial scale in which they operate. This is not due to any theoretical or conceptual constraint but rather a function of the methodology associated with each line of research (Table 1). The majority of trapline studies deal with systems that are no larger than a few square kilometers. This is due to the fact that most traplining research was developed with pollinators in mind and therefore the methods of describing traplines (such as the drawing of schematic flight maps) are best suited to the spatial scales that represent pollinators’ movement. Path recursion deals with much larger spatial scales. The field was developed using high-resolution locations data from GPS collars, and such data are mostly found for large animals covering very large areas. Studies on the ecology of fear vary in scale from small-scaled systems that are usually studied under laboratory or semi-natural conditions to large-scaled systems studies in the wild.

**Conceptual model**

There are several prerequisites for recursive movement behavior to take place. First, in order to be able to return to a previously visited patch, an animal needs to have some basic cognitive skills. The animal needs to be able to perceive and identify resource patches in order to be able to orient itself towards them (Nathan et al. 2008, Fagan et al. 2013), and to remember both the location and the quality of multiple food patches (Greggers and Menzel 1993, Morales et al. 2010, Lihoreau et al. 2011, Fagan et al. 2013). These skills are needed for any kind of non-random movement, but especially crucial for recursive movement. An animal needs to be able to predict the rate of resource recovery in order to know how long to wait before returning to a previously visited patch. This makes having a good spatio-temporal memory a crucial prerequisite for recursive movement behavior to take place (see The role of cognition… below). Second, the environment has to be heterogeneous at least to some degree. Memory has little benefit in spatially homogeneous environments (McNamara and Houston 1987, Fagan et al. 2013), and there should be no motivation to return to a previously visited patch if all patches are the same. Memory will also be useless in a rapidly and unpredictably changing environment (McNamara and Houston 1987, Fagan et al. 2013) and therefore some degree of environmental predictability is another prerequisite of recursive movement. For this reason, animals feeding on renewable resources whose rate of renewal is unpredictable (e.g., desert rodents feeding on seeds brought by the wind; Ben-Natan et al. 2004) should not develop recursive
movement behavior. Lastly, resources in the patches have to show recovery after depletion. Without resource recovery there is no reason for an animal to return to a patch once the patch’s resources have been depleted.

There are numerous kinds of recoverable resources that may drive animals’ movement. The most studied ones are food and water—herbivores feeding on grass or leaves, primates feeding on fruits, bees feeding on pollen or nectar, and even birds feeding on insects are all feeding on renewable food resources, which may be one of the reasons recursive movement is such a wide spread phenomenon. However, many other, less material, renewable resources exist. Prey’s complacency behavior is one such resource, as described above. Potential mates’ sexual receptivity is another such resource and if it has a spatial component it may also promote recursive movement patterns (e.g., the lek system of the Little Bustard, *Tetrax tetrax*, in which the females show fidelity to lek sites while the males

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**Fig. 1.** Illustrative examples of recursive movement patterns in different systems of renewable resources. A bee moving between nectar-giving flowers in a trapline manner (top panel; sensu Thomson et al. 1997); a buffalo herd moving between different patches of grass (middle panel; sensu Bar-David et al. 2009); an egret flying between ponds containing prey fish (bottom panel; sensu Katz et al. 2013). The figure was drawn by Zohar Ganot.
continuously move between them; Alonso et al. 2000, Bretagnolle et al. 2011). Parasitic load can also lead to recursive movements. Animals living in large groups can suffer from increased parasite load in areas in which they aggregate (Rifkin et al. 2012). In the absence of available host animals, parasite density is expected to decrease with time and therefore animals may be driven to alternate between resting stops in a systematic manner in order to reduce the parasitic load. In this case the renewable resource is the ‘cleanness’ of an area in regards to parasites (Hausfater and Meade 1982).

Regardless of the type of recoverable resource, our synthesis shows that the same general rules govern the creation, stability and complexity of recursive movement patterns (Fig. 2). We consider our conceptual model of recursive movement to be a derivative of Nathan et al. (2008) movement ecology paradigm. Whereas the paradigm aims to describe the drivers of movement in general, our model represents a subset of external and internal factors that will lead to the creation of a specific type of movement—recursive movement. We recognize three main external factors, and one internal factor controlling recursive movement. The rate of resource recovery is perhaps the most important external factor determining recursions. There can be no recursions without resource recovery, and the slower the rate of recovery, the longer and more complex (i.e., containing more resource sites that may be arranged in a more complicated spatial configuration) the recursion path needs to be in order to allow the animal to return to each resource patch at the optimal time. Of course, a very slow rate of resource recovery will be regarded by the animal as no recovery for all practical purposes and no recursions will take place. Similarly, a very fast rate of recovery will eliminate the need for recursive movement since the best strategy in terms of resource gain will probably be to stay in close vicinity to one resource patch. The predictability of recovery and the heterogeneity of resources are the two additional external factors controlling recursive behavior. As noted above, in order for recursions to occur the environment needs to be at least somewhat heterogeneous and predictable. The

Fig. 2. A conceptual model of the factors affecting the emergence and complexity of recursive movement patterns. The white “buffer zone” represents conditions in which recursion movement is not feasible. Darkening color represents an increase in recursion complexity, i.e., recursions that contain more resource sites which may be arranged in increasingly complicated spatial configurations. Each axis represents an independent qualitative effect: the bottom axis represents the cognitive abilities of the moving animal. The other three factors represent external factor affecting recursion—the rate of resource recovery, the predictability of resource recovery and the environmental heterogeneity.
more heterogeneous and predictable the environment is, the more complex the recursion patterns can become. Lastly, the internal factor controlling recursive movement behavior is the cognitive capabilities of the animal which are central for the creation and maintenance of recursions. The higher the perception and memory capabilities of an animal are, the more complex its recursions may become.

We did not include inter- and intra-specific interactions in our model despite the fact that interactions such as competition and predation clearly have a profound effect on the occurrence of recursive movements, and in some specific cases, such as territorial movement, are the main drivers for recursions. However, the exact way in which such interactions influence recursive movement is still moot (see below for a discussion of the effects of competition), and in the majority of the cases there are not enough studies to support any conclusion. Further research into the role of competition and predation in governing the movement in general and recursive movement in particular is greatly needed.

Our model can be applied to other forms of recursive movements. Seasonal migration is a classic example of recursive movement behavior that is widespread across species and spatio-temporal scales (Dingle 2014). Mueller and Fagan (2008) proposed a conceptual framework of movement, at the individual and population level, suggesting indeed that large-scale heterogeneity, high predictability of resources, and high cognitive capacity may lead to migration patterns. Another example of recursive movement behavior to which our model can be applied is territorial defense movement in which animals patrol their territories to defend them from intruders (e.g., Watts and Mitani 2001). It has been shown that for species that use scent-marking (e.g., wolves and foxes), conspecific avoidance and scent-mediated interactions can give rise to the formation of stable home ranges (Briscoe et al. 2002, Potts et al. 2012). For these species, rate of scent decay could be connected to rate of resource recovery and may promote recursive movement behavior along the territory borders.

New research directions

The realization that traplining, path recursion, and fear management by predators all describe the same space-use pattern opens up a vast array of opportunities. Sharing the large amount of knowledge that was accumulated within each line of research can advance our understanding of behavioral and ecological processes and provide new lines of investigation. Moreover, each line of research brings with it its own unique methodology (Table 1). While each of the methodologies has proved very useful, they have also defined the limits of the information that could have been gained in each sub-field. Having access to new methodologies and new systems can allow researchers to look into various questions they could not have investigated up to this point. Below we give several examples of how synthesizing the different lines of research on recursive movement patterns can serve to advance current knowledge, improve our understanding of behavioral and ecological processes, and provide new research directions.

Experimental validation of theoretical recursion models.—Several statistical and simulation models have been suggested in the path recursion line of research to explain the recursive behaviors of large herbivores (e.g., Bar-David et al. 2009, Benhamou and Riotte-Lambert 2012, Li and Han 2014) and to examine the role of various factors (such as the ones illustrated by our conceptual model) on recursive patterns. These models are later validated by applying them to real movement data collected from GPS collars worn by wild animals (usually large herbivores, but also migrating birds), and getting consistent and interpretable results. While this adds credibility to the suggested model, it is still only correlative data, and therefore serves as weak evidence for the validity of the model. Experimentally manipulating the environment or the movement behavior of an animal in order to test predictions made by the model in question can provide much stronger evidence for the soundness and relevance a model, but in most cases it is nearly impossible to experimentally manipulate the large-scale systems in which the movement of large herbivores occur. By applying the same path recursion model to movement data collected from smaller animals (small predators or pollinators), manipulating the environment becomes a feasible option, which will allow researchers to...
test the validity of their models with much more rigor.

The role of competition in driving or impeding recursive movements.—Within the ecology of fear framework, the role of competition among predators is assumed to have a negative effect on the chances to catch prey, because an increase in the amount of predators should theoretically increase the wariness of exposed prey. This assumption explains why big carnivores should be and are rare (Brown et al. 1999). The traplining literature considers the effects of recursive behavior on foraging success in competitive environments much more closely and has actually shown that by moving among food patches in a systematic manner, a forager reduces the detrimental effects of competition by reducing the mean yield encountered by other individuals and by gaining experience which can be translated into a competitive advantage over less experienced individuals (Garrison and Gass 1999, Ohashi et al. 2008). Applied to the ecology of fear framework, this means that a random competing predator wandering into a recently visited patch may not be able to catch any prey and may therefore be discouraged from returning to this patch. These insights taken from the traplining research challenge the way competitive interactions among predators in predator–prey systems is viewed and present a new venue for their investigation through modeling and experimentation.

Traplining is competitively advantageous since the traplining forager has knowledge of the resource patches which other random foragers do not possess. However, what happens when more than one individual or group share knowledge regarding resource sites (a scenario which is more likely in larger systems)? Does recursive movement remain a competitively superior strategy? These are still open questions that are yet to be answered.

The role of cognition in determining movement patterns across species.—Another common theme that unites the three lines of research is that of them require the animal to exhibit cognitive skills such as perception and memory. Movement behavior should therefore be strongly affected by the animal’s cognitive abilities or constraints (Saleh and Chittka 2007, Nathan et al. 2008). While the ultimate reason to perform recursive movement behavior should be in most cases similar—improving one’s fitness by ensuring resource patches are of high quality—the large differences in biology, life history and spatio-temporal scales of species suggest that the proximate cognitive mechanisms controlling this behavior should vary greatly between systems.

It is clear that medium and large herbivores use spatial memory and associations between cues and rewards to return to profitable areas and avoid undesirable areas (Bailey et al. 1996, Edwards et al. 1996). In fact, it has been suggested that impeding the spatial memory of grazing cattle, by frequent movements among grazing units or by training cattle to expect high rewards in unpredictable locations, could improve grazing patterns since this will reduce the animals’ systematic recursive movements and allow for more uniform grazing patterns (Laca 1998). It has also been established that phylogenetically advanced predators have a good spatial and temporal cognitive memory that allows them to adjust their movement strategy according to the behavior of their prey (Lima 2002, Katz et al. 2013). In contrast, traplining behavior in bees was historically considered to be the result of simple heuristics, such as always moving to the closest resource site (nearest neighbor), coupled with basic spatial memory (Anderson 1983, Higgins and Strauss 2004, Gibson et al. 2007). However, recent studies present a more complex situation. Analyses of bee traplining behavior clearly show that they do not follow nearest-neighbor solutions (Lihoreau et al. 2012a) or any other simple rule of thumb, but rather develop their trapline through trial and error by combining exploration, learning and sequential optimization (Ohashi and Thomson 2009, Lihoreau et al. 2012b). Whether this is true only for bees, or can be extended to other traplining species such as birds or primates is currently unknown and should be explored further.

Spatial memory is clearly a fundamental aspect of recursive movement behavior across species. Therefore, analyses of recursive behavior can help identify memory-driven movement processes (Fagan et al. 2013) in order to better understand the role of memory in ecological processes. A valuable step towards this goal is a recent model by Schlagel and Lewis (2014) in which they demonstrate how an organism’s
spatial memory, represented by the time since the last visit to a location, can shape movement processes, in particular returns to previously visited locations.

**Conclusions**

The ultimate goal of movement ecology research is to develop a unified framework of the ecology and evolution of movement across species (Nathan et al. 2008). Our synthesis integrates empirical and theoretical knowledge of a range of species with different ecology and natural history traits to create a conceptual model for recursive movement patterns across species. We hope that this synthesis will encourage academic collaborations between the ecological sub-disciplines investigating the different forms of recursive movement patterns. Such collaborations can yield novel insights into ecological and behavioral processes and provide exciting new opportunities for further research.

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