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Dynamic Range Size Analysis of Territorial Animals: An Optimality Approach

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Key words: movement ecology, optimal behavior, home range, territoriality

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 towards 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.

1 Introduction

2 Home range typically refers to a spatially bounded area routinely used by an organism or
3 collective of individuals over a certain amount of time to fulfill its various needs (Burt 1943; Powell
4 and Mitchell 2012). For territorial animals, home ranges may be structurally divided into a heavily
5 traversed internal area, i.e., territory, which the owners defend against intruders by means of
6 systematical patrol and aggressive evictions, and an external area, which is used primarily during
7 their foraging bouts (Samuel and Green 1988; Vander Wal and Rodgers 2012). Such spatially
8 constrained movement types are widespread among animal species, with key ecological consequences
9 at population and community levels (reviewed in Börger et al. 2008).

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

21 However, as noted by many authors (Tomkiewicz et al. 2010; Cagnacci et al. 2010; Kie et al.
22 2010), the new empirical tools and results have created both opportunities and challenges for
23 developing appropriate theoretical approaches that take advantage of this new information. As
24 noted in the provocative paper by Powell and Mitchell (2012), even defining a home range requires
25 explicit consideration of the spatial and temporal aspects of animal movements and their purpose.
26 Our goal here is to develop theoretical approaches that will accomplish this task. These approaches
27 are useful not only for interpreting data to determine a home range, but also for drawing meaningful
28 biological insights from this determination of the home range.

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

40 Range size dynamics can be more mechanistically interpreted as the spatial expressions of
41 animals’ changing movement behaviors with respect to their internal and external home range
42 areas, given that the internal areas are much less susceptible to temporal fluctuations (Börger
43 et al. 2006), including the case where the internal area is defended (“territory”; reviewed in Börger
44 et al. 2008). Local ecological factors likely affect these movement behaviors in different ways (e.g.,
45 Indermaur et al. 2009). Seasonal changes in forage abundance appear to generally drive expansions
46 into the external home range areas (Börger et al. 2006), resulting in range size seasonality as
47 observed in wild giant pandas (*Ailuropoda melanoleuca*) (Zhang et al. 2014), white-faced capuchin
48 (*Cebus capucinus*) (Campos et al. 2014), and diverse ungulate species (Morellet et al. 2013; Rivrud
49 et al. 2010; Reinecke et al. 2014; van Beest et al. 2011). Conversely, sensing potential trespassers
50 may provoke territorial retreat for defensive purpose, as demonstrated in seminal studies on pied
51 wagtail (*Motacilla alba*) and coyotes (*Canis latrans*) (Davies and Houston 1981; Moorcroft et al.
52 2006). However, intraspecific differences in range size imply that these movement responses are not
53 necessarily universal; the decided actions could be additionally influenced by the territorial quality
54 typically accessible to each age class, often scaled positively with age (see examples in Clutton-
55 Brock and Guinness 1982; Andersen et al. 1998). In summary, expansions and contractions of
56 animal home range stem from a series of behavioral outcomes governed by both individual and
57 environmental conditions.

58 To date, most analytical home range models have not explicitly incorporated range size dynam-
59 ics, nor have they been constructed within a mathematical framework that could be easily modified
60 to perform such analyses. This stands in contrast to a growing number of statistical (Börger et al.
61 2006; Naidoo et al. 2012; Lyons et al. 2013) and numerical models (Van Moorter et al. 2009; Potts
62 et al. 2012) that include an explicit time component. Nevertheless, temporal details are often
63 gained at the cost of model tractability, leaving the ecological mechanisms not easily inferable and
64 the general patterns of range size dynamics unclear.

65 *Model concept*

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

71 We addressed the first question from the perspective of classic behavioral ecology, which assumes
72 that evolutionary forces led animals to optimize their behaviors with respect to a predefined payoff
73 function (Stephens and Krebs 1986; Stephens et al. 2007). Although optimality analysis has been an
74 important tool for understanding long-term behavioral emergence (e.g., McElreath and Strimling
75 2006), it remains largely under-utilized in developing spatially explicit, dynamic movement theories
76 (Börger et al. 2008; Nathan et al. 2008). Here, we suppose that an animal makes its movement
77 decision by following one of several possible behavioral strategies (see Wang and Grimm 2007;
78 Fryxell et al. 2008), each consists of a set of directions on where and how far to move upon
79 sensing certain ecological cues. We further conceived that the animal is behaviorally plastic and
80 may maximize the payoff of its movement decision by repeatedly selecting its behavioral strategy
81 at regular intervals. The selection process was modeled within an optimization framework that
82 functionally relates all potential payoffs to the individual's state variable and its condition of forage
83 and competition.

84 Once the optimal strategy is determined, we then addressed the second question and presumed

85 that the animal’s subsequent movement path follows a biased random walk process, in which the
 86 degree of centralized movement depends on whether the individual has decided to forage or defend.
 87 Based on first principles (Grünbaum 1999), we can derive the animal’s resultant space use pattern,
 88 commonly expressed as an utilization distribution $u(\mathbf{x}, t)$, which predicts the individual’s location
 89 \mathbf{x} at time t in terms of a probability surface (Okubo and Levin 2001; Moorcroft and Lewis 2006).
 90 Under the basic assumption that the magnitude of centralized bias is spatially independent, $u(\mathbf{x}, t)$
 91 satisfies the Fokker-Planck equation:

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

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

97 **Methods**

98 *Behavioral optimization*

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

109 The seasonal feeding ground lies within some radius beyond the territory, producing supple-

110 mentary resource value $k(t)$ after foraging bouts. We assumed annual cycles for extra-territorial
 111 forage abundance such that $k(t) = k_0 + \alpha(\sin 2\pi t + 1)$, and α determines the degree of temporal
 112 resource heterogeneity. We assumed that individuals are omniscient as to the resource conditions
 113 across territorial boundaries and make movement decisions that maximize their immediate resource
 114 payoff.

115 We then introduced constraints on extra-territorial foraging behavior by assuming that an
 116 undefended territory may be subject to intrusion from conspecifics, which then reduces $w(z)$ to
 117 $w(z)h$, where h denotes the proportion of resource that is leftover until replenishment at the next
 118 time step. Intruders' presence and absence occur with probabilities $\Pr(I_p) = p$ and $\Pr(I_a) = 1 - p$.
 119 We assumed that an individual is able to successfully and completely repel intruders if it detects
 120 their presence correctly and decides to act defensively. However, the initial detection of conspecifics
 121 may be misled by information noise that affects the animal's visual, auditory, olfactory, and other
 122 sensory inputs. Under such information uncertainty, our focal individual is modeled to perceive
 123 the status of intruding conspecifics incorrectly f proportion of the time.

124 Animals repeatedly choose the optimal strategy to make their movement decisions, which con-
 125 sists of a set of rules that determine the movement behaviors given limited information about local
 126 conspecifics. We characterize three possible strategies that an animal can employ: *reactive*, *forag-*
 127 *ing*, and *defensive*. Following the reactive strategy, an individual switches from foraging beyond its
 128 territory, D_f , to territorial defense, D_d , whenever it senses intrusion risk (Fig 1). We can calculate
 129 the mean resource payoff of an individual of age z that applies this strategy at discrete time t by
 130 weighting over four possible scenarios, including chances for failed detection, pf , and false alarm,
 131 $(1 - p)f$:

$$132 \quad W_r(z, t) = p \left\{ (1 - f)w(z) + f[k(t) + w(z)h] \right\} + (1 - p) \left\{ (1 - f)[k(t) + w(z)] + fw(z) \right\}. \quad (2)$$

133
 134 Alternatively, the individual can decide to stick to a single movement behavior irrespective of its
 135 knowledge of the local environment. We expect one of the two other strategies to be favored when
 136 the sensory signals have become unreliable (see Galanthay and Flaxman 2012). For the defensive

137 strategy, the mean resource payoff at time t is therefore:

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

138 whereas the foraging strategy yields

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

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

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

143

144 OR

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

145

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

150 *Home range derivation*

151 For analytical convenience, we assumed the animals to move isotropically around its territorial
 152 center, which then allows us to convert an individual's utilization distribution into symmetric polar
 153 coordinates $u(r, z, t)$, where r measures the radial distance from the central point attractor. To
 154 differentiate movement behaviors between extra-territorial foraging D_f and territorial defense D_d ,
 155 we characterized them using respective centralizing parameters, β_d and β_f , such that $\beta_d > \beta_f$.
 156 Under optimal strategies, $u(r, z, t)$ is regulated by the functional parameter $\beta(z, t) = T_d(z, t)\beta_d +$
 157 $T_f(z, t)\beta_f$. Since Eq 1 has no practical closed-form solution, we made the simplifying assumption

158 that $u(r, z, t)$ quickly converges to space use equilibrium $\hat{u}(r, z)$ under a constant resource level $k(t)$
 159 within a time step. Therefore, we can approximate

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

160

161 Finally, an individual's temporal home range size, $S(z, t)$, truncated at the outer radius that en-
 162 compasses 90% of space use coverage, can be numerically solved from the conservational condition

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

163 *Simulation analyses*

164 We considered an animal population of size n , where each individual i of age z_i inhabits a specific
 165 local environment described by the parameter set $O_i = \{p_i, f_i, \alpha_i\}$. Range size time-series have been
 166 observed to undergo pronounced seasonal variations on a log scale (Börger et al. 2006), we therefore
 167 defined the range size of an averaged individual at time t as $V_n(t) = (1/n) \log \prod_{i=1}^n S(z_i, O_i, t)$,
 168 with n being the size of a sample population. We subsequently performed Monte Carlo simulations
 169 and modeled range size time-series $V_n(T) = \{V_n(t_0), V_n(t_1), V_n(t_2), \dots\}$ across a discretized timeline
 170 $T = \{t_0, t_1, t_2, \dots\}$. From the simulated results, we applied least-square model fitting to optimize
 171 the parameters of a sinusoidal curve, $\tilde{V}(t) = m + q \sin 2\pi t$, where m and q approximate the annual
 172 mean and seasonal variation of individual range size, respectively.

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

178 Animal range size has also been empirically shown to vary in its level of seasonal variation, from
 179 being temporally static to highly oscillatory, with respect to a number of environmental features
 180 that includes resource distribution, population density, and information uncertainty (e.g., Börger
 181 et al. 2006; Mueller and Fagan 2008). In our second analysis, we tested these predictions by simu-
 182 lating range size time-series $V_n(T)$ under random population structure for different combinations of

183 environmental parameters f , α , and p (here acting as a proxy measure for local population density)
184 and examined whether the consequent seasonal variation q correlates with these habitat descriptors
185 in ways that are consistent with several published observations.

186 Our final analysis assumes the classic theory of ideal-free distribution (e.g., see Kacelnik et al.
187 1992), which predicts that foragers should aggregate heavily in resource-rich habitats. In this
188 scenario where resource abundance and population density are positively correlated, such that
189 $p(t) = p_0 + \gamma k(t)$, where γ measures the strength of population aggregation, we expected some
190 would-be foragers to turn more territorial and contract their range size in order to defend against
191 the seasonal influx of intruders. We then simulated range size time-series $V_n(T)$ from weakly to
192 strongly aggregated systems for distinct demographic values z , while keeping the non-seasonal
193 parameter f random within the populations, and evaluated individual range size response to forage
194 opportunity as indicated by the derivative $d\tilde{V}/dk$.

195 Results

196 We first investigated the parametric conditions under which the three contrasting movement
197 strategies each becomes optimal. Individuals in the lowest end of the age range, i.e., juveniles, show
198 a fairly consistent preference for the foraging strategy irrespective of seasonal changes in forage
199 opportunity or sensory drawback in judging intrusion pressure. In contrast, adults are shown to be
200 the major supporters of the defensive strategy, particularly when forage payoff is low and intrusion
201 pressure uncertain (Fig 3). The rest of the demographics, who we classified as subadults, tend to
202 spend a significant portion of time abiding by the reactive strategy, making movement decisions
203 that are highly sensitive to forage condition; periodically, they may briefly switch their strategies to
204 one of the two other options (Fig 3). In relationship to external factors, noisy sensory information
205 generally discourages the reactive strategy from being adopted at any point during the year, thus
206 causing many individuals to suddenly flip their movement behavior over time (Fig 3). Temporal
207 resource heterogeneity, on the other hand, is shown to promote individual participation in every
208 strategy, including adults selecting the foraging strategy when the payoff is sufficiently enticing
209 (Fig S1). Under heightened intrusion pressure, the defensive strategy becomes almost universally

210 favored except by juveniles, especially when combined with imperfect sensory information (Fig S2).
211 More specifically, when intruders are present without interruption, forage is never profitable unless
212 the resource gained by the excursion exceeds the inevitable lost due to intrusion.

213 The time-series resulting from our simulations showed that mean individual-level range size can
214 undergo distinct seasonality even if the environmental condition is partially stochastic (Fig 4a). We
215 may further gather from the variation in range size distribution that this seasonal effect contains two
216 simultaneous phenomena: periodic surges in popularity for either foraging or defensive movement,
217 and a perennial presence of both behaviors at lower occurrences (Fig 4a). Seasonal differences can
218 also be reflected in the utilization distributions of individuals, here showing evident contrast in the
219 case of a subadult that makes its decisions under a constant condition of information uncertainty
220 (Fig 4b). Evaluating space use patterns in the context of optimality can therefore facilitate a
221 spatio-temporally explicit understanding of demographic and environmental effects on movement
222 range.

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

230 Constant intrusion pressure in the absence of aggregation behavior easily produces home range
231 expansion during peak forage season by all individuals (Fig 7). When aggregation tendency is in-
232 corporated, juvenile movement remains largely unaffected; however, the foraging strategy becomes
233 suboptimal for subadults and adults due to the concurrent rise of intrusion probability due to
234 conspecific arrival. In a weakly aggregative population, this leads to range sizes that respond less
235 sensitively to forage opportunity (Fig 7). In a strongly aggregative population, the massive influx
236 of conspecifics exerts a net negative forage effect on the older individuals, resulting in them switch-
237 ing from the reactive to the defensive strategy (Fig S3). Therefore, counter-intuitively, their home
238 ranges contract in response to increasing foraging level. If this latter phenomenon is present at all,

239 it appears to encompass a large proportion of the age demographic at once; the youngest age at
240 which it manifests in the population lowers with the strength of aggregation (Fig 7).

241 Discussion

242 Here we present a home range model that predicts the range size dynamics of territorial animals
243 faced with foraging and defensive requirements. Our model recognized range size as the spatial
244 product of optimal movement strategy that reflects the conflict between two fitness-enhancing be-
245 haviors: to forage beyond one's territory or to defend the territory from conspecific intrusion. When
246 a territorial individual detects nearby rivals, it is shown to sacrifice forage payoff for territorial de-
247 fense. This change in movement behavior is supported by experimental tests in captive Great
248 tits (*Parus major*), where intruder presence was found to induce territorially vigilant movement
249 in replacement of forage-efficient movements (Kacelnik et al. 1981). Behavioral changes are also
250 caused by differences between the resource values on each side of the territorial boundary. Studies
251 of red-winged blackbirds (*Agelaius phoeniceus*) reported that lowered food supply inside one's ter-
252 ritory leads to increased foraging frequency and shorter time spent on guarding against trespassers
253 (Westneat 1994). In addition, the model predicted increased intraspecific variance in behavioral
254 preference under sensory uncertainty. This is evidenced in the case of northern pike (*Esox lucius*
255 L.), a species found to exhibit a higher degree of movement diversity in turbid waters compared to
256 less murky habitats (Andersen et al. 2008).

257 By combining behavioral optimization and utilization distribution, we provided an analytical
258 framework that examined how home range areas may be affected by movement decisions, as well
259 as the ecological conditions underpinning those decisions. Our model design conformed to the
260 movement ecology framework proposed by Nathan et al. (2008), which conceptualizes movement
261 mechanisms of individuals as interactions amongst one's internal state (here, age), external factors
262 (environmental parameters), motion and navigation capacities (grouped in the measure of central-
263 ization). This integrative approach allowed us to specifically search for a rich suite of dynamical
264 range size patterns.

265 *Demographic effects*

266 For animals that can secure increasingly valuable territory with age, their home ranges appear
267 to decrease in size over lifetime; their range sizes meanwhile undergo the largest degree of seasonal
268 variability between the onset of independent mobility and full maturity. Our results are consistent
269 with previous empirical works on roe deer (*Capreolus capreolus*) home range dynamics, as reported
270 in Andersen et al. (1998), Strandgaard (1972), Pettorelli et al. (2003), and Börger et al. (2006).
271 Fawns are usually non-territorial; compared to older individuals, their movements are expansive and
272 driven by the need to constantly forage within the local landscape. Territoriality begins to emerge in
273 younglings near maturity; on average, range sizes become reduced compared to fawns but fluctuate
274 more with seasonality. Fully matured and senescent adults are highly sedentary; range sizes become
275 mostly restricted to their territories and are less affected by seasonal conditions. Similar range size
276 patterns can also be found in other ungulates (e.g., see Clutton-Brock and Guinness 1982) and
277 more distant taxonomic groups. Eagle owls (*Bubo bubo*), for instance, demonstrate large range size
278 dynamics at the intermediate age class before permanently retreating into their territories in later
279 years (Campioni et al. 2013). Similarly, the Malaysian flying lizards (*Draco volans sumatranus*)
280 shift from being territorial intruders to territorial guardians over their lifetimes (Mori and Hikida
281 1993).

282 *Environmental effects*

283 Our model indicated that several environmental features can either stabilize or destabilize in-
284 dividual range size dynamics. In habitat types characterized by seasonal growth of rich forage
285 patches, we demonstrated that local animals show a noticeable degree of range size variation with
286 seasonal periodicity over the course of the year. Furthermore, we predicted the emergence of even
287 larger range size fluctuation, given the added condition that the sensory information necessary for
288 assessing the risk of territorial intrusion is unreliable. In contrast, sensory-compromised individuals
289 surrounded by a dense population of conspecifics may have their range size dynamics significantly
290 reduced.

291 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) 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 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 spent advertising their territorial presence (Randall 1984). Finally, resource, density, and sensory effects are jointly evaluated in 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., setaside).

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

319 contingent on widespread crowding behavior in the population, we hypothesize that it may be more
320 commonly observed in environments where the majority of high quality resource is concentrated
321 within small regions.

322 To our knowledge, there has been no previous age structure analysis of range size dynamics with
323 respect to resource seasonality. However, sex differences, which are also associated with unequal
324 territory qualities in many animals (see Campioni et al. 2013), have been suggested to generate
325 divergent range sizes both during and outside of breeding seasons. Case studies, based partly on
326 measures of home range overlap, include red deer (*Cervus elaphus*) (Reinecke et al. 2014), field
327 voles (*Microtus agrestis*) (Pusenius and Viitala 1993), and raccoons (*Procyon lotor*) (Gehrt and
328 Fritzell 1998). As further expected from our hypothesis, territorial individuals may become more
329 area restricted in systems where the resources are unevenly distributed (e.g., Jensen et al. 2005;
330 Schoener 1987; Markham et al. 2013).

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

338 *Utilization distributions: bimodality and transient dynamics*

339 Our model highlights two dynamical qualities of utilization distribution that are increasingly
340 emphasized in mechanistic movement analysis: bimodality and transient dynamics. The first con-
341 cept stems from the two statistical clusters, or modes, that are often distinctive in movement data
342 (e.g., exploratory vs. encamped) (Morales et al. 2004; Beyer et al. 2013). Modal transitions oc-
343 cur nonrandomly (Schmitt et al. 2006) and reflect changes in both landscape conditions and an
344 animal's internal state (Morales et al. 2004, 2005). However, few mathematical models have inte-
345 grated bimodality into space use patterns. Blackwell (1997) derived the utilization distributions

346 of animals that switch between core-area movement and excursion according to a Markov Chain.
347 More recently, the “exchange model” developed by Skalski and Gilliam (2003) also made space use
348 predictions by including the amount of time an individual spent in one of two movement states into
349 an advection-diffusion movement process. Both models helped advance the theoretical foundation
350 of modal transitions, which we have now extended on the basis of payoff maximization.

351 Transient analyses are employed to describe the temporal variation in ecological dynamics, such
352 as time-series fluctuations, before the system settles into permanent equilibria. Recognizing the
353 importance of transient dynamics has contributed an essential explanatory aspect in understanding
354 population and community patterns, thereby helping to generate more reliable predictions within
355 short-term, ecologically relevant timescales (Hastings 2004, 2010). In agent-based movement mod-
356 els, transient dynamics of animal space use can be simulated as consequences of spatial memory
357 processes (Van Moorter et al. 2009; Riotte-Lambert et al. 2015) and scent-mark avoidance behavior
358 (Potts et al. 2013). However, analytical models centered around utilization distributions are hand-
359 icapped in this regard mainly due to the technical barrier in solving Fokker-Planck equations in
360 time. Our model adopted the sidestepped approach in Moorcroft et al. (2006) and Bateman et al.
361 (2015), which allows space use variation to equilibriate at the chosen time steps, driven by terrain
362 gradient, neighbor removal, or group fission. In other words, we approximate transient range size
363 dynamics by sequentially perturbing the steady-state solutions, with the implications that (1) the
364 animal optimizes its movement behavior faster than its spatial convergence and that (2) both pro-
365 cesses occur immediately relative to the governing ecological dynamics. Although many terrestrial
366 systems support these timescale disparities (e.g., see Bateman et al. 2015), future work could aim
367 to incorporate powerful numerical differential equation solvers that can relax this constraint, thus
368 broaden our current picture of range size patterns.

369 *Future extensions*

370 Our model exchanged mechanistic complexity for heuristic transparency; in the future, this
371 optimality framework could be enhanced in a number of ways. For example, the centralizing pa-
372 rameter currently fixed for each type of movement behavior could be more realistically modeled as a

373 continuous function of demographic variables, assuming a state-dependent spectrum of locomotive
374 efficiency and navigation experience. We also strongly encourage the development of mechanis-
375 tically analogous agent-based simulations, which would help generalize the dynamical process by
376 addressing the effects of multiple home range attractors (see Don and Rennolls 1983).

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

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

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

401 Glossary

402 D Movement decision.

403 I Intruder status.

404 V Individual range size averaged from a sample population.

405 W Expected resource payoff of enacting a particular movement strategy.

406 α The amount of seasonal change in extra-territorial resource value k .

407 β Degree of centralization in movement behavior.

408 f Probability that the sensory information about intruders yields false conclusion.

409 h Proportion of territorial resource value that remains after intrusion occurs.

410 k Extra-territorial resource value.

411 m Approximated mean annual individual range size.

412 n Sample population size.

413 p Probability of intruders being present near a territory.

414 q Approximated seasonal variation of individual range size.

415 w Baseline resource value of a territory.

416 z State variable that represents an animal's age.

APPENDIX

417

418

419

Revision of home range solution in Moorcroft and Lewis (2006).

420

421

422

423

We derived an alternate expression for the equilibrium to the one published in Moorcroft and Lewis (2006, page 33, equations 3.14-3.15). Our solution (see Appendix) fixed the error we detected in the original derivations that was later confirmed by the authors (Mark Lewis, personal communication).

424

425

Taking the polar Laplacian transform of steady-state advection-diffusion equation in Cartesian coordinates:

$$\vec{\nabla}^2 u - \beta \vec{\nabla} \cdot (u \vec{x}) = 0, \quad (\text{A1})$$

426 such that

$$\vec{r} = (r \cos \theta, r \sin \theta), \quad (\text{A2})$$

427 and

$$-\hat{r} = \frac{-\vec{r}}{|\vec{r}|} = -(\cos \theta, \sin \theta). \quad (\text{A3})$$

428

429 The centrally oriented advection term should then be expressed as

$$\vec{\nabla} \cdot (u(-\hat{r})) = \vec{\nabla} \cdot (u(-\cos \theta, -\sin \theta)) \quad (\text{A4})$$

$$= - \left[\frac{\partial}{\partial x}(u \cos \theta) + \frac{\partial}{\partial y}(u \sin \theta) \right] \quad (\text{A5})$$

$$= - \left[\frac{\partial}{\partial r}(u \cos \theta) \frac{\partial r}{\partial x} + \frac{\partial}{\partial \theta}(u \cos \theta) \frac{\partial \theta}{\partial x} + \frac{\partial}{\partial r}(u \sin \theta) \frac{\partial r}{\partial y} + \frac{\partial}{\partial \theta}(u \sin \theta) \frac{\partial \theta}{\partial y} \right] \quad (\text{A6})$$

$$= - \left[\cos^2 \theta \frac{\partial u}{\partial r} - \frac{\sin \theta}{r} \frac{\partial}{\partial \theta}(u \cos \theta) + \sin^2 \theta \frac{\partial u}{\partial r} + \frac{\cos \theta}{r} \frac{\partial}{\partial \theta}(u \sin \theta) \right] \quad (\text{A7})$$

$$= - \left[\cos^2 \theta \frac{\partial u}{\partial r} - \frac{\sin 2\theta}{2r} \frac{\partial u}{\partial \theta} + \frac{u}{r} \sin^2 \theta + \sin^2 \theta \frac{\partial u}{\partial r} + \frac{\sin 2\theta}{2r} \frac{\partial u}{\partial \theta} + \frac{u}{r} \cos^2 \theta \right] \quad (\text{A8})$$

$$= - \left[\frac{\partial u}{\partial r} + \frac{u}{r} \right] \quad (\text{A9})$$

$$= - \frac{1}{r} \frac{\partial}{\partial r}(ru). \quad (\text{A10})$$

430 Substituting the corrected advection term into (A1), the latter in polar coordinates becomes

$$\frac{\beta}{r} \frac{\partial}{\partial r}(ru) + \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial u}{\partial r} \right) = 0, \quad (\text{A11})$$

431 or simply,

$$\frac{\partial^2 u}{\partial r^2} + \frac{\partial u}{\partial r} \left(\beta + \frac{1}{r} \right) + \frac{\beta}{r} u = 0. \quad (\text{A12})$$

432 The form of the differential equation is sufficient to continue with the Frobenius Method (Boas

433 2006), which gives a solution that is the same as the series for $(\beta^2/2\pi) \exp(-\beta r)$.

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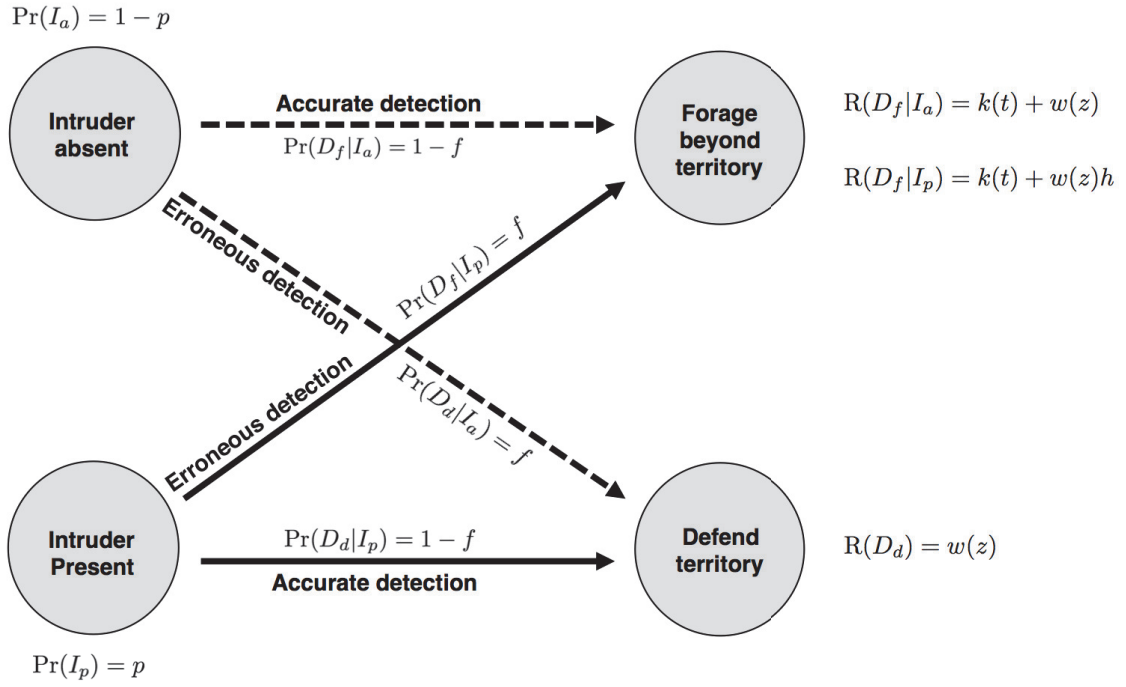


Figure 1: Flowchart depicting how an individual decides between extra-territorial foraging, D_f , and territorial defense, D_d , according to the reactive strategy, which produces expected resource payoff $W_r(z, t)$. Intruders' presence and absence are indicated by I_p and I_a , respectively. The resource reward, $R(\cdot)$, associated with each scenario of intrusion risk and sensory noise is expressed on the right side of the diagram. The decisional flowchart of the foraging strategy consists of the two upper 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 $\Pr(D_d|I_a) = \Pr(D_d|I_p) = 1$.

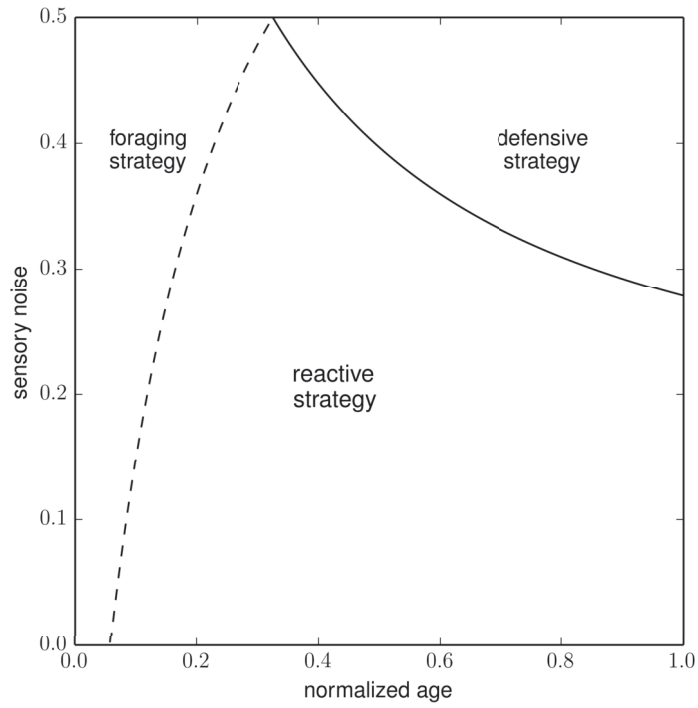


Figure 2: Parametric regimes of the three optimal strategies as a function of age z and sensory noise f . Parameter space above the solid and dashed lines satisfy Eqs 5 and 6, respectively. Environmental parameters $p = 0.2$ and $k(t) = 0.05$, which is approximately 8% of maximal territorial resource value, $w(1)$; intrusion penalty $h = 0.1$

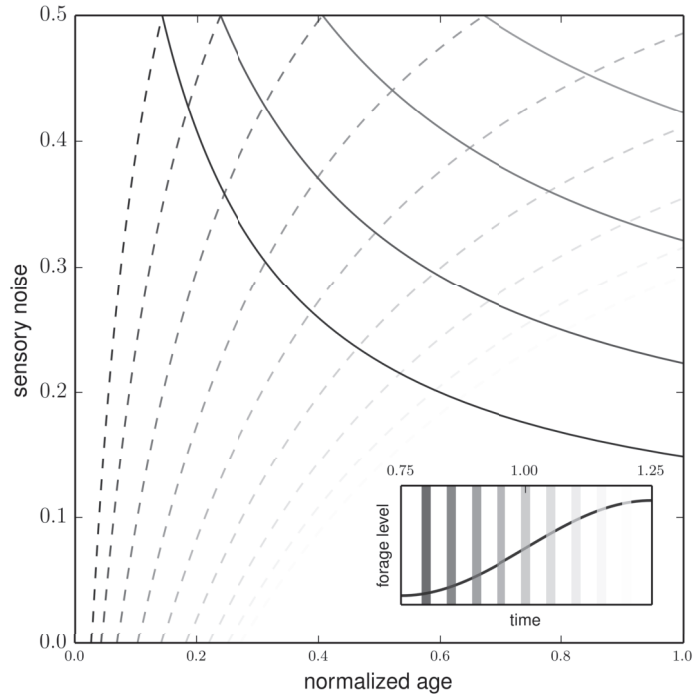
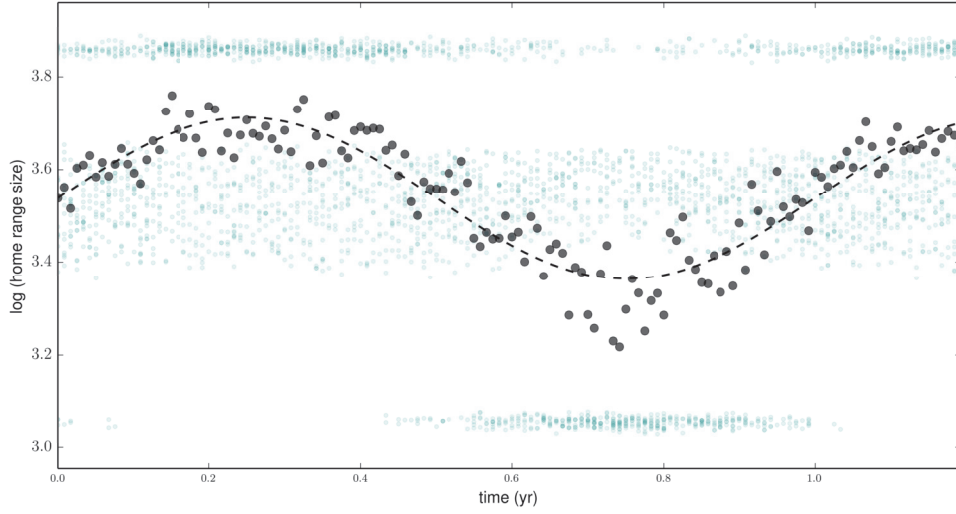
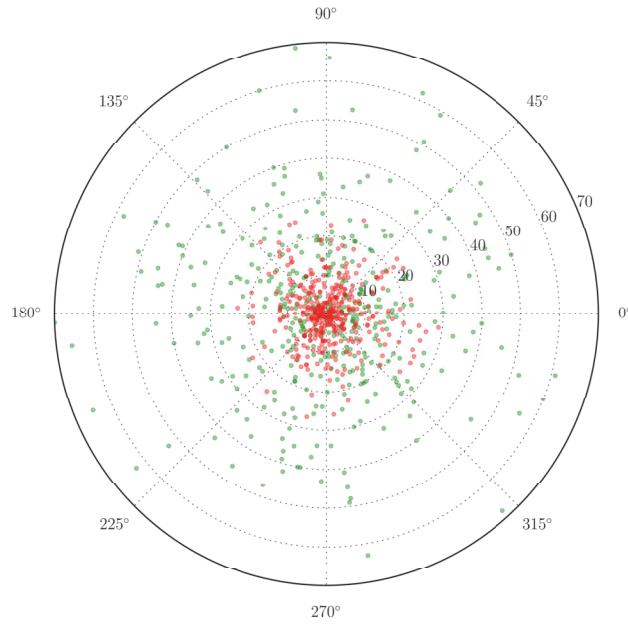


Figure 3: Parametric regimes of optimal strategies plotted over time $T = \{0.8, 0.85, \dots, 1.2\}$ (from dark to light) as a function of age z and sensory noise f . The corresponding phases in forage level $k(T)$ are marked by vertical lines in the inset figure using the same shading scheme. Environmental parameters $k_0 = 0.02$, $\alpha = 0.05$, and $p = 0.2$; intrusion penalty $h = 0.1$.



(a)



(b)

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 the circles; the dashed line shows the sinusoidal range size estimation $\tilde{V}(t)$. (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).

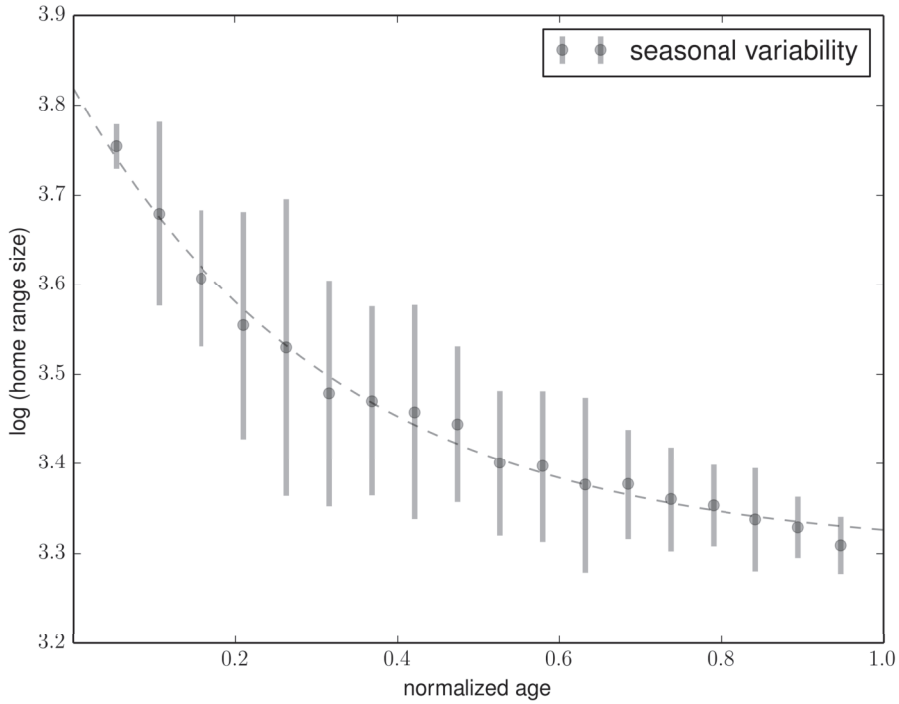


Figure 5: Demographic effects on range size dynamics. Base forage level $k_0 = 0.02$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2, \beta_f = 0.08$. Under constant age variable z , a sample population of $n = 5$ is simulated at each time step for a period of one year. Environmental 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 , shown in circles, are fitted with 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.

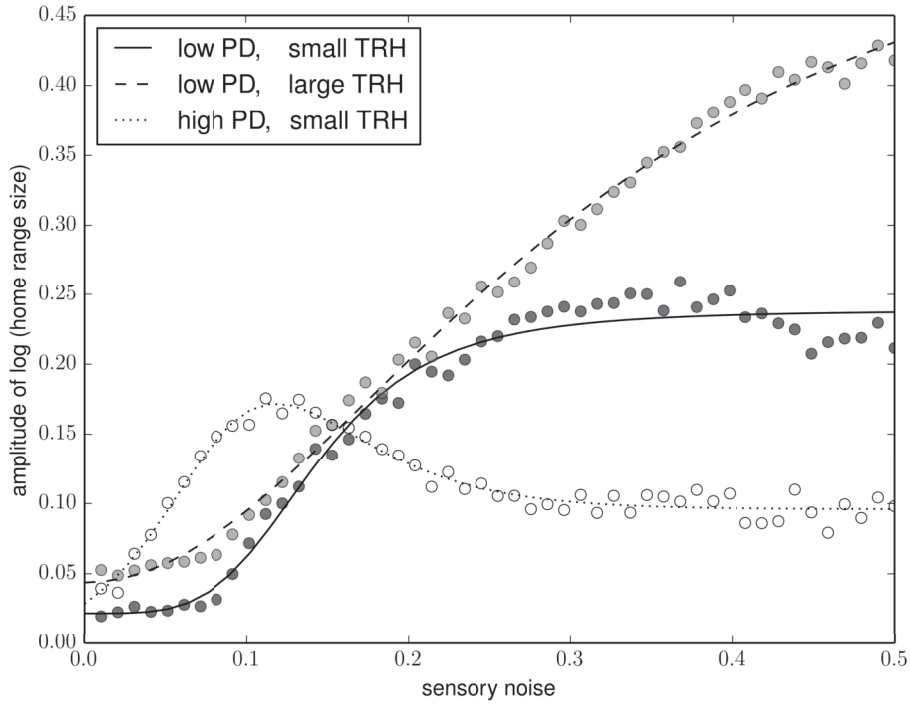


Figure 6: Environmental effects on range size dynamics. Base forage level $k_0 = 0.02$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2, \beta_f = 0.08$. Under constant environmental condition $O = \{p, f, \alpha\}$, a sample population of $n = 20$ is simulated at each time step for a period of one year. Small and large temporal resource heterogeneities (TRH) correspond to parameter values $\alpha = 0.1$ and 0.2 , respectively; low and high population densities (PD) 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 , shown in circles, are fitted to logistic and double-logistic regression curves as a function of sensory noise f .

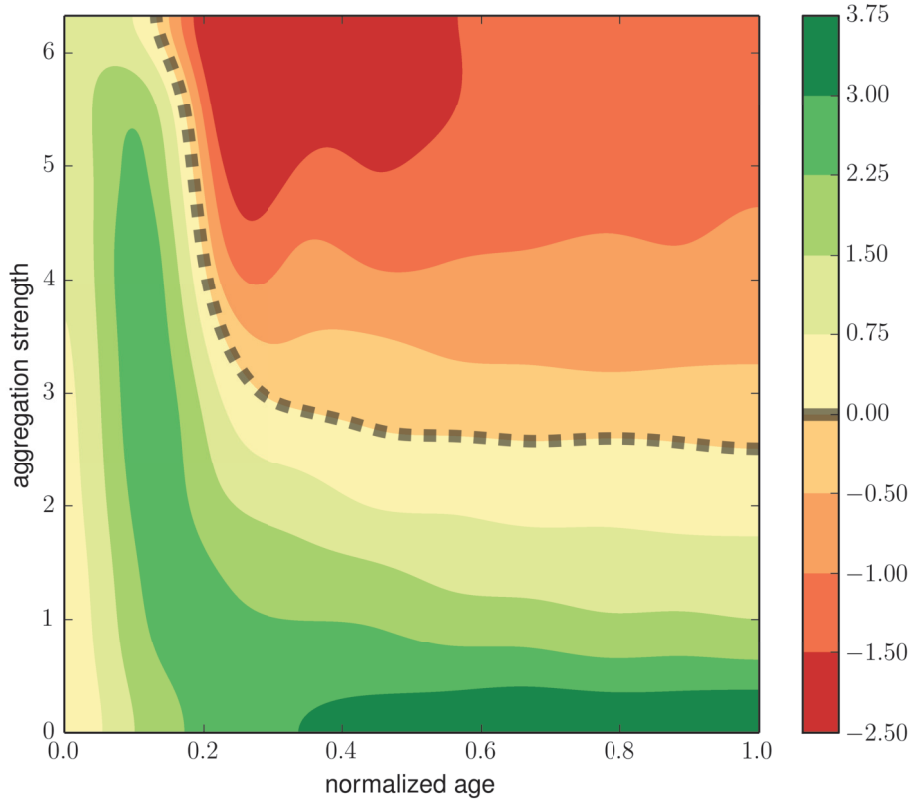
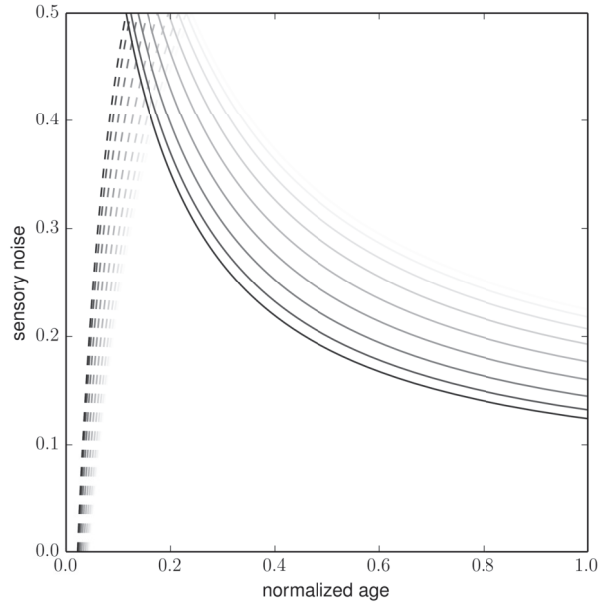
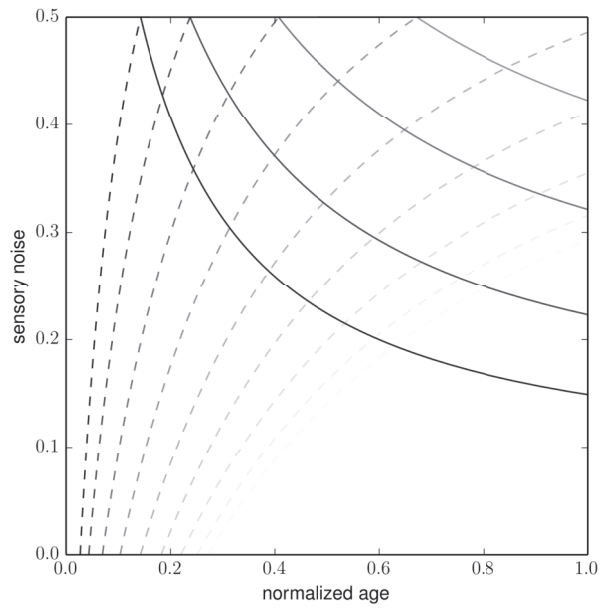


Figure 7: Individual range size response to forage opportunity as a function of age and aggregation strength. Base forage level $k_0 = 0.02$; base intrusion pressure $p_0 = 0.1$; temporal resource heterogeneity $\alpha = 0.15$; intrusion penalty $h = 0.1$; centralizing parameters $\beta_d = 0.2, \beta_f = 0.08$. 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 one 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 $d\tilde{V}/dk$, respectively; the dashed line demarcates the threshold of demographic divergence.

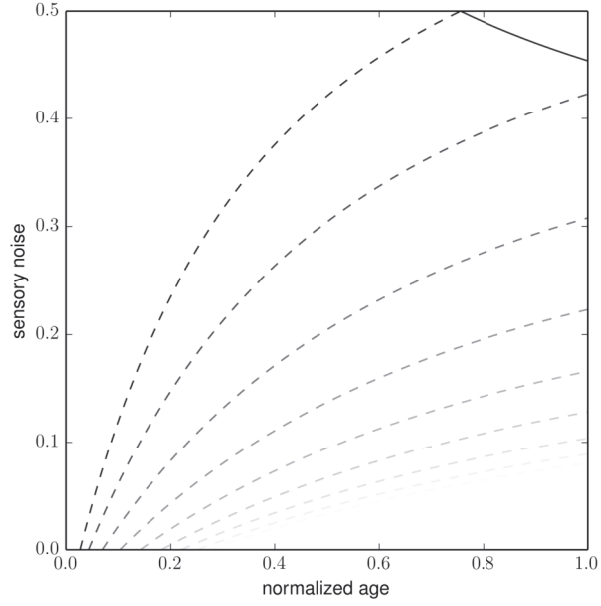


(a)

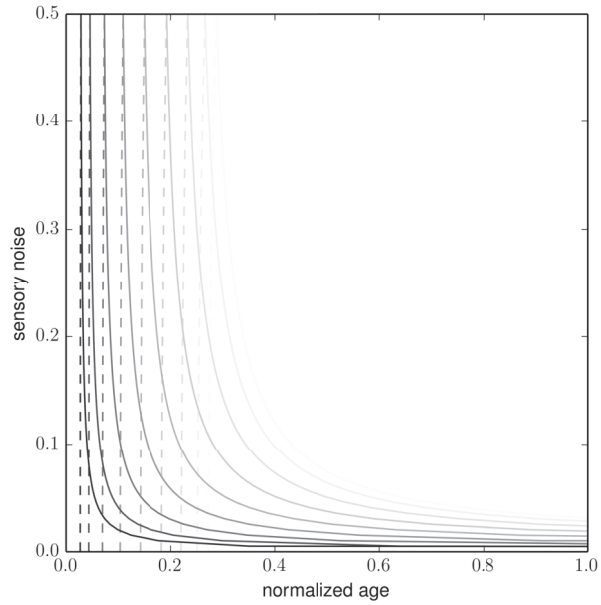


(b)

Figure 8: **S1**. Parametric regimes of optimal strategies plotted over time $T = \{0.8, 0.85, \dots, 1.2\}$ (from dark to light) as a function of age z and sensory noise f . Intrusion penalty $h = 0.1$; environmental parameters $k_0 = 0.02$, $p = 0.2$, and (a) $\alpha = 0.01$; (b) $\alpha = 0.1$.



(a)



(b)

Figure 9: **S2**. Parametric regimes of optimal strategies plotted over time $T = \{0.8, 0.85, \dots, 1.2\}$ (from dark to light) as a function of age z and sensory noise f . Intrusion penalty $h = 0.1$; environmental parameters $k_0 = 0.02$, $\alpha = 0.05$, and (a) $p = 0.05$; (b) $p = 0.95$. The values of the two boundaries at $p = 1$ satisfy $k(t) = w(z)(1 - h)$.

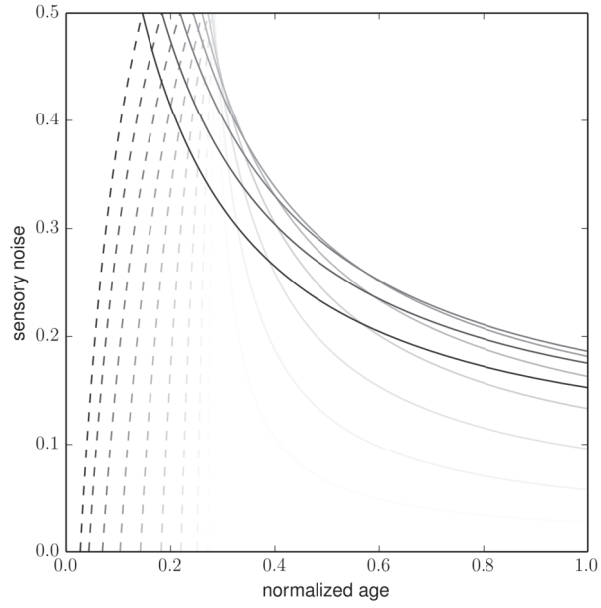


Figure 10: **S3**. Parametric regimes of optimal strategies under aggregation, plotted over time $T = \{0.8, 0.85, \dots, 1.2\}$ (from dark to light) as a function of age z and sensory noise f . Environmental parameters $k_0 = 0.02$, $\alpha = 0.1$, and $p_0 = 0.1$; intrusion penalty $h = 0.1$; aggregation strength $\gamma = 4$.