Home ranges and the value of spatial information

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Animals concentrate their activities within areas we call home ranges because information about places increases fitness. Most animals, and certainly all mammals, store information about places in cognitive maps—or neurally encoded representations of the geometric relations among places—and learn to associate objects or events with places on their map. I define the value of information as a time-dependent increment it adds to any appropriate currency of fitness for an informed versus an uninformed forager, and integrate it into simple conceptual models that help explain movements of animals that learn, forget, and use information. Unlike other space-use models, these recognize that movement decisions are based on an individual's imperfect and ever-changing *expectancies* about the environment—rather than omniscience or ignorance. Using simple, deterministic models, I demonstrate how the use of such dynamic information explains why animals use home ranges, and can help explain diverse movement patterns, including systematic patrolling or "traplining," shifting activity or focal areas, extra-home-range exploration, and seemingly random (although goal-directed and spatially contagious) movements. These models also provide insights about interindividual spacing patterns, from exclusive home ranges (whether defended as territories or not) to broadly overlapping or shared ranges. Incorporating this dynamic view of animal expectancies and information value into more-complex and realistic movement models, such as random-walk, Bayesian foraging, and multi-individual movement models, should facilitate a more comprehensive and empirical understanding of animal space-use phenomena. The fitness value of cognitive maps and the selective exploitation of spatial information support a general theory of animal space use, which explains why mammals have home ranges and how they use them.

Key words: cognitive map, foraging, hippocampus, home range, information, learning, movements, space use, spacing, territory

How animals distribute their activities in space and time is of central importance in behavioral and population ecology. Biologists track animals to estimate the sizes and shapes of home ranges, movement patterns within home ranges, home-range overlap among individuals, and how home-range boundaries vary over time (Fieberg and Börger 2012; Fieberg and Kochanny 2005; Powell and Mitchell 2012). Theoretical biologists have developed diverse theories to explain space-use patterns at different spatiotemporal scales, ranging from the transient movement decisions of individual foragers (e.g., Charnov 1976; Moorcroft 2012; Moorcroft and Lewis 2006; Pyke 1984; Stephens and Krebs 1986), to patterns in the cumulative area an animal uses over time (Fieberg and Börger 2012; McNab 1963; Powell 2000, 2004; Waser and Wiley 1979; Worton 1989), to how individuals distribute themselves as populations relative to habitat characteristics and each other (Bacon et al. 1991; Brown and Orians 1970; Fretwell 1972; Mitchell and Powell 2003, 2007, 2012; Morales et al. 2010; Powell 1989, 2000; Rosenzweig 1991; South 1999; With and

Crist 1996; Wynne-Edwards 1962). Population spacing patterns, in turn, strongly influence theories concerning the evolution of social systems (Carr and Macdonald 1986; Horn 1968; Orians 1969; Slobodchikoff 1984; Smith 1968; Waser and Wiley 1979; Wittenberger 1979).

Despite these diverse approaches to understanding animal space-use patterns, a "unified theory" of animal space use that integrates across these multiple scales and phenomena of interest remains elusive (Börger et al. 2008; Moorcroft 2012; Powell and Mitchell 2012) and ecologists have struggled to explain why nearly all animals form home ranges (i.e., area restricted or spatially contagious space use by individuals) despite the great diversity of ecological niches, movement patterns, and population spacing patterns observed among

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species (Börger et al. 2008; Van Moorter et al. 2009). Many space-use models assume home-range existence a priori rather than treating it as an emergent property of animal movements; and mechanistic (random-walk) movement models do not produce home-range behavior unless constrained by sometimes ad hoc mechanisms, such as reflective boundaries or attraction to particular places (review in Börger et al. 2008).

Recently, a growing number of animal movement modelers have recognized the importance of learning and memory in animal space-use decisions (e.g., Boyer and Walsh 2010; Dalziel et al. 2008; Morales et al. 2010; Van Moorter et al. 2009), which I contend is key to developing a "unified theory" of animal space use and explaining the near universality of home-range behavior. I (Spencer 1992) proposed a conceptual theory of animal space-use behavior for animals that gain and use information that is integrated into "cognitive maps" (Jacobs 2003; O'Keefe and Nadel 1978; Peters 1978; Powell 2004; Powell and Mitchell 2012; Tolman 1948) and illustrated the theory with simple, conceptual movement models that demonstrate how exploiting information in a partially predictable and dynamic world can help explain diverse space-use patterns across multiple scales—from momentary movement decisions, to travel paths, to home-range utilization distributions, to shifting home-range areas, to patterns of home-range overlap among individuals. Here I review these concepts and models, and argue that a unified theory of animal space use requires understanding the cognitive processes animals use to exploit information. This approach emphasizes that what we call the home range is an emergent property of the movements of an animal that benefits from spatial information. In other words, home ranges exist because information about places is useful—and the home range may best be defined as that area over which an animal regularly exploits and updates information stored in a cognitive map.

In the next section ("Foundations and Assumptions"), I review information about how animals gather, integrate, and use information in cognitive maps, and I define the value of information as a dynamic variable for use in movement models. I next illustrate how the value of dynamic information, together with resource depression and renewal functions, can be used to create *decision profiles* (Spencer 1992) that predict when spatial information should be used, and demonstrate the implications for animal space-use decisions ("Temporal Decision Profiles and Optimal Return Times"). I then illustrate these concepts using simple movement models for individuals using a 1-dimensional (1-D), homogenous habitat, followed by extensions to consider heterogeneous habitats and 2-dimensional (2-D) habitats. In the "Discussion," I synthesize the findings and their implications for understanding home-range behavior, relate the predictions to empirical research, and suggest how the approach can be incorporated into more-complex, realistic, and empirical space-use models.

FOUNDATIONS AND ASSUMPTIONS

Animal space-use models assume that individuals space themselves and move through their environments in ways that increase fitness via the efficient exploitation of resources and avoidance of risks (e.g., Fretwell 1972; Mitchell and Powell 2004, 2008; Powell 2004; Rosenzweig 1991; Schoener 1981; Stephens et al. 2007; Stephens and Krebs 1986). Until recently, most models have assumed that foragers are either ignorant or omniscient about resource distributions. For example, most optimal foraging models assume that encounters with resources are random in space or time (e.g., Benhamou and Bovet 1989; Bovet and Benhamou 1991; Charnov 1976; Cody 1971, 1974; Pyke 1978, 1981; Turchin 1991) or that foragers distribute themselves or direct their movements between resource locations in omniscient and systematic ways (Anderson 1983; Ford 1983; Fretwell 1972). In reality, resource availability in space and time is usually only partly predictable, due to numerous ecological and stochastic processes, such as birth, death, growth, phenology, movement, or exploitation by other foragers. Consequently, I assume that space-use patterns are functions of foragers' imperfect *expectancies* about resource distributions based on prior learning, rather than functions of the *actual* distributions at any given time. For such expectancies to be useful (i.e., to increase fitness), they must correlate with actual distributions at least some of the time, but the correlation will usually be imperfect and will change (often decrease) over time.

Cognitive maps and the nature of spatial information.—My theory applies broadly to foragers that create and use cognitive maps (O'Keefe and Nadel 1978; Peters 1978; Tolman 1948)—that is, neurally encoded representations of the geometric relations among places. This ability has been widely demonstrated in mammals and other vertebrates (Gallistel 1990; Rodríquez et al. 2002) and perhaps some insects (Gould 1986; Menzel et al. 2005; but see Cruse and Wehner 2011). In mammals, cognitive mapping is made possible by the hippocampus (Fyhn et al. 2004; Jacobs 2003; Kjelstrup et al. 2008; O'Keefe and Nadel 1978; Sargolini et al. 2006; Solstad et al. 2008; Squire and Schacter 2002). Because memories are associated with places on the map, mammals and other vertebrates can integrate information about the geographic relations among places with expectations (or "place hypotheses"—Krechevsky 1932; O'Keefe and Nadel 1978) about what is in those places, based on prior experience. Places per se do not move around or disappear, and spatial memories can be highly resistant to memory decay (Kamil and Roitblat 1985; Nadel 1991; O'Keefe and Nadel 1978; Staddon 1983). In contrast, the things or events associated with places may move or change over time. Thus, the use of cognitive maps involves integrating temporally stable and temporally variable information (Olton 1985). In my theory, cognitive maps allow for navigation from place to place, whereas expectancies based on learned, site-specific information influence an animal's motivations for where and when to go.

As animals move they build and improve cognitive maps and update expectancies about sites on maps. They may

approach or avoid sites in a goal-directed fashion (Nadel et al. 1985; Tolman 1932) as motivated by expectancies and internal states (e.g., hunger or fear) and as facilitated by map information (Spencer 1992). Repeated use of an area increases the richness and accuracy of map information, which allows more efficient navigation among sites.

These assumptions and observations are consistent with an ecological view of cognition as reflecting adaptations to an animal's niche (Gallistel 1990; Healy and Braithwaite 2000; Real 1993; Staddon 1983; Stephens 2008). Because space and time are common to all niches, diverse taxa adapt to the temporal and spatial properties of the environment in similar ways, whereas their cognitive processes for dealing with niche-specific or species-specific characteristics vary (Staddon 1983). Because the physical environment and geometric relations among places are generally stable, animals can learn the locations of fitness-affecting features in a single encounter and remember them for long periods, whereas learning tasks that are ecologically arbitrary may take many trials (O'Keefe and Nadel 1978; Olton 1985; Staddon 1983).

Spatial predictability and the value of information.—I define the value of spatial information as the time-dependent increment it adds to any appropriate currency of fitness (e.g., foraging returns, exposure to predation, or probability of mating) for an informed versus an uninformed forager in the same area; thus, information has value only if it affects behavior in ways that increase payoffs or decrease risks (see also Eliassen et al. 2009; McNamara and Dall 2010; Stephens 1989, 2008). For simplicity, I initially define information in terms of foraging returns. Thus, learned information about resource locations has value at a later time if anticipating resource locations increases foraging returns (e.g., by increasing search efficiency, harvest rate, or capture probability). Animals may have some average or a priori expectancy about places they have never visited, but they are assumed to have specific information only about those they have visited.

Predictability is likely to decline over time after learning because of prey movements, phenological changes, exploitation by other foragers, and so on. Loss of predictability favors using information before conditions change. Exploited or depressed (sensu Charnov et al. 1976) resources require time to renew, however, favoring delayed return (Davies and Houston 1981; Kamil 1978). The optimal time to return to a resource site should, therefore, be a compromise between that favored by decreasing information and that favored by resource renewal (Spencer 1992).

TEMPORAL DECISION PROFILES AND OPTIMAL RETURN TIMES

Define a site as a finite area that may contain resources, such as a discrete patch or a smaller unit within a patch (for example, a single fruiting shrub within a clump of shrubs). Define the expected value, V, of a site as the net gain in resources a forager expects during a visit as a function of

resource availability, R. Assume that V increases with R as the proportion, Δ, of R that the forager removes during a visit (i.e., assume a type I functional response [Holling 1959]):

$$V = \Delta R,$$

where $0 < \Delta < 1$. During the visit the forager reduces R and V to ending values of R_0 and V_0. All else being equal (i.e., ignoring travel costs) a forager ought not to return to an exploited site until that site's expected value increases from V_0 to at least the expected value at unexploited sites, which are all equal in expected value to some mean for the environment as a whole. Previous foraging models have assumed an optimal rule is to delay return for as long as possible to maximize resource renewal between revisits (e.g., Davies and Houston 1981; Kamil 1978). If a forager in those previous models has unlimited sites available to it, it would do best by moving continuously to unexploited sites. If sites are limiting (e.g., due to territorial neighbors or habitat boundaries), then sites must be revisited, and the forager should maximize time between visits to allow for maximal resource renewal, thus developing a circuit or "traplining" strategy (Anderson 1983; Spencer 1992). Now consider that while exploiting a site, the animal gains information that can increase its foraging efficiency during a subsequent visit. For example, it may map effective foraging perches, places where wind-blown seeds collect, hiding places for prey, or which shrubs produce prodigious amounts of fruit or nectar. The value of this information, I, is an increment it adds to V:

$$V = \Delta R (1 + I).$$

The intrinsic value of this information is, however, dynamic. In many cases, information value should decline at decelerating (i.e., exponential) rates, such as when changes in resource locations occur independently and randomly over time. Decelerating declines are observed, for example, in availability of seed caches to scatter-hoarding rodents due to pilfering by other individuals (Vander Wall et al. 2006). Assume that the value of information decays exponentially with time (t) from a maximum when the information is 1st learned (I_0—Spencer 1992):

$$I_t = I_0 e^{-dt},$$

where I_t is the increment to foraging returns that an informed forager expects relative to an uninformed forager at time t given decay rate d.

Assume that resources renew according to a negative exponential function with the intrinsic rate of resource renewal, r. Then, the expected value of a site x to a forager at time t is:

$$V_{x,t} = \Delta[R_0 + (1 - R_0)(1 - e^{-rt})](1 + I_0 e^{-dt}). \quad (1)$$

Expected value varies over time as shown in Fig. 1A, which I call a *temporal decision profile* (Spencer 1992). The expected value of the site to the forager is initially lower than that of unexploited sites because of its reduced resource density. With time, the expected value rises above the unexploited background value, peaks, and finally asymptotes on the background
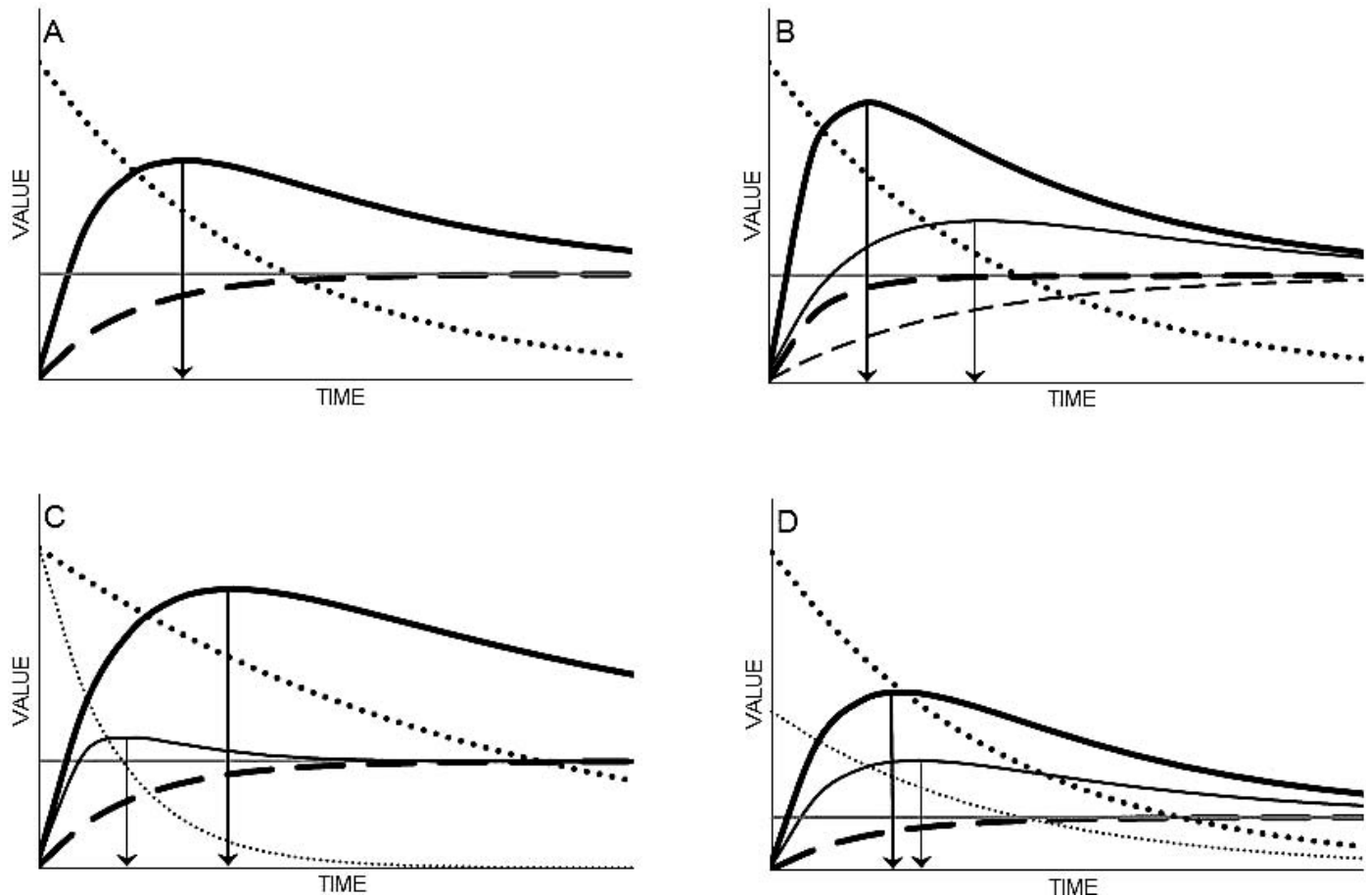
FIG. 1.—Temporal decision profiles showing optimal return times given that resources renew and information values decay with time since a previous visit. In all figures, the decreasing dotted curve(s) is an animal's decaying information about resources, the monotonically increasing dashed curve(s) is the renewing resources, and the solid humped curve(s) represents the forager's expected foraging returns based on both resource level and information (from equation 1). The horizontal line represents the average expected returns for a forager that does not use information. Vertical arrows show optimal return times. A) Standard curves with exponential information decay and negative exponential resource renewal. B) Effects of resource renewal rate: faster renewal leads to earlier optimal return time and higher expected value. C) Effects of information decay rate: faster decay leads to earlier optimal return time but lower expected value. D) Effects of initial information value: higher initial value leads to earlier optimal return time and higher expected value.

value as information value declines toward zero. The optimal time to reuse a site is at the peak in the V_t hump, which is always earlier than predicted by resource renewal alone. Logically, as the rate of resource renewal increases, optimal return time comes earlier (Fig. 1B). If information value declines rapidly, optimal return time also decreases but with lower expected value than for sites with slower information decay (Fig. 1C). Higher initial value of information also favors earlier return time, potentially with large returns (Fig. 1D).

The shape of a temporal decision profile depends on parameter values (as shown in Fig. 1) and on the forms of resource depletion and renewal functions (e.g., linear, sigmoidal, or exponential). Nevertheless, all forms of depletion and renewal functions can result in a humped value curve and yield qualitatively similar predictions to those described here for linear depletion and exponential renewal (Spencer 1992).

An important general conclusion results from humped decision profiles: So long as acquired information has value,

an informed forager should revisit sites and therefore limit its use of space to a finite set of sites even if available sites are infinite. Hence, exploiting information leads to formation of a home range within which the forager can update its cognitive map in a positive feedback process.

MOVEMENTS OF FORAGERS WITH 1-D COGNITIVE MAPS

Before further discussing use of information in complex environments, I 1st illustrate use of decision profiles in some simple movement models (Spencer 1992) for foragers constrained to (quasi) 1-D environments, such as a pied wagtail (*Motacilla alba yarrellii*—Davies and Houston 1981) or a mink (*Mustela vison*—Gerell 1970; Yamaguchi and Macdonald 2003) foraging along a riverbank. At any moment, such a forager has 3 options: proceed forward, stay put, or turn to retrace its previous route.

Assume that the forager is naïve initially about resource distribution (e.g., it has just immigrated) but that it has an average expectancy about resource density, perhaps estimated from average densities experienced elsewhere or inherited from ancestors (McNamara and Dall 2010). Thus, all sites along the linear environment are initially equivalent in expected value. Further assume that geometric information (the locations of specific sites along the linear environment) neither improves nor decays once obtained, so that changing information values represent changes in foraging rate due only to gaining and losing site-specific resource information and can be ignored (but see below for inclusion of travel costs).

Define a site, x, as an arbitrarily small unit length of habitat. The resource value of any site x along the linear habitat is V_x. For simplicity, assume that travel costs are constant and can be ignored, and that the forager moves at a constant rate, α, in 1 direction along the habitat. Its expected total net gains after time T spent foraging are:

$$V = \int_0^{\alpha T} V_x dx = \alpha T V_x.$$

V_x equals ΔR if the naïve forager takes a constant proportion, Δ, of encountered prey or food (a type I functional response). Because α and ΔR are constants, let $\alpha = 1$ and $V_x = \Delta R = 1$ to simplify the following equations and to facilitate comparisons. Note, however, that future models could replace these constants with more biologically justified functions, such as making Δ a function of information and having travel speed or cost vary with resource density, harvest rates, or other factors.

After passing through x, the forager leaves an ending value of resources, V_0:

$$V_0 = (1 - \Delta)R.$$

Resources renew following exploitation along a negative exponential trajectory. As long as $\Delta > 0$ and resource renewal is not instantaneous, a forager that turns around immediately experiences reduced returns relative to expectations for continuing forward. However, the forager also may gain information during its pass through x that could elevate foraging returns in x despite resource depression. This advantage may pertain both to that proportion of resources, Δ, that were eaten on the 1st pass and that are replaced by renewal, as well as to resources, $1 - \Delta$, that were encountered but not eaten (e.g., prey that escaped an initial encounter). The question is: Under what conditions does the value of this information more than compensate for the negative effects of resource depression if the forager turns around? That is, when does it pay to turn back and use information?

Let $I_{x,t}$ be the increment to foraging at site x due to information about x used at time t. $I_{x,0}$ is the value of this information given perfect predictability, that is, before the resource distribution at x changes. $I_{x,t}$ declines from this maximum as the distribution changes.

In the presence of a lone forager, the value of any place x at time t is:

$$V_{x,t} = \Delta R_{x,t}(1 + I_{x,t}).$$

For the naïve forager (having not yet turned around), $I_{x,t} = 0$, and expected foraging returns $V_{x,t} = \Delta R_{x,t}$. Hence, naïve foraging returns within a site are directly proportional to expected resource density there (as in most previous foraging models). If the forager turns around, it faces depressed resources but, if $I_{x,t} > 0$, it can exploit those resources more efficiently. Furthermore, resources are renewing, and the farther back the forager goes after turning the longer each site has had to renew.

The forager cannot transport itself to any site instantly but must retrace its steps. Hence, the decision to turn around is based upon the expected value of each site upon return to the site, rather than at the time of decision:

$$\overleftarrow{V}_{x,t} = \Delta R_{x,2t}(1 + I_{x,2t}), \tag{2}$$

where x,t is the value of x expected upon arrival but evaluated at the current time.

The total returns the forager expects from continuing forward until time T are:

$$V_{\text{continue}} = \int_0^T V_x dx = T,$$

(because $V_x = \Delta R = 1$), whereas the total returns expected for a return trip become:

$$V_{\text{return}} = \int_T^0 \overleftarrow{V}_{x,t} dx.$$

Obviously, the forager should turn around only if $V_{\text{return}} > V_{\text{continue}}$.

Spatial decision profiles.—Alternative spatial decision profiles generated by equation 2 for foragers using linear cognitive maps reveal qualitative conditions under which spatial information will motivate a forager to turn around. In spatial decision profiles, the x-axis is distance (or location) and values represent those *expected upon arrival* at each site, rather than at the time of evaluation, because site value will continue to change with resource renewal and information decay after a forager has decided to turn around. Hence, the forager's expectancies reflect the total round-trip time (or cost) to a site rather than the time passed when it makes the decision to turn around. If the forager travelled a long way in 1 direction in a homogeneous, previously unexploited habitat, the returns it expects at each previously visited site if it turns back are (again assuming a constant travel speed of $1x/1t = 1$, a type I functional response, and exponential renewal):

$$\overleftarrow{V}_{x,t} = \left[V_{x,0} + (1 - V_{x,0})(1 - e^{-2rt})\right](1 + I_{x,0}e^{-2dt}).$$

An example of this scenario (Fig. 2A, with conditions as in Fig. 1A) shows how the forager would have fared by turning early. The forager should not turn until it has passed a *minimum* distance, $x_{\min}$, in the initial direction, at which point the reduction in cumulative value it would experience due to revisiting depleted sites close behind (a "missed opportunity
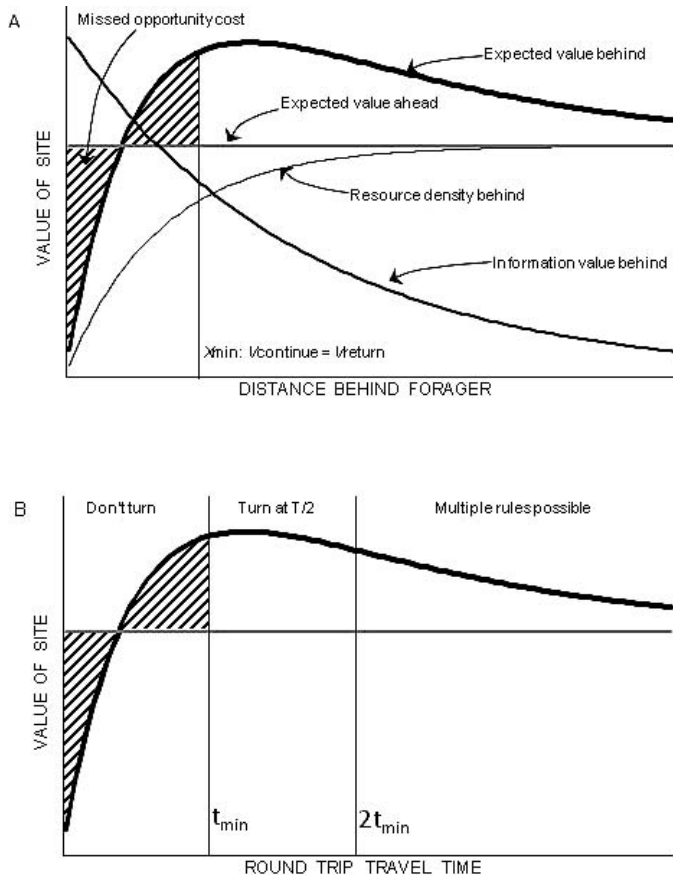
Fig. 2.—Spatial decision profiles for a forager with a linear cognitive map. A) Resource density, information value, and expected site value at a moment in time as a function of distance back over the length of habitat just covered, compared with the value of unexploited sites ahead. x_{min} indicates the minimum distance moved in the initial direction before it pays to turn around, because by the time the forager returns to the origin, its expected gains due to information value will just balance the temporary reduction in foraging returns due to reexploiting recently depleted sites (the "missed opportunity cost"). Going farther than x_{min} and then returning will increase expected returns relative to continuing indefinitely in 1 direction. B) Optimal turnaround decisions for the forager in Fig. 2A if it faces a deadline of length T. If $T < t_{min}$ the forager should not turn to use information; if $t_{min} < T < 2t_{min}$ the forager should turn once at $T/2$. Longer T leads to many possible rules depending on other assumptions, as discussed in the text.

cost" of turning around versus continuing ahead) is at least balanced by the elevated value of sites it will eventually experience farther back, as illustrated by the hatched areas in Fig. 2A, which are equal.

The forager should not turn before $t = t_{turn} = x_{min}$, and the minimum time necessary to complete the round-trip is $t_{min} = 2t_{turn}$, where t_{min} is the minimum time necessary for information to pay. If the forager turns earlier than t_{turn} (or has less than t_{min} available for foraging), the potential gains it foregoes for the 1st sites revisited exceed the elevated gains of the remaining sites. Once $V_{return} = V_{continue}$ (at x_{min}), the increased benefits reaped from the information at distant sites

going back balance the initial "missed opportunity cost." Thus, a forager able to integrate expected future returns can adopt a superior strategy to a forager that makes decisions based on instantaneous returns (Spencer 1992).

Nevertheless, solving for a globally optimum (or evolutionarily stable—Maynard Smith 1982) turnaround strategy requires additional assumptions about the time available to the forager, how the forager perceives time, and whether the forager can predict its own influence on future resource values or whether the forager can plan more than 1 turn in advance (Spencer 1992). For a simple example, consider a forager with a deadline, such as a diurnal forager that must maximize returns by sunset and does not anticipate its future effects on resource values beyond 1 turnaround. Fig. 2B illustrates the gains expected using the decision profile in Fig. 2A, except that the x-axis has been rescaled to reflect round-trip time. T is the length of the available foraging period. For $T < t_{min}$, the forager should not turn around. If $t_{min} < T < 2t_{min}$, the forager should move in 1 direction for $T/2$ and then return to the starting point by time T. As T becomes larger, solving for the optimum decision rule becomes a complex problem best handled by simulation, because each turn changes the decision profile nonsymmetrically (Fig. 3). Nonetheless, early in a long foraging period ($T > t_{min}$), the forager benefits from integrating expected returns over a relatively long time horizon and from using this information by sometimes turning around. As the deadline approaches ($T < t_{min}$), however, the forager should stop turning.

For a forager not facing an imminent deadline, if it pays once to turn around to use information, it pays eventually to turn again. Because the forager's expectancies were assumed to be homogenous at time 0, they also were symmetrical. If the forager turns after moving for t in 1 direction, a time t' ($0 < t' < 3t$) must come when it pays to turn again (i.e., when the forager has gone no more than twice the distance in the opposite direction after turning). Extending this argument, as long as the value of information creates an advantage to turning around at least once, a forager should turn repeatedly after moving some distance each time. The movement pattern generated is not necessarily periodic or cyclic, however, with the forager continually covering the same stretch of habitat. The time and distance moved after each turn varies, because the decision profile changes with each pass, as demonstrated by the following simple simulation models (Spencer 1992).

Movement simulations and home ranges in linear environments.—Consider a forager in a 1-D environment using the simple rule "turn when the *current, cumulative* value of sites behind is expected to *exceed* that of the sites ahead" foraging in an environment of 100 initially identical sites along a line segment closed into a polygon by joining the ends (e.g., as the shoreline of a lake). This allows the forager either to continue foraging around the environment in 1 direction (a circuit) or to turn around and forage back over recently covered ground. If information is useful but its value declines, and if resources renew quickly enough, it may pay for the forager to
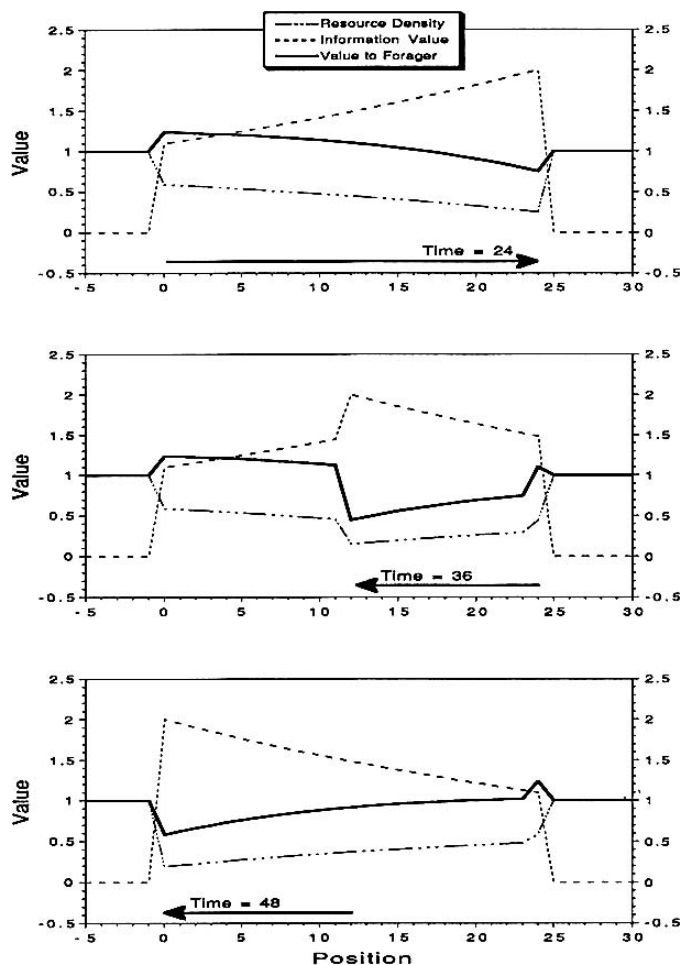
FIG. 3.—Value profiles for a forager at 3 times during a trip up and back over a length of habitat starting at position 0. Arrows indicate the forager's direction of movement over the previous time periods. A) Just before the forager turns for the 1st time, at time = 24. B) The forager is half way back to the start point at time = 36. Note asymmetries in resource density, the value of information, and expected value to forager. C) The forager is back to its starting point at time = 48. Note that the further reduction of resources on the return trip makes turning again at position 0 a poor strategy, so the forager will continue moving farther left before eventually turning again.

turn back sometimes and use that information; alternately, continuing in a unidirectional circuit may be better.

The forager starts at a random site at time 0, which it depletes by Δ, while simultaneously gaining information of value I_0. The forager then moves at rate $\alpha = 1$ to an adjacent site, again foraging and learning, while resources begin renewing at the 1st site at rate r and information begins decaying in value at rate d. The forager does not face an absolute deadline but integrates expectations over a finite time period T. Thus, at each step the forager sums the current value of each site, ahead and behind, out a distance set by T, then moves in the direction of greater expected returns. The cycle of forage, evaluate, and move continues to the time limit T.

Several major patterns of movement, with variations on each theme, result from varying parameter values to create

qualitatively different decision profiles and varying foraging horizons T (Fig. 4). (Similar sets of movement patterns result from sigmoidal or linear resource renewal functions [Spencer 1992].) As expected, a forager that does not benefit from information—either because information never pays (Fig. 4A, case 3) or because time is too short—never turns (Fig. 4C). Foragers that benefit immediately from information (Fig. 4B, all cases) turn with every step (Fig. 4E), roughly equivalent to a "sit-and-wait foraging strategy" (Huey and Pianka 1981). Note that this is not necessarily an evolutionarily stable strategy, because a forager that delays turning until resources renew even more may experience higher returns than one that turns as soon as information becomes useful (note the humps in expected value in Fig. 4B).

The most interesting and probably most general cases concern foragers that benefit from information after a time delay to allow for resource renewal (Fig. 4A, cases 1 and 2). Such foragers should turn repeatedly (Fig. 4D) given $T > t_{\min}$. They do not, however, move back and forth over the same length of habitat, at least until they establish a dynamic equilibrium between resource depression and renewal. The length of habitat thus covered generally expands with each turn before settling into a repeating pattern or cycle when renewal balances depletion (Spencer 1992). Thus, after a period of exploration and expanding home-range size, the forager eventually establishes and systematically covers a stable home range, *despite that doing so reduces resource density relative to unexploited sites*, because the forager can exploit resources within the home range more efficiently.

Nevertheless, the equilibrium home range may not maximize foraging returns, because a forager that establishes a larger home range may actually experience higher returns than one using the equilibrium range size (Spencer 1992). Optimal range length and total expected value both decrease with increasing rates of information decay and resource renewal, both of which push the hump in the decision profile down and to the left (Fig. 5). If, however, the range size that maximizes efficient use of spatial information is smaller than that needed to support the forager in the long term, the forager should subdivide its home range into multiple "foraging ranges" or "core areas" within which it concentrates its activities in the short term before moving to another (Spencer 1992). Such "foraging ranges" are not necessarily discernible habitat or resource patches in the traditional sense (e.g., Charnov 1976; Van Moorter et al. 2009) but, rather, are areas defined by short-term contagion in the forager's movements within the larger home range. Equilibrium home-range size also decreases as maximum information value (I_0) and rate of resource renewal (r) increase, but increases with rate of resource depletion (Δ).

At slow information decay rates, a forager can wait for resources to renew more fully while still having some information advantage. By turning around occasionally but not travelling all the way back before turning again, a forager produces a shifting or drifting home range. At very high decay rates, resources may not renew quickly enough for information to pay off, and the forager does just as well by ignoring
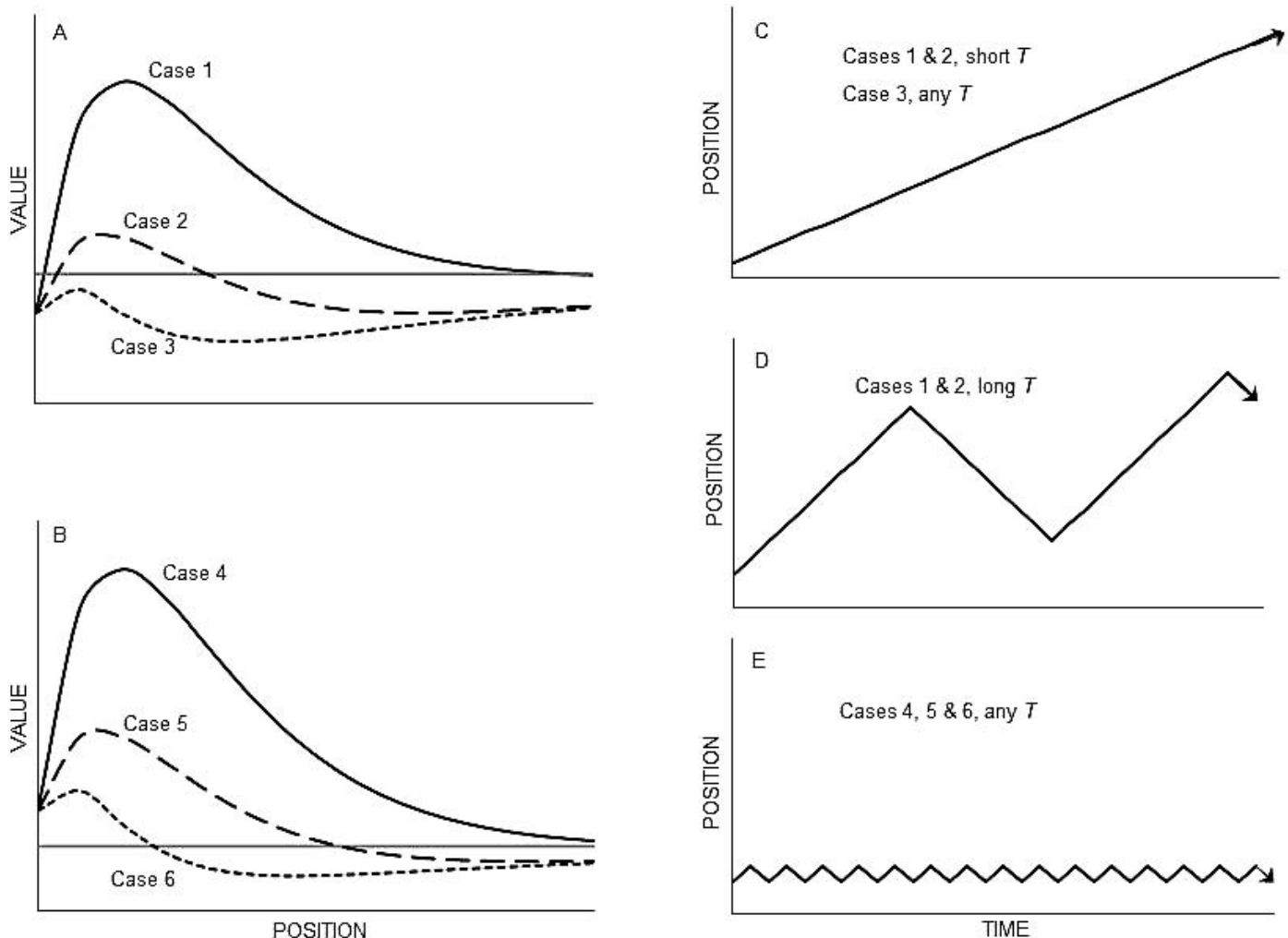
FIG. 4.—The types of movements that result from exponential decision profiles as a function of foraging horizon length, T, given the rule to turn back when current $V_{continue} > V_{return}$. A and B) The 6 types of decision profiles possible with exponential resource renewal and information decay. In the 3 cases in panel A, the forager faces reduced site value immediately following exploitation because the value of information does not immediately exceed the effects of resource depression. In the 3 cases in panel B, the forager experiences an immediate increase in site value because the value of information exceeds effects of resource depression (although waiting longer to use information increases value even more). C, D, and E) The forager's movements, shown as position versus time, depending on type of decision profile and T. C) The forager never turns to use information given cases 1 and 2 if $T < t_{min}$, and case 3 for all T. D) The forager turns repeatedly given cases 1 and 2 for $T > t_{min}$. E) The forager turns at every step for cases 4, 5, and 6, regardless of T.

information and continuing to wander into unexploited habitat (Spencer 1992).

Effects of habitat heterogeneity.—Habitat heterogeneity in a linear environment causes complex behaviors. A simulated forager in an environment with suitable (initial resource density = 2) and unsuitable (resource density = 0) resource patches and initially unaware of the distribution of patches has expectancies that resource values equal the average value for the entire environment (= 1) until it gains information via exploitation. Fig. 6 illustrates a circular environment of 100 sites with 1 patch each of suitable and unsuitable habitat. The forager initially explores the entire environment before turning to use information and settling into a home range that it appears to subdivide into 2 foraging ranges, with a movement pattern that

is nearly 2-cyclic but that does not repeat itself precisely—a hallmark of chaos (Gleick 1987).

Figures 7 and 8 illustrate the effects of resource renewal (Fig. 7) and information decay (Fig. 8) rates in a patchy environment. At low rates of resource renewal (Fig. 7A), a forager explores the entire environment, sometimes turning back for short distances within patches of suitable habitat; once the forager has mapped all patches, it tends to remain longer in them during a visit. As renewal rate increases, visits within patches lengthen and movements between patches become more systematic (Fig. 7B), eventually contracting to a home range that is a subset of the available (and previously explored) patches (Fig. 7C). At very high renewal rates, the forager stays in the 1st patch encountered, remaining ignorant of surrounding habitat and perhaps even settling in a portion of the patch
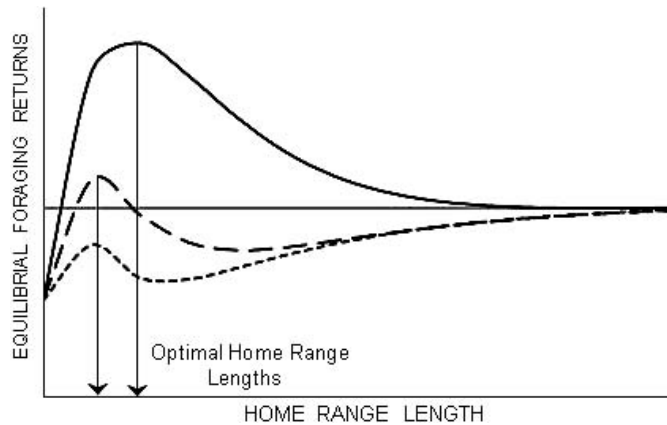
FIG. 5.—Equilibrial foraging returns as a function of home-range length and 3 information decay rates (corresponding with cases 1–3 from Fig. 4A). Faster information decay favors smaller home ranges unless decay is so fast relative to resource renewal that information never benefits the forager.
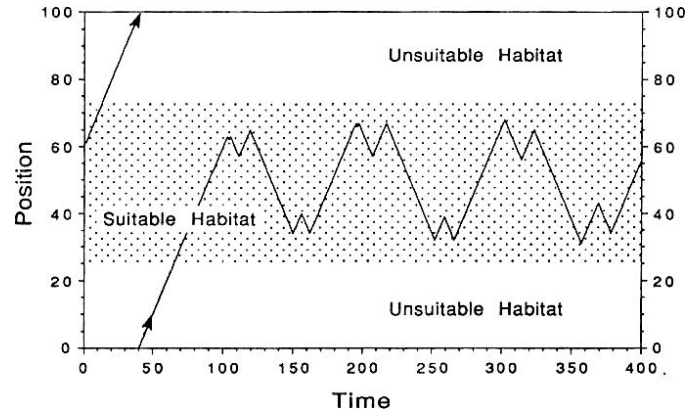

FIG. 6.—Movements of a forager exploring suitable and unsuitable habitat patches in a linear environment closed into a circle (positions 0 and 100 are identical). The forager starts at position 60 in suitable habitat (shaded) and completely explores the environment before establishing a home range in the suitable habitat. Note that movements within the home range approach a stable 2-cycle pattern, but have chaotic tendencies influenced by the forager's awareness of habitat boundaries.

(Fig. 7D). Finally, when renewal rate is so high that it immediately compensates for resource depletion, the forager becomes a sit-and-wait predator (not shown—Spencer 1992).

At low rates of information decay (Fig. 8A), the forager traverses the entire environment, sometimes lingering in patches. The duration of patch visits generally increases once patches are identified by exploration. As information decay rates increase, the forager spends longer in each patch and contracts its home range to fewer patches to take advantage of information before it becomes obsolete (Figs. 8B and 8C). At very high decay rates, the forager remains in a single patch following initial exploration and in the extreme may become a sit-and-wait predator (Fig. 8D).

MOVEMENTS OF FORAGERS WITH 2-D COGNITIVE MAPS

In 1-D models, foragers lack some major benefits of cognitive mapping, such as interpreting shortcuts or novel routes among or within sites to increase travel efficiency and to revisit sites at the optimal times. Thus, in a 2- or 3-D environment, a forager with cognitive mapping abilities can significantly increase foraging returns with information. In addition, because travel paths are quasi-1-D, lacunae (areas of little or no use) can develop by chance within a 2- or 3-D home range. Once these lacunae are formed, their presence may be reinforced via the positive feedback nature of information, which raises the value of previously explored sites relative to unexplored sites and encourages their preferential reuse. Such lacunae may allow individuals in a population to interlace or overlap their home ranges without ever foraging in the same sites, such as seen in foraging fruit bats (*Artibeus jamaicensis*—Morrison 1978) and black bears (*Ursus americanus*—Mitchell and Powell 2008).

Consider a 2-D environment containing many potential foraging sites that a forager with cognitive mapping abilities can link into circuits for systematic revisiting. Each circuit is mathematically equivalent to the 1-D circuit around a lake, except that here the circuit is not imposed by the physical environment but defined cognitively by the forager. Optimal circuit length is $x^* = t^*$, where t^* is the optimal return time and assuming constant travel speed $1x/1t$. The initial visit to each site in a circuit yields the background payoff value of 1; the 2nd, informed visit yields the maximum payoff of V^*, at the peak of the decision profile (Fig. 9A). Thus, if information has value, the forager should always complete at least 2 cycles before shifting to a new circuit. If resources renew completely in $<t^*$, the forager experiences V^* forever and the optimal rule is to follow the circuit perpetually. If resources do not renew completely in $<t^*$, resource density and, hence, foraging returns, decline toward a nonzero asymptote from 1 cycle to the next. Within each cycle, the foraging rate is constant, resulting in stepwise changes in foraging returns with each cycle (Fig. 9B). Eventually, foraging rate may equilibrate as renewal balances depletion between cycles.

The forager should travel its circuit until the foraging rate expected on the next cycle falls below the average for establishing and using a new circuit; that is, when:

$$V_{c+1} < \frac{\sum_1^c V_c}{c}, \qquad (3)$$

where c is the number of cycles completed. At this point, the forager should explore and establish a new circuit. If inequality equation 3 is always false, the per-cycle foraging rate equilibrates above the background value of establishing a new circuit and the forager never explores a new circuit. If moving to a new circuit pays and the forager does so, resource
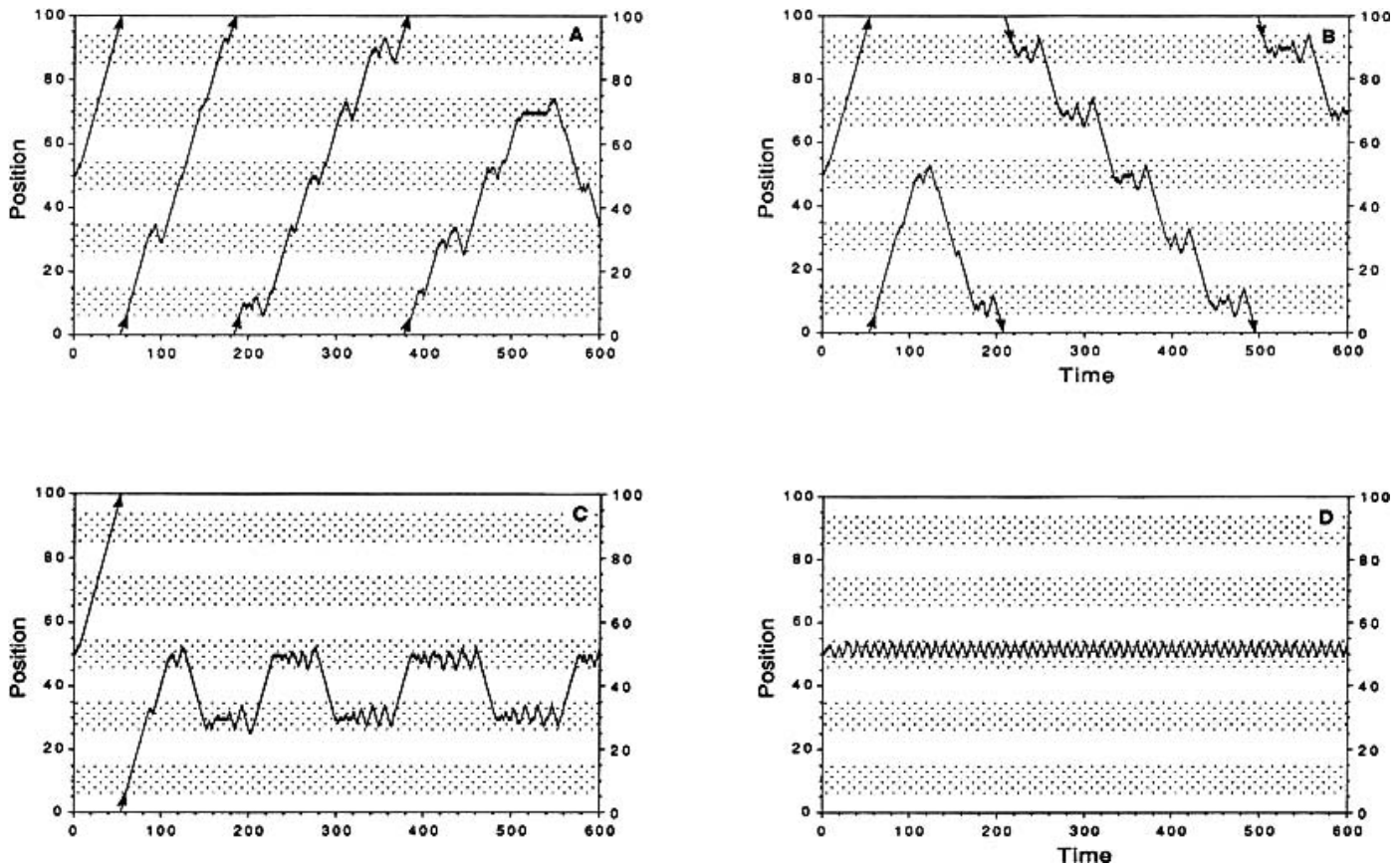
FIG. 7.—Effects of exponential resource renewal rate (*r*) on movements in a patchy, linear environment. As renewal rate increases, the forager contracts its home range to fewer patches (shaded) and spends greater durations in each. A) $r = 0.001$. The forager explores the entire environment, sometimes tarrying in patches; stays in patches are slightly longer after the entire space has been explored. B) $r = 0.005$. The forager explores and uses the entire environment but spends longer time in each patch than for smaller *r*. C) $r = 0.01$. After exploring the entire environment, the forager alternates between 2 patches, spending increasing time in each. D) $r = 0.05$. The forager never explores beyond the 1st patch, settling into a portion of it.

levels in the 1st circuit continue to renew. If renewal is rapid relative to information decay, the forager may eventually benefit by returning to its 1st circuit. It may continue adding new circuits to its home range until establishing an overall equilibrium with renewal. The result is a network of circuits, each of which the forager treats similarly to Charnov's (1976) patch in that the forager should leave a circuit when the foraging rate with the circuit falls to the average rate for the entire set of circuits. In addition, if sites do not all renew at the same rate, the forager can mix-and-match sites into new circuits that it can use efficiently.

The major differences between this and most patch-use models are here the "patch" (circuit) is intrinsically defined by the forager rather than by the environment; changes in foraging rate within the circuit are discontinuous because the forager covers the circuit systematically rather than randomly; foraging returns increase between the 1st and 2nd cycles in a circuit (patch depletion models assume continuously decreasing returns); and foragers preferentially revisit circuits (traditional patch-use models have no such tendency). This formulation produces novel predictions relative to previous patch-use models in foraging theory (e.g., Charnov 1976): a learning

forager should systematically revisit patches, as opposed to moving randomly from patch to patch, and, hence, will develop a home range; movements within a patch should be systematic, so foraging returns are not smoothly decelerating; at intermediate and large patch sizes, foraging returns will accelerate as information becomes useful; and large patches should be subdivided for effective exploitation of information. In addition, the tendency to stay in a patch or to revisit known patches should increase with increasing I_0, d, and r; increase with increasing variance in T_{pn} and the foragers' sensitivities to this variance; and decrease with increasing Δ (Spencer 1992).

DISCUSSION

Building a "unified approach" to understanding animal space-use and home-range behavior (Börger et al. 2008) requires that animal movement models make realistic assumptions about how animals gain and use information in dynamic environments. Until recently, most movement models have assumed that animals are either omniscient or ignorant about the distribution of resources in space and time. Recent modelers have recognized the importance of memory in animal
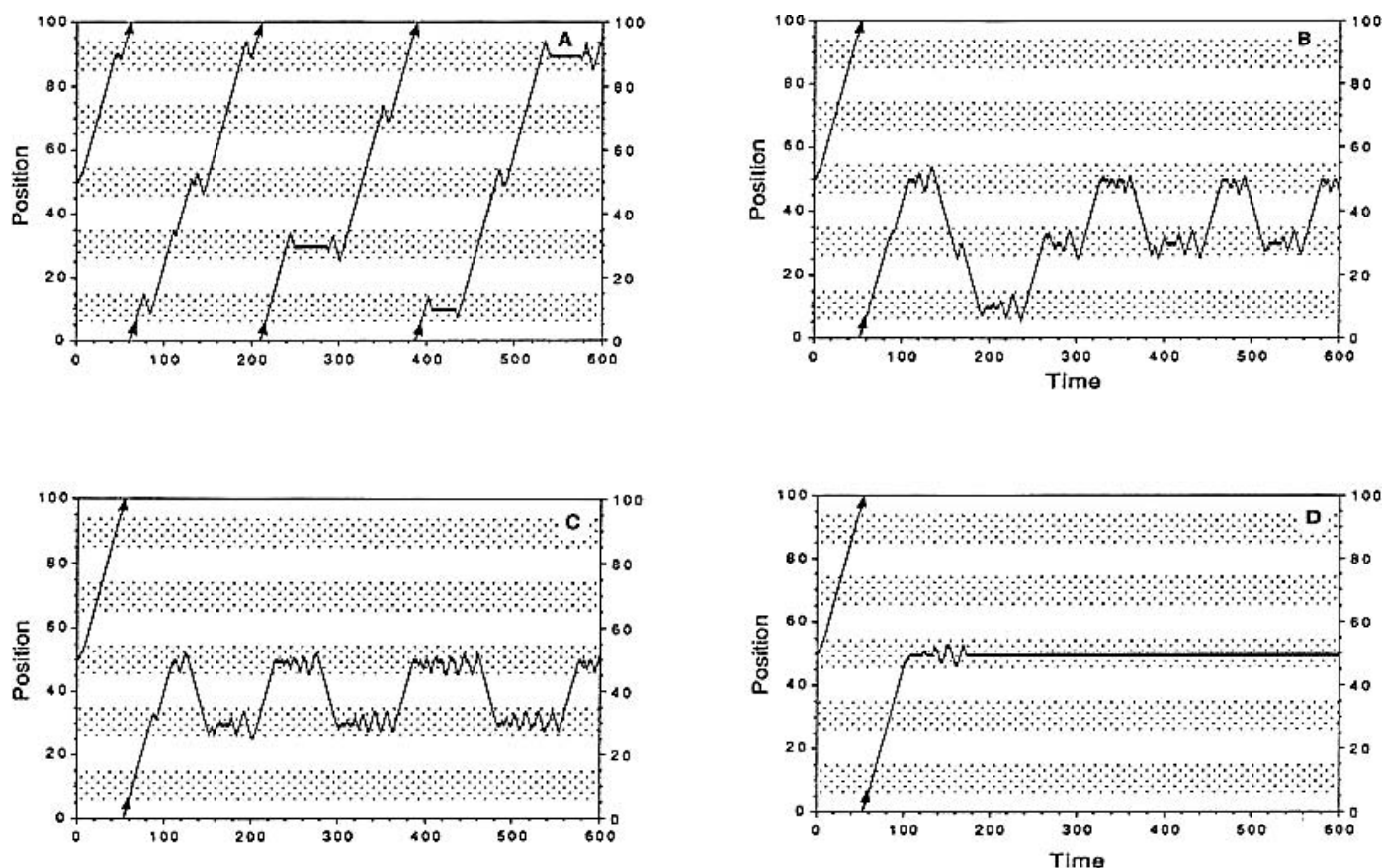
Fig. 8.—Effects of rate of information decay (*d*) on movements in a patchy, linear environment with exponential resource renewal. As information decays faster, the forager contracts its home range to fewer patches (shaded) and spends greater durations in each. A) $d = 0.001$. The forager explores the entire environment, sometimes tarrying in patches; stays in patches tend to be longer once the entire space has been explored. B) $d = 0.005$. The forager explores the entire environment, but thereafter alternates among 3 and eventually 2 patches. C) $d = 0.01$. After exploring the entire environment, the forager alternates between 2 patches, spending increasing time in each. D) $d = 0.05$. After exploring the entire environment, the forager settles into the 1st patch encountered, eventually adopting a sit-and-wait strategy.

movements and have begun introducing learning and memory algorithms into mechanistic movement models (e.g., Boyer and Walsh 2010; Dalziel et al. 2008; Morales et al. 2010; Smouse et al. 2010; Tan et al. 2002; Van Moorter et al. 2009). This promising approach should continue to advance by integrating new scientific understanding of the cognitive processes underlying movement decisions.

I assume that movement decisions are based on imperfect *expectancies* about environmental distributions that reflect the dynamic value of learned information. Models based on this approach can demonstrate how a wide array of space-use phenomena—from momentary movement decisions, to sub–home-range movement patterns, to patterns of home-range overlap and population spacing—can emerge from mechanistic optimality models. Integrating these assumptions about expectancies and dynamic information value into more sophisticated movement models, such as Bayesian foraging (Iwasa et al. 1981; McNamara et al. 2006; Valone 2006) and correlated random-walk models (Boyer and Walsh 2010; Moorcroft 2012; Moorcroft and Lewis 2006; Van Moorter et al. 2009), should prove fruitful.

Why home ranges exist.—Despite the tremendous variety of movements and spacing patterns observed among animals across diverse taxa, niches, and scales, 1 fundamental characteristic is near universal: animals concentrate their movements within areas we call home ranges rather than wandering aimlessly (Brown and Orians 1970; Burt 1943; Jewell 1966; Powell 2000; Seton 1909; Siniff and Jessen 1969; Waser and Wiley 1979). Numerous models have been devised to understand this emergent property of animal movements, including mechanistic movement models (Moorcroft 2012; Moorcroft and Lewis 2006), functional models based on optimal foraging theory (Mitchell and Powell 2012), and statistical models that estimate probability density functions and delineate home-range boundaries from animal location data (Fieberg and Börger 2012). Börger et al. (2008) synthesized this literature and argued that a general, mechanistic understanding of home-range behavior (or why home ranges exist) is still lacking. I contend that such understanding requires explicit recognition of the cognitive processes involved in animal movement decisions and the fitness value of information (Powell 2012; Powell and Mitchell 2012). In short, home ranges exist because information about
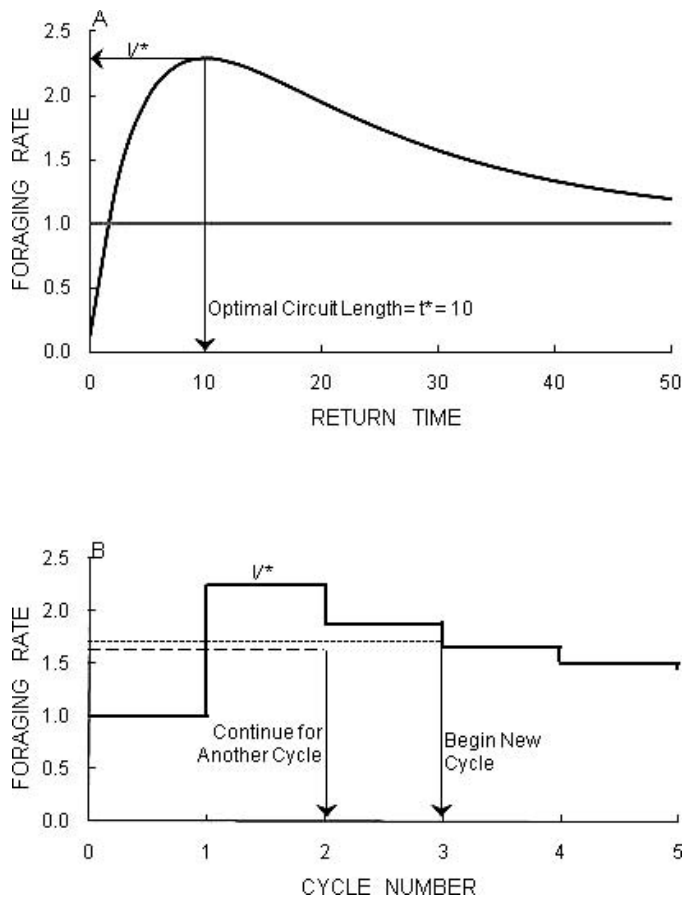
FIG. 9.—Predicting the number of cycles around a foraging circuit. A) A decision profile for a forager that should develop a circuit of 10 sites that takes $t^* = 10$ time units per cycle. The 1st (exploratory) cycle yields foraging returns $= 1$ (the average expected returns for an uninformed forager). The 2nd cycle yields maximum returns $= V^*$. B) Foraging returns as a function of cycle number for the circuit. Foraging returns are constant within a cycle but change between cycles. Foraging returns for cycles 1 and 2 come from Fig. 9A; thereafter, foraging returns fall asymptotically as resource depletion exceeds renewal between cycles. The forager should quit the circuit and start a new one when expected foraging returns on the next cycle (in this example, the 4th cycle) would fall below the average of preceding cycles (dashed lines showing average returns for the first 2 and 3 cycles).

places increases fitness, and a home range may best be defined as that area over which an animal regularly exploits and updates spatial information as stored in a cognitive map.

Nevertheless, exactly how that home range is used (i.e., patterns of movement within the home range, home-range stability, extra–home-range exploration, and home-range overlap) should vary adaptively with the particular sorts of space-use problems presented by each animal's niche (Mitchell and Powell 2012; Moorcroft 2012; Powell 2000, 2004, 2012; Powell and Mitchell 2012; Spencer 1992). As demonstrated by my simple models (Spencer 1992), a variety of home-range utilization patterns can result from different spatiotemporal distributions of resources—which influence the optimal timing of information use—even though spatial contagion (or home-

range behavior) is a general emergent result whenever spatial information has value.

Situations where an animal immigrates or is introduced to an area where it has no prior experience offer empirical evidence for the role of information in home-range establishment. In such cases, individuals generally develop stable home ranges after initial periods of homing, or "floating," and exploration (e.g., American martens [*Martes americana*—Davis 1983], fishers [*Martes pennanti*—Proulx et al. 1994], wolves [*Canis lupus*—Ream et al. 1985; Weise et al. 1979], wapiti [*Cervus elaphus*—Fryxell et al. 2008; Wolf et al. 2009], and black bear [*U. americanus*—Costello 2010]). Ream et al. (1985) tracked for 30 months a lone female wolf that dispersed a great distance into an area that had lacked wolves for many years. After a period of apparent exploration, the wolf settled into a "well-defined home range" with 2 intensively used core areas, despite the lack of obvious constraints on her movements (she was not pregnant or lactating and had no territorial neighbors). Ream et al. (1985) suggested 2 hypotheses for this behavior: the wolf was the sole survivor of a pack that had lived there years before and her "distinct movement pattern represented a vestige of their territorial behavior" (p. 234); or she established a home range to saturate it with her scent, which "increased the probability that a dispersing male might find her" (p. 234). I suggest a more fundamental hypothesis: after exploring a new part of the world, she found a good place, got to know it, and settled down.

Home-range size, structure, and stability.—Temporal patterns in the predictive value of learned information can influence the size and stability of a home range, as well as how an animal structures its within–home-range movement patterns. Body size, diet, and resource density explain much variance in home-range sizes among mammals (Adams 2001; Calder 1984; Jetz et al. 2004; Mace et al. 1983; McNab 1963; Powell 2012; Powell et al. 1997). I predict that, after controlling for these factors, home-range size varies inversely with the maximum value of information and with the rate of information decay. Furthermore, interindividual variance in home-range sizes should decrease with increasing information value and rate of information decay, because high I_0 and d narrow the hump in foraging returns plotted against range size and, therefore, deviations from the range size that maximizes foraging returns are likely to be most costly when the timely use of information strongly affects fitness. If information has marginal utility or decays very slowly, foraging returns vary little with increasing area (beyond a minimum threshold) and other factors may constrain movements (Spencer 1992).

So long as information is useful, optimal return times should be earlier than expected from resource renewal alone, as was empirically demonstrated by Wolf et al. (2009) for wapiti. Factors that favor early return, such as high information value coupled with rapid information decay (e.g., as resource distributions change), should concentrate an animal's activity into a smaller area than would be predicted by resource availability alone, and potentially smaller than required to supply the individual's resource needs in the long term. In such

cases, we should see a "shifting core" or "shifting foraging area" pattern of home-range use, as the forager concentrates its movements in the short term to take advantage of recent information, but shifts to other areas over the longer term because the initial area cannot support its needs indefinitely. This pattern has been described in numerous mammals (e.g., Altmann and Altmann 1970; Doncaster and Macdonald 1991; Fryxell et al. 2008; Gerell 1970; Jones 1989; Milton 1980; Powell et al. 1997; Rabinowitz 1986; Terborgh 1983; Waser 1976). It seems particularly prevalent in carnivores, which require large home ranges for their body sizes (Jetz et al. 2004; McNab 1963) and often hunt elusive prey. Capture success is generally low for active predators (e.g., raptors [Craighead and Craighead 1956], fishers [Powell 1993], and wolves [Mech 1970]) and predator–prey encounters often result in hiding, alert, or otherwise defensive prey (Jędrzejewski and Jędrzejewska 1990; Stillman et al. 2000; Ylönen 1989). Depending on how long this behavioral resource depression lasts, a predator may benefit from returning soon, or from foraging elsewhere and returning later. I once observed a radiocollared marten (*M. americana*) fail to capture a ground squirrel (*Callospermophilus* [*Spermophilus*] *lateralis*) on an initial encounter. After continuing to forage away from the site, the marten returned directly to the encounter site 1 h later, appeared to stalk the location, detected the reemerged squirrel, and captured it (Spencer and Zielinski 1983). Martens in that study would use a portion of their home range intensively for several days, often revisiting specific locations, and then rapidly shift to another area, presumably as they depressed local prey availability to where the advantages of short-term information no longer compensated for the effects of resource depression.

Factors that favor delayed revisits to previously visited sites (e.g., stable, predictable resource locations and slow resource renewal), should favor more systematic coverage of the home range to maximize time for renewal between visits. For animals that exploit stationary resource patches that renew in place, such as nectarivores or frugivores, traplining or circuit foraging is advantageous (Gill 1988; Gill and Wolff 1977; Kamil 1978; Kodric-Brown and Brown 1978; Paton and Carpenter 1984). For animals that eat many small items that are more evenly distributed or not spatially predictable, such as insectivorous carnivores on the Serengeti Plain (Waser 1981), remembering locations of previous prey encounters provides little advantage, and they should constantly shift foraging areas to avoid reuse of recently exploited areas.

Home-range overlap and territoriality.—I hypothesize that the value of spatial information generally promotes population hyperdispersion (as opposed to random dispersion) and can help explain exclusive use of space by individuals in the absence of territorial defense. In general, home-range overlap should decrease with increasing information values, because a forager encountering sites recently exploited by another may experience the costs of resource depression without the commensurate benefits of updated information. Imagine, for example, a disperser entering the home range of an established

resident. The disperser has no site-specific expectancies in the area and it suffers poor foraging returns because the resident, which can exploit its home range efficiently due to information, has depressed local resource availability. The disperser is therefore likely to move on, or to return to previously visited sites where it experienced better conditions. Thus, the self-reinforcing relationships between site-specific expectancies, information value, and movement patterns should cause individuals to gradually develop relatively exclusive use areas (home ranges or foraging ranges), even if they never encounter one another or experience territorial defense. In fact, vertebrates often occupy home ranges with no evidence of aggression, advertisement, or even exclusivity (Brown and Orians 1970; Powell 2000; Waser and Wiley 1979). Contrary to assumptions of some territory-use models (Adams 2001; Brown 1969, 1975; Carpenter 1987), territoriality per se is not an evolved trait, but an emergent *result* of site tenacity that may be reinforced secondarily with aggressive behavior or advertisement (Powell et al. 1997). The benefits of spatial information can be the sole catalyst for exclusive use of space.

Calculating the value of information.—Animals with site-specific information appear to search more efficiently than naïve animals, increasing their probabilities of capturing elusive prey or of returning to productive sites before they are exploited by competitors (e.g., Croze 1970; Gill and Wolff 1977; Schaller 1972; Vander Wall et al. 2006). If P_n is the probability of a naïve forager obtaining a particular resource item and P_i is the probability for an informed forager, then the value of information (I) is $I = P_i/P_n - 1$. I has been calculated for diverse foragers, with ranges from $I \approx 0.25$ for territorial sunbirds (Gill and Wolff 1977), to $I = 31.7$–42.3 for scatter hoarders (Balda 1980; Vander Wall 1982; Vander Wall et al. 2006). Using data collected by Jacobs and Liman (1991), I calculated I for eastern gray squirrels (*Sciurus carolinensis*) as 1.2 at 2 days after caching, 1.3 after 4 days, and 0.8 after 12 days (Spencer 1992), consistent with the assumption of information decay.

Assumptions about cognitive mechanisms.—My assumptions about cognitive mechanisms and memory are well supported by the literature, including the ability to associate stimuli with places (Gallistel 1990; O'Keefe and Nadel 1978; Olton 1985; Tolman 1948), to develop in maplike representations (O'Keefe and Nadel 1978; Tolman 1932, 1948), to weight experience by time (Beling 1929; Bolles and Moot 1973; Clayton and Dickinson 1998; Gallistel 1990; Gill 1988; Olton 1985; Raby et al. 2007; Zielinski 1986, 1988), and to create time- and space-specific expectancies that motivate goal-directed behavior (O'Keefe and Nadel 1978; Tolman 1932). My assumptions also are consistent with ecological views on learning (Gallistel 1990; Healy and Braithwaite 2000; Johnston 1981; Johnston and Pietrewicz 1985; Kamil and Roitblat 1985; Real 1993; Staddon 1983). Cognitive mapping can involve 1-time, all-or-nothing learning (O'Keefe and Nadel 1978), and can allow an individual to infer relationships not directly experienced (e.g., shortcuts). These characteristics contrast strongly with, for example, classical

and operant conditioning tasks, which may require many trials to learn (Kamil and Roitblat 1985; Pavlov 1927; Staddon 1983). Place memories appear more resistant to decay than other memories (Nadel 1991; O'Keefe and Nadel 1978) and memories of geometric relationships between places are preserved even if the things found in those places change or are forgotten. Consequently, I assume that decay in geometric information is slow (or absent), whereas site-specific information decays more rapidly. Nonetheless, the accuracy and precision of an animal's representation of geometric relations improves with repeated experience (Ellen et al. 1982; Thinus-Blanc et al. 1991), so future models could allow geometric information in a cognitive map to increase asymptotically with experience, and to decay independently (and more slowly) than information about resources.

Relation to other theories.—Powell (2000, 2004) noted that knowledge of resources and cognitive maps are inherent in Burt's (1943) definition of home range, and postulated that the cognitive map of a mammal might be envisioned as an integration of contour maps for fitness-affecting features, such as food resources, escape cover, or potential mates. Powell's (2000, 2004) formulation is similar to mine in that it relates an animal's cognitive map to fitness (via a "fitness landscape") and recognizes that the cognitive map may change as resource distributions change. My formulation builds on Powell's by making more explicit (based largely on the animal cognition literature) the difference between temporally stable and temporally variable features in cognitive maps, and how expectancies and the value of spatial information may vary with time. Moreover, my formulation demonstrates how movement decisions motivated by dynamic expectancies can generate home ranges as emergent properties of movements, while also helping explain how animals exploiting resources with different spatiotemporal distribution patterns should structure their movements within home ranges and space themselves relative to other individuals. Although a growing number of optimal foraging models allow foragers to learn, in many the foragers are learning about resource *density* in a patch during exploration. Thus, these models still implicitly assume that foragers are ignorant about the *locations* of prey or patches (Bernstein et al. 1991; Eliassen et al. 2009; Green 1980, 1984; Iwasa et al. 1981; Mangel and Clark 1986; McNamara 1982; McNamara and Houston 1985; Oaten 1977; Stamps and Krishnan 1999; Stephens 2008; Valone 1990). Other models, inspired largely by studies of nectarivores, allow foragers to learn resource locations and to delay return until resources have renewed (Armstrong et al. 1987; Cole et al. 1982; Davies and Houston 1981; Gill and Wolff 1975; Kamil 1978; Paton and Carpenter 1984). These models assume that foragers *avoid sites of low expected value*, whereas my approach assumes that informed foragers move *toward sites of high expected value*.

Although these rules may seem equivalent under certain circumstances, the difference is important, because avoiding areas of low expected value does not by itself lead to spatial contagion (home-range behavior). Preferentially moving toward sites of high expected value seems a more general rule,

although most animals undoubtedly move in response to multiple types of expectancies, such as avoiding potentially risky areas while approaching areas with high expected resource values or potential mates (Powell 2000, 2004).

Mechanistic movement models using random-walk algorithms (e.g., Dalziel et al. 2008; da Silva et al. 2006; Gautestad and Mysterud 2005; Paraan and Esguerra 2006; Schutz and Trimper 2004; Siniff and Jessen 1969; Tan et al. 2002; Turchin 1998) produce home-range behavior only if they employ reflective boundaries or an "attraction to place" bias, such as attraction to a particular location (e.g., a central den site) or to previously visited sites (Moorcroft 2012). Until recently, algorithms used to create spatial contagion in random-walk models have been mostly ad hoc and biologically unjustified (Börger et al. 2008; Moorcroft 2012). For example, Tan et al. (2002) assumed that animals remember *lists* of sites in the order visited, eventually reaching a dynamic balance between forgotten (older) and remembered (recently visited) sites, which is inconsistent with studies of serial learning functions (Ebbinghaus 1885) or episodic memories (Clayton et al. 2001a, 2001b; Griffiths et al. 1999; Raby et al. 2007). Gautestad and Mysterud (2005) used a similar "return-to-a-previously visited location" rule, but their site-fidelity algorithm chose the revisitation sites randomly from all visited sites at fixed time intervals. Such rules ignore how animals integrate and utilize spatial and temporal information in cognitive maps (O'Keefe and Nadel 1978; Olton 1985).

Very recently, modelers have begun to incorporate more defensible memory algorithms into movement models, consequently yielding more realistic and useful predictions (e.g., Boyer and Walsh 2010; Gautestad and Mysterud 2010; Van Moorter et al. 2009). For example, Van Moorter et al. (2009) developed a correlated random-walk model that produces a variety of realistic space-use patterns using assumptions similar to those I used to define decision profiles. In their model, movement decisions are based on a time-dependent attraction to patches based on a decaying "reference memory" of maximum values and avoidance of patches based on "working memory" of when a patch was last visited. This formulation is equivalent to my assumptions that the "expected value of a site" varies as information decays and resources renew. Their model produces stable home ranges, especially when working memory (renewal rates) decays more rapidly than reference memory (cognitive map), which is consistent with my assumptions and with the learning and memory literature (O'Keefe and Nadel 1978). Nevertheless, my formulation makes explicit that reference memories within a cognitive map can include a variety of temporally stable and temporally dynamic information, and that declines in information value can occur due either to changes in resource distribution or to memory decay. Because forgetting can be a maladaptive limitation of memory, future models should distinguish between the cognitive processes of *forgetting* (either as a limitation or an adaptive mechanism [Kraemer and Golding 1997]) and *adaptive adjustment of expectations* based on experience (which Van Moorter et al. [2009] did not simulate).

Building on the theory.—This conceptual approach to understanding animal space use is not tied to the simple environments, functional forms, or deterministic equations I used to illustrate it. For linear environments, qualitative predictions about space-use patterns remain unchanged so long as resource uptake increases monotonically with resource density (i.e., type I, II, or III, but not type IV, functional responses [Holling 1959]), the resource renews monotonically with time, the value of information decreases monotonically with time, and time to forage is not perceived as infinite (Spencer 1992). Future models in 2- or even 3-D environments should incorporate more biologically justified assumptions and more explicitly address how mismatches between expected values and actual or experienced values affect foragers. My models assume that expected site values correlate with actual values, so that, on average, a forager basing movement decisions on its expectations will experience higher foraging returns than one that does not. Future models could replace this deterministic assumption using probability functions to describe resource patterns and with Bayesian updating of expectations (Iwasa et al. 1981; McNamara and Dall 2010; McNamara et al. 2006; Valone 2006). Future models also could replace the simplifying assumptions in my equations with variable travel costs and harvest rates, multiple types of resources and risks, resource gradients, diurnal or other temporal cycles, and so on, to better represent real-world niches. Hypotheses generated by such models, as well as the various predictions I make herein concerning the influence of dynamic information values on space-use patterns, could be tested with field data collected using global positioning system technology (Moorcroft 2012; Wolf et al. 2009) to further our understanding of animal space-use and home-range behavior.

Animals respond to myriad spatial and temporal distributions of varying predictability, but even imperfect information about such patterns can increase fitness (Eliassen et al. 2009; McNamara and Dall 2010). Understanding the fitness value of spatial and temporal information, and how animals exploit such information using cognitive maps, is essential to a general theory of animal space use. It explains why mammals have home ranges and how they use them.

ACKNOWLEDGMENTS

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