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Paper:

Tao, Y., Börger, L. & Hastings, A. (2016). Dynamic Range Size Analysis of Territorial Animals: An Optimality
Approach. *The American Naturalist, 188*(4), 460-474.

http://dx.doi.org/10.1086/688257

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Dynamic Range Size Analysis of Territorial Animals: An Optimality Approach

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ABSTRACT: Home range sizes of territorial animals are often observed to vary periodically in response to seasonal changes in foraging opportunities. Here we develop the first mechanistic model focused on the temporal dynamics of home range expansion and contraction in territorial animals. We demonstrate how simple movement principles can lead to a rich suite of range size dynamics, by balancing foraging activity with defensive requirements and incorporating optimal behavioral rules into mechanistic home range analysis. Our heuristic model predicts three general temporal patterns that have been observed in empirical studies across multiple taxa. First, a positive correlation between age and territory quality promotes shrinking home ranges over an individual's lifetime, with maximal range size variability shortly before the adult stage. Second, poor sensory information, low population density, and large resource heterogeneity may all independently facilitate range size instability. Finally, aggregation behavior toward forage-rich areas helps produce divergent home range responses between individuals from different age classes. This model has broad applications for addressing important unknowns in animal space use, with potential applications also in conservation and health management strategies.

Keywords: movement ecology, optimal behavior, home range, territoriality.

Introduction

Home range typically refers to a spatially bounded area routinely used by an organism or collective of individuals over a certain amount of time to fulfill its various needs (Burt 1943; Powell and Mitchell 2012). For territorial animals, home ranges may be structurally divided into a heavily traversed internal area (i.e., territory), which the owners defend against intruders by means of systematical patrol and aggressive evictions, and an external area, which is used pri-

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marily during their foraging bouts (Samuel and Green 1988; Vander Wal and Rodgers 2012). Such spatially constrained movement types are widespread among animal species, with key ecological consequences at population and community levels (reviewed in Börger et al. 2008).

Recent developments in technology have greatly advanced the study of animal home ranges, with modern, cost-effective tracking devices now being widely employed to collect increasingly finer-scaled relocation data (Cagnacci et al. 2010; Kie et al. 2010; Tomkiewicz et al. 2010). This increase in detailed movement information allows for the study of home ranges as dynamical systems that reflect an animal's changing interactions with its environment. A striking observation has been the fluid nature of bounded space use patterns as a function of time, including variations in spatial location (Bohrer et al. 2014), boundary geometry (Bateman et al. 2015), internal structure, and area coverage (Börger et al. 2006). Such temporal variations have been observed to correlate broadly with demographic descriptors, such as age or group size (Singh et al. 2012; Campioni et al. 2013; Kittle et al. 2015), as well as with ecological conditions, such as population density (Wang and Grimm 2007) and weather events (Birkett et al. 2012; Weimerskirch et al. 2012).

However, as noted by many authors (Cagnacci et al. 2010; Kie et al. 2010; Tomkiewicz et al. 2010; Börger 2016), the new empirical tools and results have created both opportunities and challenges for developing appropriate theoretical approaches that take advantage of this new information. As noted in the provocative article by Powell and Mitchell (2012), even defining a home range requires explicit consideration of the spatial and temporal aspects of animal movements and their purpose. Our goal here is to develop theoretical approaches that will accomplish this task. These approaches are useful not only for interpreting data to determine a home range but also for drawing meaningful biological insights from this determination of the home range.

Our ability to accurately capture and predict changes in home range size or area coverage is especially important

when evaluated in the context of ecology and disease transmission. For small vertebrates living in densely populated habitats, individual-based simulations have suggested that a rapid decrease in mean range size may be a readily measurable indicator of major directional shifts in the population's age and sex structure (Wang and Grimm 2007). Furthermore, knowing how strictly an animal's space use is bounded over its lifetime can help design more effective protected areas (Moffat et al. 2001). In addition, zoonotic outbreaks have been repeatedly traced to transmission opportunities created by the reservoir hosts expanding their range sizes in response to local agricultural practices (Pulliam et al. 2012). Understanding the causes, mechanisms, and consequences of temporal variation in animal home range size is thus essential for informing both conservation management and global health initiatives.

Range size dynamics can be more mechanistically interpreted as the spatial expressions of animals' changing movement behaviors with respect to their internal and external home range areas, given that the internal areas are much less susceptible to temporal fluctuations (Börger et al. 2006), including the case where the internal area is defended (territory; reviewed in Börger et al. 2008). Local ecological factors likely affect these movement behaviors in different ways (e.g., Indermaur et al. 2009). Seasonal changes in forage abundance appear to generally drive expansions into the external home range areas (Börger et al. 2006), resulting in range size seasonality as observed in wild giant pandas (*Ailuropoda melanoleuca*; Zhang et al. 2014), white-faced capuchin (*Cebus capucinus*; Campos et al. 2014), and diverse ungulate species (Rivrud et al. 2010; van Beest et al. 2011; Morellet et al. 2013; Reinecke et al. 2014). Conversely, sensing potential trespassers may provoke territorial retreat for defensive purpose, as demonstrated in seminal studies on pied wagtail (*Motacilla alba*) and coyotes (*Canis latrans*; Davies and Houston 1981; Moorcroft et al. 2006). However, intraspecific differences in range size imply that these movement responses are not necessarily universal; the decided actions could be additionally influenced by the territorial quality typically accessible to each age class, often scaled positively with age (see examples in Clutton-Brock and Guinness 1982; Andersen et al. 1998). In summary, expansions and contractions of animal home range stem from a series of behavioral outcomes governed by both individual and environmental conditions.

To date, most analytical home range models have not explicitly incorporated range size dynamics, nor have they been constructed within a mathematical framework that could be easily modified to perform such analyses. This stands in contrast to a growing number of statistical (Börger et al. 2006; Naidoo et al. 2012; Lyons et al. 2013) and numerical (Van Moorter et al. 2009; Potts et al. 2012) models that include an explicit time component. Nevertheless,

temporal details are often gained at the cost of model tractability, leaving the ecological mechanisms not easily inferable and the general patterns of range size dynamics unclear.

Model Concept

We present an analytical home range model that predicts a territorial animal's seasonal range size dynamics on the basis of its demographic descriptor and local environmental features. The model consists of two parts that correspond to two aspects of movement behaviors: why an individual would choose to engage in particular movement activities (forage vs. territorial defense) and how its movement decisions are then translated into home-ranging space use patterns.

We addressed the first question from the perspective of classic behavioral ecology, which assumes that evolutionary forces led animals to optimize their behaviors with respect to a predefined payoff function (Stephens and Krebs 1986; Stephens et al. 2007). Although optimality analysis has been an important tool for understanding long-term behavioral emergence (e.g., McElreath and Strimling 2006), it remains largely underutilized in developing spatially explicit, dynamic movement theories (Börger et al. 2008; Nathan et al. 2008). Here, we suppose that an animal makes its movement decision by following one of several possible behavioral strategies (see Wang and Grimm 2007; Fryxell et al. 2008), each consisting of a set of directions on where and how far to move upon sensing certain ecological cues. We further conceived that the animal is behaviorally plastic and may maximize the payoff of its movement decision by repeatedly selecting its behavioral strategy at regular intervals. The selection process was modeled within an optimization framework that functionally relates all potential payoffs to the individual's state variable and its condition of forage and competition.

Once the optimal strategy is determined, we then addressed the second question and presumed that the animal's subsequent movement path follows a biased random walk process, in which the degree of centralized movement depends on whether the individual has decided to forage or defend. On the basis of first principles (Grünbaum 1999), we can derive the animal's resultant space use pattern, commonly expressed as an utilization distribution $u(\mathbf{x}, t)$, which predicts the individual's location $\mathbf{x}$ at time t in terms of a probability surface (Okubo and Levin 2002; Moorcroft and Lewis 2006). Under the basic assumption that the magnitude of centralized bias is spatially independent, $u(\mathbf{x}, t)$ satisfies the Fokker-Planck equation:

$$\frac{\partial u}{\partial t}(\mathbf{x}, t) = \nabla^2 u - \beta \nabla \cdot (u\vec{\mathbf{x}}), \qquad (1)$$

where $\vec{\mathbf{x}}$ is a unit vector pointing toward the home range center. β is the measure of centralization, which we assumed to be higher for the more sedentary territorial defenders (Morales et al. 2004; Beyer et al. 2013). We then defined home range according to convention as the minimal region that encompasses a chosen percentage of $\int u(\mathbf{x}, t) d\mathbf{x}$ when the time derivative equals 0 (Moorcroft and Lewis 2006).

Methods

Behavioral Optimization

We considered a model animal that holds a circular, fixed-sized territory containing temporally invariant resource value. This value, $w(z)$, depends on z, where z is defined as a relative age from the onset of independent mobility ($z = 0$) to full adulthood ($z = 1$). Territory quality (e.g., access to mates) is contingent on dominance status in both sexes, as studies have found in sea lions (*Zalophus wollebaeki*) and red deer (*Cervus elaphus*; Bebié and McElligott 2006; Wolf and Trillmich 2007). Observations of pikas (*Ochotona princeps*) and white-throated sparrows (*Zonotrichia albicollis*) further suggest that dominance status in territorial species is often correlated with age and may increase sharply during one's early years before gradually leveling off (Kawamichi 1976; Piper and Wiley 1989). We therefore modeled territorial resource value as an asymptotic function of age, such that $w(z) = 1 - \exp(-z)$.

The seasonal feeding ground lies within some radius beyond the territory, producing supplementary resource value $k(t)$ after foraging bouts. We assumed annual cycles for extraterritorial forage abundance such that $k(t) = k_0 + \alpha(\sin 2\pi t + 1)$, and α determines the degree of temporal resource heterogeneity. We assumed that individuals are omniscient as to the resource conditions across territorial boundaries and make movement decisions that maximize their immediate resource payoff.

We then introduced constraints on extraterritorial foraging behavior by assuming that an undefended territory may be subject to intrusion from conspecifics, which then reduces $w(z)$ to $w(z)h$, where h denotes the proportion of resource that is leftover until replenishment at the next time step. Intruders' presence and absence occur with probabilities $\Pr(I_p) = p$ and $\Pr(I_a) = 1 - p$. We assumed that an individual is able to successfully and completely repel intruders if it detects their presence correctly and decides to act defensively. However, the initial detection of conspecifics may be misled by information noise that affects the animal's visual, auditory, olfactory, and other sensory inputs. Under such information uncertainty, our focal individual is modeled to perceive the status of intruding conspecifics incorrectly f proportion of the time.

Animals repeatedly choose the optimal strategy to make their movement decisions, which consists of a set of rules that determine the movement behaviors, given limited information about local conspecifics. We characterize three possible strategies that an animal can employ: reactive, foraging, and defensive. Following the reactive strategy, an individual switches from foraging beyond its territory, D_f, to territorial defense, D_d, whenever it senses intrusion risk (fig. 1). We can calculate the mean resource payoff of an individual of age z that applies this strategy at discrete time t by weighting over four possible scenarios, including chances for failed detection, pf, and false alarm, $(1 - p)f$:

$$W_r(z, t) = p\{(1 - f)w(z) + f[k(t) + w(z)h]\}$$
$$+ (1 - p)\{(1 - f)[k(t) + w(z)] + fw(z)\} \quad (2)$$

(for full glossary, see table 1). Alternatively, the individual can decide to stick to a single movement behavior, irrespective of its knowledge of the local environment. We expect one of the two other strategies to be favored when the sensory signals have become unreliable (see Galanthay and Flaxman 2012). For the defensive strategy, the mean resource payoff at time t is therefore

$$W_d(z, t) = w(z), \quad (3)$$

whereas the foraging strategy yields

$$W_f(z, t) = p[k(t) + w(z)h] + (1 - p)[k(t) + w(z)]. \quad (4)$$

We can find the optimal strategies (i.e., the strategy with the maximal payoff for any given set of parameters) and their associated movement behaviors, using a map partitioned into at most three parametric regimes (fig. 2). On the basis of our resource payoff functions, the defensive and foraging strategies are chosen if

$$z > -\ln\left[1 - \left(\frac{k(t)}{1 - h}\right)\left(\frac{1 - f}{f}\right)\left(\frac{1 - p}{p}\right) - \frac{k(t)}{1 - h}\right] \quad (5)$$

or

$$z < -\ln\left[1 - \left(\frac{k(t)}{1 - h}\right)\left(\frac{f}{1 - f}\right)\left(\frac{1 - p}{p}\right) - \frac{k(t)}{1 - h}\right], \quad (6)$$

respectively. In either of those cases, the proportional amount of time spent on the respective movement behaviors, $T_d(z, t)$ and $T_f(z, t)$, would be binary over the immediate time step. If neither inequality is satisfied, then the reactive strategy is the optimum, which gives $T_d(z, t) = p + f - 2pf$ and $T_f(z, t) = 1 - T_d(z, t)$.

Home Range Derivation

For analytical convenience, we assume that the animal moves isotropically around its territorial center, which then allows us to convert an individual's utilization distribution into symmetric polar coordinates $u(r, z, t)$, where r measures the ra-
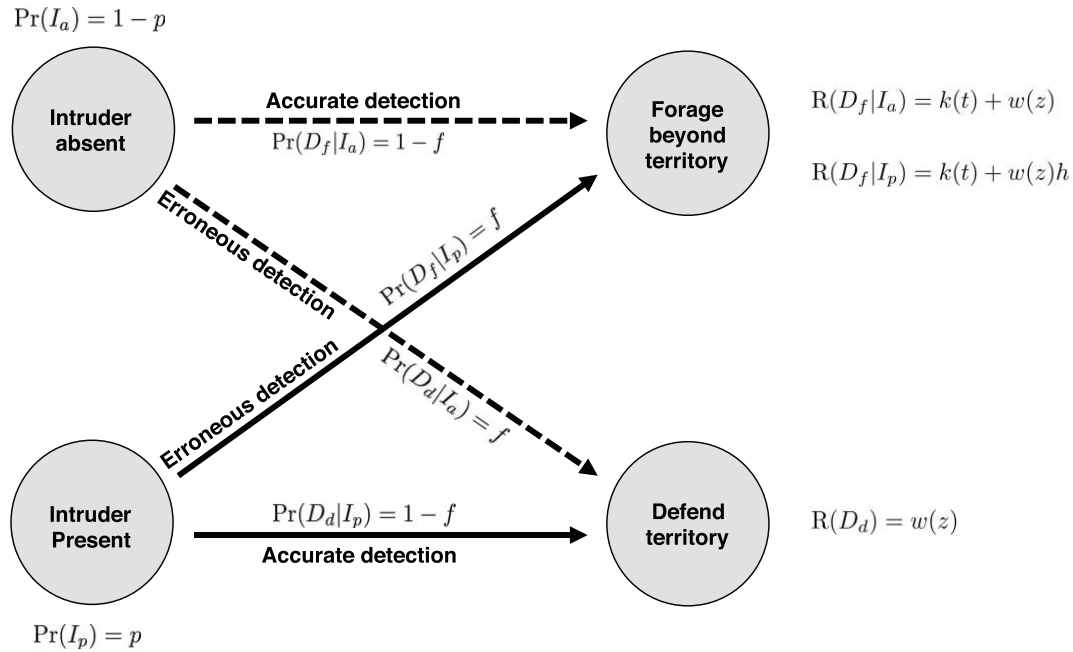
Figure 1: Flowchart depicting how an individual decides between extraterritorial foraging, D_f, and territorial defense, D_d, according to the reactive strategy, which produces expected resource payoff $W_r(z, t)$. Intruders' presence and absence are indicated by I_p and I_a, respectively. The resource reward, $R(\cdot)$, associated with each scenario of intrusion risk and sensory noise is expressed on the right. The decisional flowchart of the foraging strategy consists of the two top arrows, with $\Pr(D_f|I_a) = \Pr(D_f|I_p) = 1$. That of the defensive strategy consists of the two bottom arrows, with $\Pr(D_d|I_a) = \Pr(D_d|I_p) = 1$.

dial distance from the central point attractor. To differentiate movement behaviors between territorial defense D_d and extraterritorial foraging D_f, we characterized them using respective centralizing parameters, β_d and β_f, such that $\beta_d > \beta_f$. Under optimal strategies, $u(r, z, t)$ is regulated by the functional parameter $\beta(z, t) = T_d(z, t)\beta_d + T_f(z, t)\beta_f$. Since equation (1) has no practical closed-form solution, we made the simplifying assumption that $u(r, z, t)$ quickly converges to space use equilibrium $\hat{u}(r, z)$ under a constant resource level $k(t)$ within a time step. Therefore, we can approximate

$$u(r, z, t) \approx \hat{u}(r, z)\Big|_{k(t)} = \frac{\beta^2(z, t)}{2\pi}\exp(-\beta(z, t)r) \quad (7)$$

(see appendix for derivation detail). Finally, an individual's temporal home range size, $S(z, t)$, truncated at the outer radius that encompasses 90% of space use coverage, can be numerically solved from the conservational condition

$$2\pi\int_0^c u(r, z, t)r\mathrm{d}r = 0.9, \text{ with } c = \sqrt{\frac{S(z, t)}{\pi}}. \quad (8)$$

Simulation Analyses

We considered an animal population of size n, where each individual i of age z_i inhabits a specific local environment described by the parameter set $O_i = \{p_i, f_i, \alpha_i\}$. Range size time series have been observed to undergo pronounced seasonal variations on a log scale (Börger et al. 2006); we therefore defined the range size of an averaged individual at time t as $V_n(t) = (1/n)\log\prod_{i=1}^n S(z_i, O_i, t)$, with n being the size of a sample population. We subsequently performed Monte Carlo simulations and modeled range size time series $V_n(T) = \{V_n(t_0), V_n(t_1), V_n(t_2), ...\}$ across a discretized timeline $T = \{t_0, t_1, t_2, ...\}$. From the simulated results, we applied least squares model fitting to optimize the parameters of a sinusoidal curve, $\tilde{V}(t) = m + q\sin 2\pi t$, where m and q approximate the annual mean and seasonal variation of individual range size, respectively.

In our first analysis, we explored how demographic factors may influence range size dynamics both seasonally and over the course of an animal's lifetime. For specific age value z, we ran year-long simulations of range size time series, $V_n(T)$, under random environmental conditions and tracked the resultant changes in both seasonal variation q and annual mean m at discrete stages of maturation.

Animal range size has also been empirically shown to vary in its level of seasonal variation, from being temporally static to highly oscillatory, with respect to a number of environmental features that includes resource distribution, population density, and information uncertainty (e.g., Bör-

Table 1: Glossary

Symbol	Description
D	Movement decision
I	Intruder status
W	Expected resource payoff of enacting a particular movement strategy
V	Individual range size averaged from a sample population
$\tilde{V}$	Individual range size sinusoidally fitted to V over time
u	Individual utilization distribution
α	Amount of seasonal change in extraterritorial resource value k
β	Degree of centralization in movement behavior
f	Probability that the sensory information about intruders yields false conclusion
h	Proportion of territorial resource value that remains after intrusion occurs
k	Extraterritorial resource value
m	Approximated mean annual individual range size
n	Sample population size
p	Probability of intruders being present near a territory
q	Approximated seasonal variation of individual range size
w	Baseline resource value of a territory
z	State variable that represents an animal's age

ger et al. 2006; Mueller and Fagan 2008). In our second analysis, we tested these predictions by simulating range size time series $V_n(T)$ under random population structure for different combinations of environmental parameters f, α, and p (here acting as a proxy measure for local population density) and examined whether the consequent seasonal variation q correlates with these habitat descriptors in ways that are consistent with several published observations.

Our final analysis assumes the classic theory of ideal-free distribution (e.g., see Kacelnik et al. 1992), which predicts that foragers should aggregate heavily in resource-rich habitats. In this scenario where resource abundance and population density are positively correlated, such that $p(t) = p_0 + \gamma k(t)$, where γ measures the strength of population aggregation, we expected some would-be foragers to turn more territorial and contract their range size in order to defend against the seasonal influx of intruders. We then simulated range size time series $V_n(T)$ from weakly to strongly aggregated systems for distinct demographic values z—while keeping the nonseasonal parameter f random within the populations—and evaluated individual range size response to forage opportunity, as indicated by the derivative $d\tilde{V}/dk$.

Results

We first investigated the parametric conditions under which the three contrasting movement strategies each become optimal. Individuals in the lowest end of the age range (i.e., juveniles) show a fairly consistent preference for the foraging strategy irrespective of seasonal changes in forage opportunity or sensory drawback in judging intrusion pressure. In contrast, adults are shown to strongly favor the defensive strategy, particularly when forage payoff is low and intrusion pressure uncertain (fig. 3). The rest of the age classes, which we classified as subadults, tend to spend a significant portion of time abiding by the reactive strategy, making movement decisions that are highly sensitive to forage conditions; periodically, they may briefly switch their strategies to one of the two other options (fig. 3). In relationship to external factors, noisy sensory information generally discourages the reactive strategy from being adopted at any point during the year, thus causing many individuals to suddenly flip their movement behavior over time (fig. 3). Temporal resource heterogeneity, on the other hand, is shown to promote individual participation in every strategy, including adults selecting the foraging strategy when the payoff is sufficiently enticing (fig. A1; figs. A1–A3 available online). Under heightened intrusion pressure, the defensive strategy becomes almost universally favored except by juveniles, especially when combined with imperfect sensory information (fig. A2). More specifically, when intruders are present without interruption, forage is never profitable unless the resource gained by the excursion exceeds the inevitable lost due to intrusion.

The time series resulting from our simulations showed that mean individual-level range size can undergo distinct seasonality even if the environmental condition is partially stochastic (fig. 4a). We may further gather from the variation in range size distribution that this seasonal effect contains two simultaneous phenomena: periodic surges in popularity for either foraging or defensive movement and a perennial presence of both behaviors at lower occurrences (fig. 4a). Seasonal differences can also be reflected in the utilization distributions of individuals, here showing evident contrast in the case of a subadult that makes its decisions
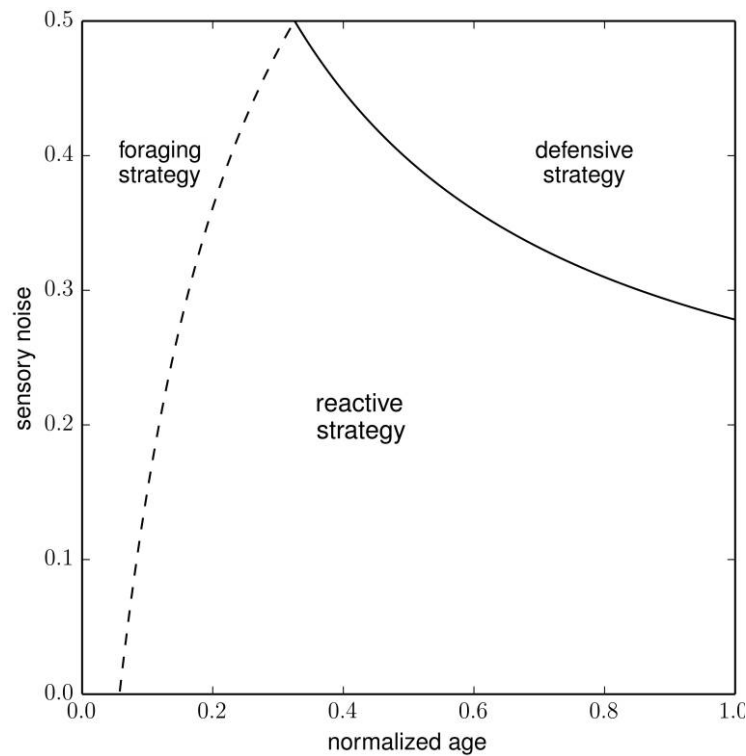
Figure 2: Parametric regimes of the three optimal strategies as a function of age z and sensory noise f. Parameter space above the solid and dashed lines satisfy equations (5) and (6), respectively. Environmental parameters $p = 0.2$ and $k(t) = 0.05$, which is approximately 8% of maximal territorial resource value, $w(1)$; intrusion penalty $h = 0.1$.

under a constant condition of information uncertainty (fig. 4*b*). Evaluating space use patterns in the context of optimality can therefore facilitate a spatiotemporally explicit understanding of demographic and environmental effects on movement range.

From the first analysis, the process of aging is found to negatively correlate with mean individual-level range size; it is also shown to be destabilizing—that is, it increases the amount of seasonal range size variation—during the first half of the animal's lifetime until the effect is progressively reversed (fig. 5). Next, simulations with respect to environmental descriptors suggest that range size destabilization can also be achieved through an increase in either sensory noise or temporal resource heterogeneity (fig. 6). Conversely, combining high values of sensory noise and population density results in more stable home range area over time (fig. 6).

Constant intrusion pressure in the absence of aggregation behavior easily produces home range expansion during peak forage season by all individuals (fig. 7). When aggregation tendency is incorporated, juvenile movement remains largely unaffected; however, the foraging strategy becomes suboptimal for subadults and adults because of the concurrent rise of intrusion probability due to conspecific arrival.

In a weakly aggregative population, this leads to range sizes that respond less sensitively to forage opportunity (fig. 7). In a strongly aggregative population, the massive influx of conspecifics exerts a net negative forage effect on the older individuals, resulting in them switching from the reactive to the defensive strategy (fig. A3). Therefore, counterintuitively, their home ranges contract in response to increasing foraging level. If this latter phenomenon is present at all, it appears to encompass a large proportion of the age demographic at once; the youngest age at which it manifests in the population lowers with the strength of aggregation (fig. 7).

Discussion

Here we present a home range model that predicts the range size dynamics of territorial animals faced with foraging and defensive requirements. Our model recognized range size as the spatial product of optimal movement strategy that reflects the conflict between two fitness-enhancing behaviors: to forage beyond one's territory or to defend the territory from conspecific intrusion. When a territorial individual detects nearby rivals, it is shown to sacrifice forage payoff for territorial defense. This change in movement be-
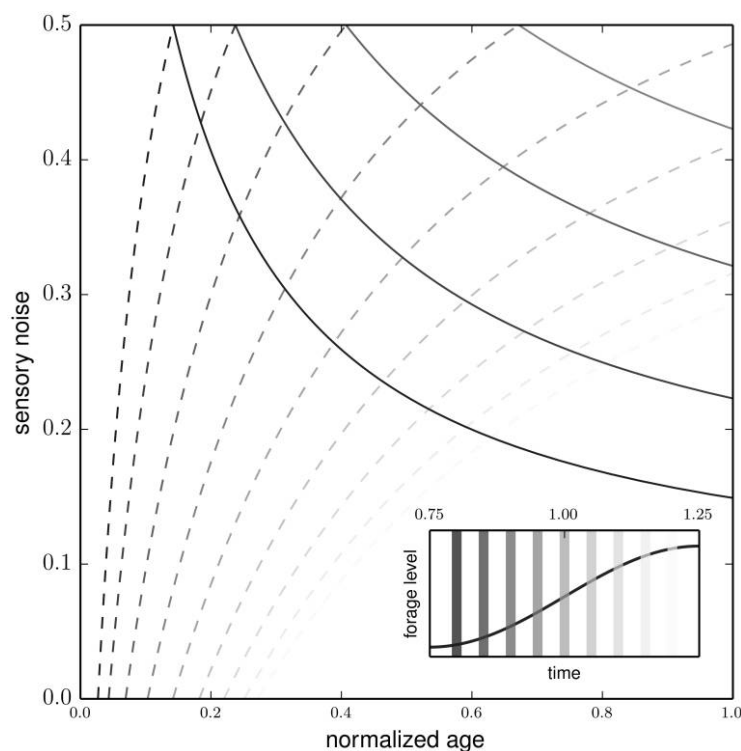
Figure 3: Parametric regimes of optimal strategies plotted over time $T = \{0.8, 0.85, \ldots, 1.2\}$ (from dark to light) as a function of age z and sensory noise f. The corresponding phases in forage level $k(T)$ are marked by vertical lines in the inset figure using the same shading scheme. Environmental parameters $k_0 = 0.02$, $\alpha = 0.05$, $p = 0.2$; intrusion penalty $h = 0.1$.

havior is supported by experimental tests in captive great tits (*Parus major*), where intruder presence was found to induce territorially vigilant movement in replacement of forage-efficient movements (Kacelnik et al. 1981). Behavioral changes are also caused by differences between the resource values on each side of the territorial boundary. Studies of red-winged blackbirds (*Agelaius phoeniceus*) reported that lowered food supply inside one's territory leads to increased foraging frequency and shorter time spent on guarding against trespassers (Westneat 1994). In addition, the model predicted increased intraspecific variance in behavioral preference under sensory uncertainty. This is evidenced in the case of northern pike (*Esox lucius* L.), a species found to exhibit a higher degree of movement diversity in turbid waters compared with less murky habitats (Andersen et al. 2008).

By combining behavioral optimization and utilization distribution, we provided an analytical framework that examined how home range areas may be affected by movement decisions as well as the ecological conditions underpinning those decisions. Our model design conformed to the movement ecology framework proposed by Nathan et al. (2008), which conceptualizes movement mechanisms of individuals as interactions among one's internal state (here, age), external factors (environmental parameters), and motion and

navigation capacities (grouped in the measure of centralization). This integrative approach allowed us to specifically search for a rich suite of dynamical range size patterns.
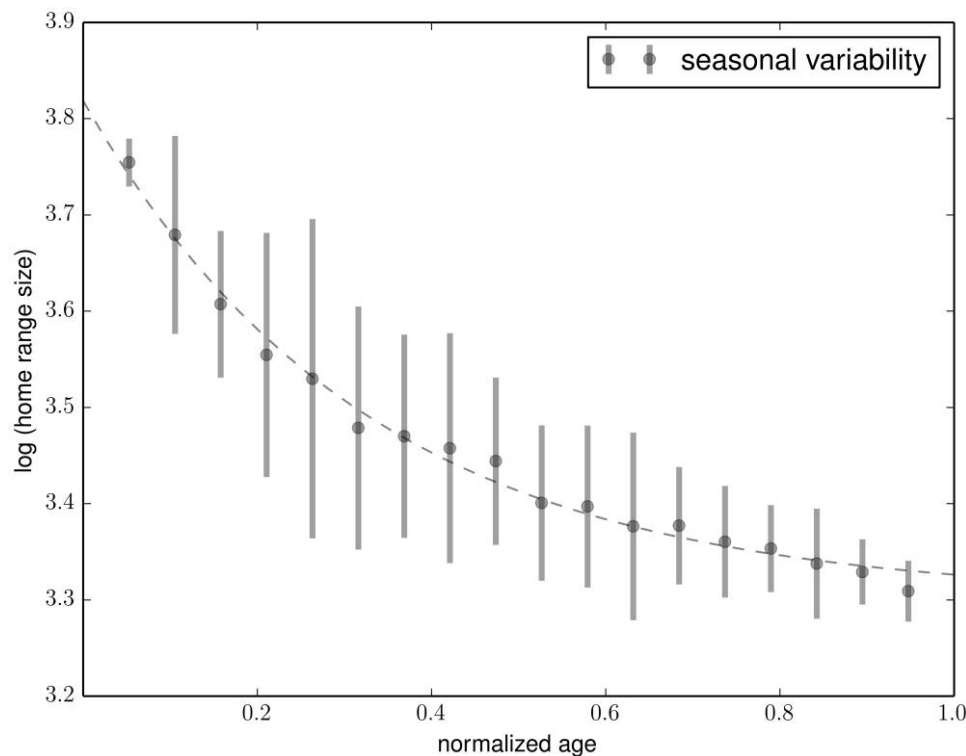
Demographic Effects

For animals that can secure increasingly valuable territory with age, their home ranges appear to decrease in size over their lifetime; their range sizes meanwhile undergo the largest degree of seasonal variability between the onset of independent mobility and full maturity. Our results are consistent with previous empirical works on roe deer (*Capreolus capreolus*) home range dynamics, as reported by Strandgaard (1972), Andersen et al. (1998), Pettorelli et al. (2003), and Börger et al. (2006). Fawns are usually nonterritorial; compared with older individuals, their movements are expansive and driven by the need to constantly forage within the local landscape. Territoriality begins to emerge in younglings near maturity; on average, range sizes become reduced compared with fawns but fluctuate more with seasonality. Fully matured and senescent adults are highly sedentary; range sizes become mostly restricted to their territories and are less affected by seasonal conditions. Similar range size patterns can also be found in other ungulates (e.g., see Clutton-Brock
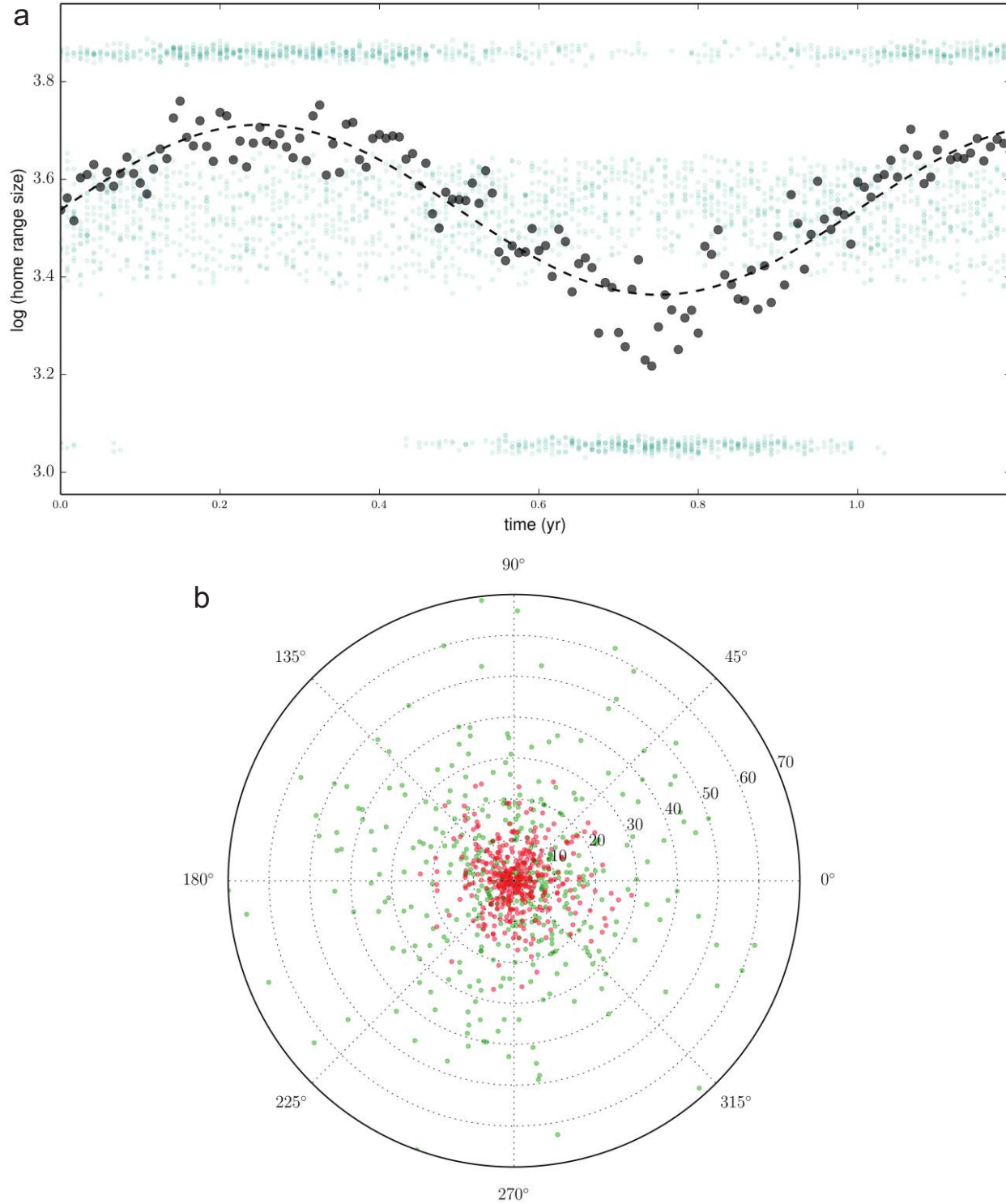
Figure 4: Temporal home range dynamics. Environmental parameters $k_0 = 0.02$, $\alpha = 0.05$, $p = 0.2$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2$, $\beta_f = 0.08$. a, Individual range size time series. A sample population with size $n = 20$ is simulated at each time step, where one's age and the information noise it experiences are randomly distributed, such that $z_i \sim U(0, 1)$ and $f_i \sim U(0, 0.5)$. The resultant log-transformed range size values $\log S(z_i, O_i, t)$ are jittered and plotted in blue. Their population-averaged values over time T, $V_n(T)$, are marked by circles; dashed line shows the sinusoidal range size estimation $V(t)$. b, Seasonal relocation from home range center. Samples are drawn from the utilization distributions of an individual ($z_i = 0.5$, $f_i = 0.4$) at times $t = 0.8$ (red) and $t = 1.2$ (green).

Figure 5: Demographic effects on range size dynamics. Base forage level $k_0 = 0.02$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2$, $\beta_f = 0.08$. Under constant age variable z, a sample population of $n = 5$ is simulated at each time step for a period of 1 year. Environmental condition $O = \{p, f, \alpha\}$ is randomized across individuals such that $p_i \sim U(0, 1)$, $f_i \sim U(0, 0.5)$, and $\alpha_i \sim U(0, 0.03)$. The approximated mean individual range sizes m (circles) are fitted with a dashed line to an exponential regression curve as a function of z. At each select age, the vertical bar measures the corresponding value of approximated seasonal variation, q, scaled to $(2q)^3$ for visual clarity.

and Guinness 1982) and more distant taxonomic groups. Eagle owls (*Bubo bubo*), for instance, demonstrate large range size dynamics at the intermediate age class before permanently retreating into their territories in later years (Campioni et al. 2013). Similarly, the Malaysian flying lizards (*Draco volans sumatranus*) shift from being territorial intruders to territorial guardians over their lifetimes (Mori and Hikida 1993).

Environmental Effects

Our model indicated that several environmental features can either stabilize or destabilize individual range size dynamics. In habitat types characterized by seasonal growth of rich forage patches, we demonstrated that local animals show a noticeable degree of range size variation with seasonal periodicity over the course of the year. Furthermore, we predicted the emergence of even larger range size fluctuation, given the added condition that the sensory information necessary for assessing the risk of territorial intrusion is unreliable. In contrast, sensory-compromised individuals

surrounded by a dense population of conspecifics may have their range size dynamics significantly reduced.

Few tracking studies have been conducted on a scope that comprehensively documents range size dynamics as a multivariate function of all three environmental features we considered. However, several patterns observed in terrestrial species may offer support for our model results. For instance, North American elk (*Cervus elaphus*) inhabiting landscapes with heterogeneous distribution of vegetational resources are projected to show increased space use variation (Morales et al. 2005). To the best of our knowledge, there has been no direct empirical studies of sensory noise alone on range size variability. However, Mueller and Fagan (2008) and Jonzén et al. (2011) suggest that when resources are temporally unpredictable, nomadism is favored, defined as a spatial pattern characterized by temporally volatile movements, contrary to sedentary ranges and migration. In the broader sense, the unpredictability of resources can be related to net forage outcome, hence extended to include uninformed interactions with territorial intruders (competitors), so Mueller and Fagan's predictions could potentially provide support for
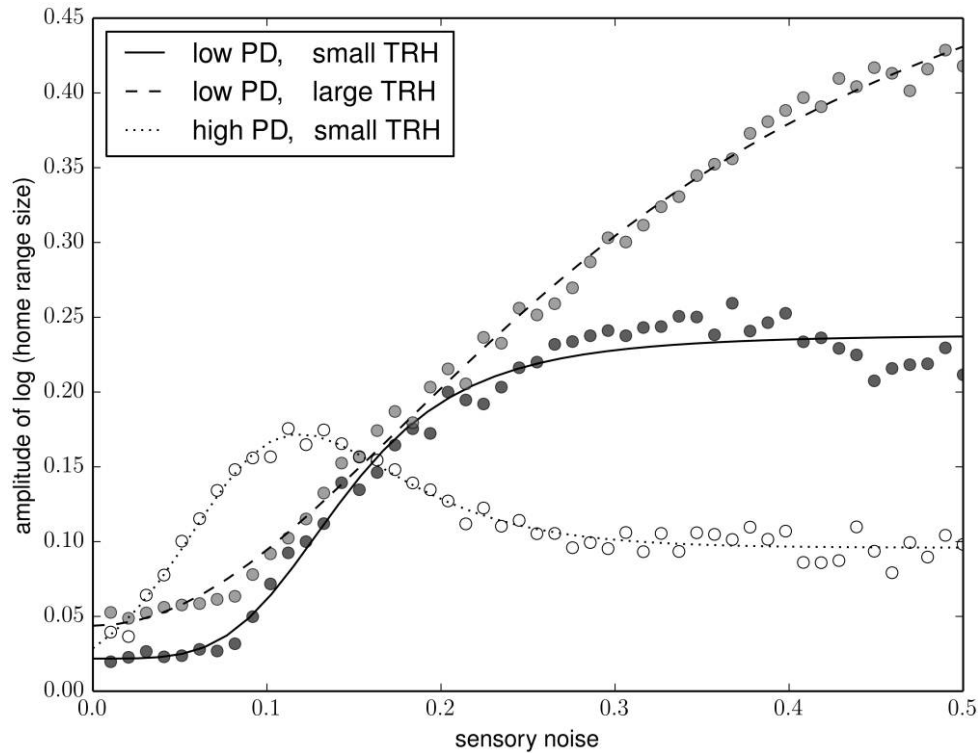
Figure 6: Environmental effects on range size dynamics. Base forage level $k_0 = 0.02$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2$, $\beta_f = 0.08$. Under constant environmental condition $O = \{p, f, \alpha\}$, a sample population of $n = 20$ is simulated at each time step for a period of 1 year. Small and large temporal resource heterogeneities (TRHs) correspond to parameter values $\alpha = 0.1$ and 0.2, respectively; low and high population densities (PDs) correspond to $p = 0.2$ and 0.4. Age variable z is randomized uniformly across individuals such that $z_i \sim U(0, 1)$. The approximated seasonal variations of individual range size q (circles) are fitted to logistic and double-logistic regression curves as a function of sensory noise f.

the range size impact of sensory noise. Evidence for the stabilizing effect of population density may be gleaned from the ranging activities of bannertail kangaroo rats (*Dipodomys spectabilis*), which are found to curtail their travel frequencies at high population densities to prolong the amount of time they spend advertising their territorial presence (Randall 1984). Finally, resource, density, and sensory effects are jointly evaluated by Börger et al. (2006), showing that for roe deer (*C. capreolus*) in naturally noisy settings, the habitat type with pronounced temporal resource heterogeneity (i.e., herbaceous crop) produces range sizes that cycle with larger amplitudes relative to the habitats where the animals often cluster (i.e., set-aside).

Demographic Divergence

If conspecifics are drawn to a resource patch according to an ideal free distribution, such that the number of animals that aggregate in a habitat is proportional to the forage quality therein, then range size dynamics may respond to forage level in opposite manners between different demographic

groups. This possible coexistence of contrasting range size responses indicates that the seasonal arrival of forage opportunity simultaneously signals different priorities that relate to the individual's demographically dependent attributes: for those physically incapable of securing high-value territories, resource elevation motivates home range expansion through spatial exploration; otherwise, it leads to home range contraction by means of territorial patrol. Since this pattern is contingent on widespread crowding behavior in the population, we hypothesize that it may be more commonly observed in environments where the majority of high-quality resource is concentrated within small regions.

To our knowledge, there has been no previous age structure analysis of range size dynamics with respect to resource seasonality. However, sex differences, which are also associated with unequal territory qualities in many animals (see Campioni et al. 2013), have been suggested to generate divergent range sizes both during and outside of breeding seasons. Case studies based partly on measures of home range overlap include red deer (*C. elaphus*; Reinecke et al. 2014), field voles (*Microtus agrestis*; Pusenius and Viitala 1993), and rac-
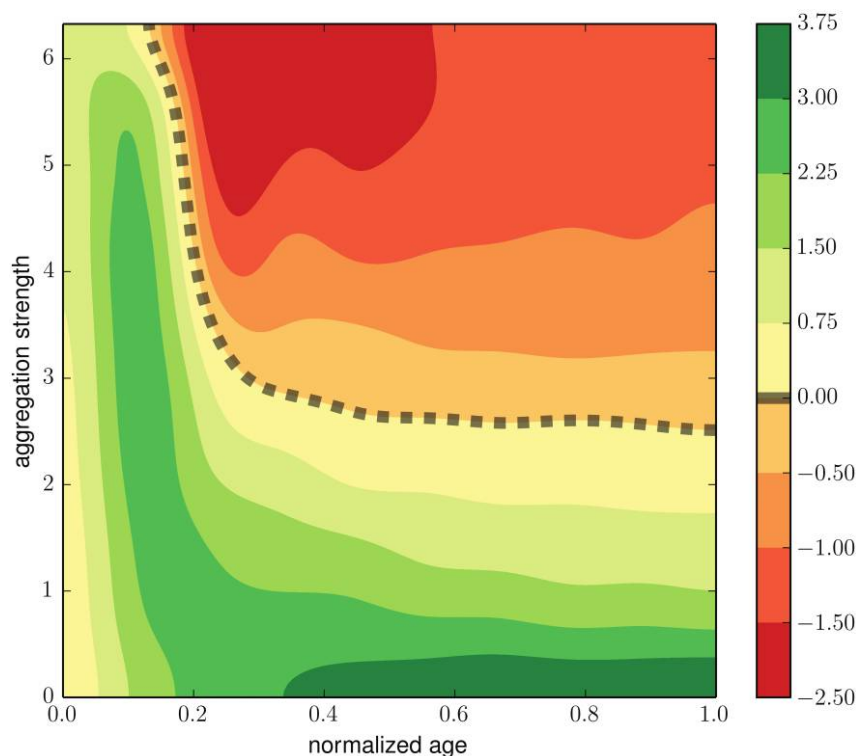
Figure 7: Individual range size response to forage opportunity as a function of age and aggregation strength. Base forage level $k_0 = 0.02$; base intrusion pressure $p_0 = 0.1$; temporal resource heterogeneity $\alpha = 0.15$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2$, $\beta_f = 0.08$. Given constant age variable z and aggregation strength γ, a sample population of $n = 100$ is simulated at each time step for a period of 1 year. Sensory noise f is uniformly randomized across individuals such that $f_i \sim U(0, 0.5)$. Expansion (green) and contraction (red) responses occur under positive and negative values of $d\hat{V}/dk$, respectively; the dashed line demarcates the threshold of demographic divergence.

coons (*Procyon lotor*; Gehrt and Fritzell 1998). As further expected from our hypothesis, territorial individuals may become more area restricted in systems where the resources are unevenly distributed (e.g., Schoener 1987; Jensen et al. 2005; Markham et al. 2013).

The occurrence of contrasting range size dynamics due to demographic state underlines important considerations for ecological applications. In the context of a wildlife sanctuary, particular cohorts or social niches could become isolated via habitat modifications that promote expansive space use for only a small number of individuals. We urge future research into other demographic variables that demonstrate bifurcated home range responses, which could help inform conservation efforts to more effectively focus on individuals whose movement patterns predominately underpin the management objectives.

Utilization Distributions: Bimodality and Transient Dynamics

Our model highlights two dynamical qualities of utilization distribution that are increasingly emphasized in mechanis-

tic movement analysis: bimodality and transient dynamics. The first concept stems from the two statistical clusters—or modes—that are often distinctive in movement data (e.g., exploratory vs. encamped; Morales et al. 2004; Beyer et al. 2013). Modal transitions occur nonrandomly (Schmitt et al. 2006) and reflect changes in both landscape conditions and an animal's internal state (Morales et al. 2004, 2005). However, few mathematical models have integrated bimodality into space use patterns. Blackwell (1997) derived the utilization distributions of animals that switch between core area movement and excursion according to a Markov chain. More recently, the exchange model developed by Skalski and Gilliam (2003) also made space use predictions by including the amount of time an individual spent in one of two movement states into an advection-diffusion movement process. Both models helped advance the theoretical foundation of modal transitions, which we have now extended on the basis of payoff maximization.

Transient analyses are employed to describe the temporal variation in ecological dynamics, such as time series fluctuations, before the system settles into permanent equilibria. Recognizing the importance of transient dynamics has

contributed an essential explanatory aspect in understanding population and community patterns, thereby helping to generate more reliable predictions within short-term, ecologically relevant timescales (Hastings 2004, 2010). In agent-based movement models, transient dynamics of animal space use can be simulated as consequences of spatial memory processes (Van Moorter et al. 2009; Riotte-Lambert et al. 2015) and scent mark avoidance behavior (Potts et al. 2013). However, analytical models centered around utilization distributions are handicapped in this regard mainly because of the technical barrier in solving Fokker-Planck equations in time. Our model adopted the sidestepped approach of Moorcroft et al. (2006) and Bateman et al. (2015), which allows space use variation to equilibrate at the chosen time steps, driven by terrain gradient, neighbor removal, or group fission. In other words, we approximate transient range size dynamics by sequentially perturbing the steady-state solutions, with the implications that (1) the animal optimizes its movement behavior faster than its spatial convergence and that (2) both processes occur immediately relative to the governing ecological dynamics. Although many terrestrial systems support these timescale disparities (e.g., see Bateman et al. 2015), future work could aim to incorporate powerful numerical differential equation solvers that can relax this constraint, thus broadening our current picture of range size patterns.

Future Extensions

Our model exchanged mechanistic complexity for heuristic transparency; in the future, this optimality framework could be enhanced in a number of ways. For example, the centralizing parameter currently fixed for each type of movement behavior could be more realistically modeled as a continuous function of demographic variables, assuming a state-dependent spectrum of locomotive efficiency and navigation experience. We also strongly encourage the development of mechanistically analogous agent-based simulations, which would help generalize the dynamical process by addressing the effects of multiple home range attractors (see Don and Rennolls 1983).

It is worth noting that our optimality approach implies a scenario in which the focal individual may defend against neighbors trespassing into its territory yet suffers no cost in cases where its forage destinations lie within conspecific territories. We anticipate that future models will expand this asymmetric framework by explicitly addressing the importance of feedback in animal-animal interactions. For instance, it may be possible for juveniles surrounded by defensive territorial owners to avoid ineffective foraging excursions and instead favor establishments of low-quality territories, as observed in bannertail kangaroo rats (*D. spectabilis*; Randall 1984). Payoff derivations based on space use feedback may also show that territorial adults spaced within foragers could maximize resource intake by exploiting others' territories that have been left weakly defended.

In addition to territorial defense and forage abundance, the range size effects of predation pressure would be another productive topic to investigate. It may simultaneously modify the fitness cost of long-distance foraging and, when the animals' sensory faculties are under heightened vigilance, raise the likelihood for false alarm (Owings and Coss 1977). By introducing predators, the list of movement strategies could also be appropriately expanded, including—among other alternatives—a punctuated forage behavior that minimizes the animals' exposure (Lima and Bednekoff 1999).

We demonstrated how animals capable of making optimal movement decisions can occupy home ranges that expand and contract on the basis of demographic and environmental conditions. With our model, we aimed to spur interest in applying optimization models as a part of our theoretical understanding of animal movement ecology. This synthesis of behavioral decisions and space use patterns—respectively representing the why and the how aspects of movement mechanisms—remains a sparsely explored yet promising field of research. As home range models continue to mature in multiple, parallel directions (see Potts and Lewis 2014), we further suggest a concerted effort to unify the optimality framework with resource selection functions (Moorcroft and Barnett 2008) and step selection functions (Potts et al. 2014).

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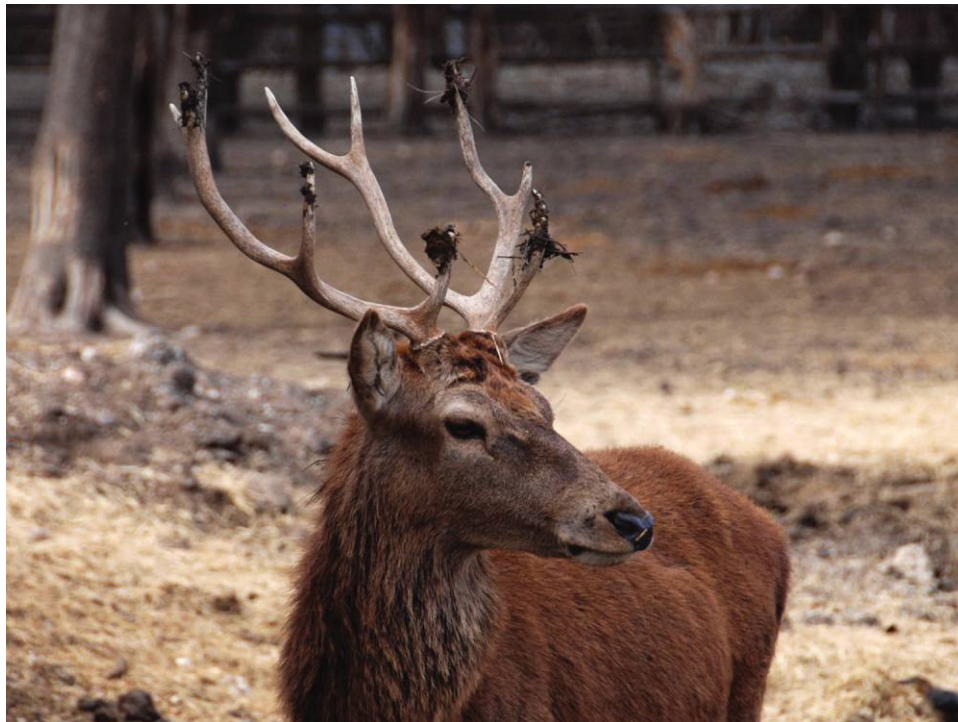
Red deer (*Cervus elaphus*), a species whose territory varies over its life span. Animal World and Snake Farm, New Braunfels, Texas. Photo © 2007 Jeff Whitlock, The Online Zoo, used with permission.