LJMU Research Online

Heathcote, RJP, Whiteside, MA, Beardsworth, CE, Van Horik, JO, Laker, PR, Toledo, S, Orchan, Y, Nathan, R and Madden, JR

Spatial memory predicts home range size and predation risk in pheasants

http://researchonline.ljmu.ac.uk/id/eprint/18893/

Article

For more information please contact researchonline@ljmu.ac.uk

Spatial memory predicts home range size and predation risk in pheasants

Robert J. P. Heathcote[1,2*]; Mark A. Whiteside[2,3]; Christine E. Beardsworth[2,4,5]; Jayden O. Van Horik[2,6]; Philippa R. Laker[2]; Sivan Toledo[7], Yotam Orchan[8], Ran Nathan[8], Joah R. Madden[2].

[1] School of Biological Sciences, University of Bristol, Tyndall Avenue, Bristol, BS8 1TQ. UK

[2] Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Perry Road, Exeter EX3 4QG. UK

[3] School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA. UK

[4] NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, Den Burg, The Netherlands.

[5] School of Biological & Environmental Sciences, Liverpool John Moores University, Liverpool, United Kingdom

[6] University of Exeter Clinical Trials Unit, College of Medicine and Health, University of Exeter Medical School

[7] Blavatnik School of Computer Science, Tel-Aviv University, Tel-Aviv 69978. Israel

[8] Movement Ecology Lab, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Faculty of Science, The Hebrew University of Jerusalem. Israel.

*Corresponding author: r.j.p.heathcote@gmail.com

23 **Abstract**

24 Most animals confine their activities to a discrete home range, long assumed to reflect the fitness

25 benefits of obtaining spatial knowledge about the landscape. However, few empirical studies have

26 linked spatial memory to home range development, or determined how selection operates on spatial

27 memory via the latter's role in mediating space use. We assayed the cognitive ability of juvenile

28 pheasants (*Phasianus colchicus*) reared under identical conditions before releasing them into a novel

29 landscape and used high-throughput tracking to record their movements as they developed their home

30 ranges, and determine the location, timing and cause of any mortality events. Individuals with greater

31 spatial reference memory developed larger home ranges. Mortality risk from predators was highest at

32 the periphery of an individual's home range, in areas they had less experience and opportunity to

33 obtain spatial information. Importantly, predation risk was lower in individuals with greater spatial

34 memory and larger core home ranges, suggesting selection may operate on spatial memory by

35 increasing the ability to learn about predation risk across the landscape. Our results reveal that spatial

36 memory, determined from abstract cognitive assays, shapes home range development and variation,

37 and suggests predation risk selects for spatial memory via experience-dependent spatial variation in

38 mortality.

39

40 **Main text**

41 *Introduction*

42 Most animals confine the majority of their activities to a relatively restricted spatial region: their

43 home range [1–4]. The patterns and dynamics of animal home ranges have fundamental consequences

44 across biology, from epidemiology [5,6] to population dynamics and predator-prey interactions [6–9], yet

45 surprisingly little work demonstrates the processes by which selection can emerge and shape home

46 range variation. A long-standing explanation for why many animals form home ranges, supported by

47 a wealth of mechanistic modelling studies (e.g. [1,10]), is that it allows a resident to learn the location of,

48 and optimally exploit, patchily distributed resources such as food and shelter [11–13]. Consequently, an

2

49 animal's ability to learn, retain and update information on the spatial location of resources within its

50 home range is assumed to be of great benefit [12,14], and is a central tenet to many definitions of the

51 home range [15,16]. Decades of work incorporating proxies of resource-based spatial memory into

52 mechanistic random-walk models of home range development results in the emergence of more

53 realistic home ranges, or better statistical power in predicting the development of real animal home

54 ranges, compared to alternative processes such as sensory detection of resources [4,17–27]. Whilst these

55 prior studies have produced convincing conclusions when incorporating artificial analogues of spatial

56 memory, they still require empirical validation in light of the extensive work from comparative and

57 classical psychology demonstrating animals often make use of multiple and distinct cognitive

58 modalities that work synergistically to process different types of information during daily life [28].

59 Indeed, the few studies that incorporate different types of spatial memory such as 'working memory'

60 (short-term memory of recently visited locations [29]) and 'reference memory' (longer-term memory of

61 landmarks [30]) suggest they work in concert to maximise the efficiency of movement patterns within a

62 home range (e.g. [21,22]), and that working memory itself may be a particularly important determinant of

63 home range size [21]. However, we still lack empirical studies that test the predictions made by these

64 simulation studies to establish the role of cognitive ability (and specifically various types of spatial

65 memory) in real home range formation and size variation.

66

67 Whilst a great deal of work has focused on the drivers of interspecific variation in home range size,

68 for instance showing that it scales as a function of body size, metabolic rate and forage type [31] as well

69 as being heavily influenced by locomotion and foraging strategies [32–34], less is known about the causes

70 and consequences of home range size at the intraspecific level, particularly with regards to how these

71 are affected by individual-level variation in different traits. Larger home ranges may infer a range of

72 benefits such as increased access to mates, refuges and resources [35], although the factors constraining

73 size are less well established empirically, particularly in species that do not suffer economic costs of

74 aggressively defending spatially distributed and non-divisible resources [22,36,37]. Spatial memory

75 ability, as a major factor enabling animals to form stable home ranges in the first place, could be a

76 potential mechanistic component limiting home range size. If animals form home ranges to exploit

77 spatial knowledge about important resources or local variation in predation risk, then all else being

78 equal, better spatial memory should translate to animals being able to utilise larger home ranges

79 without suffering associated costs caused by poor knowledge about the landscape such as inefficient

80 travel between resources [21,22] or suboptimal vigilance whilst travelling across regions of varying

81 predation risk [38]. Whilst some biologically-plausible mechanistic models incorporating multiple

82 cognitive modalities have indeed suggested that better spatial memory can translate into the

83 emergence of larger home ranges [21,22], this needs validation from field-based studies of real animals.

84

85 Here, we use a unique system in common pheasants (*Phasianus colchicus*) where we can rear large

86 numbers of individuals under standardised conditions, assay them across a battery of cognitive tasks,

87 tag all individuals with high spatial and temporal resolution radio tags, and release them into a novel

88 wild landscape to track their movements as they develop their home ranges. This approach reduces

89 variation in early life environmental effects on subsequent behavioural traits, allowing us to test key

90 predictions about the causes and consequences of movement ecology (although, as with any

91 experimental control, this comes at the potential expense of reducing ecological realism). Specifically,

92 we aimed to test how individual-level variation in three cognitive modalities (associative learning,

93 spatial working memory, and development of a spatial reference memory) obtained from

94 psychometric assays predict variation in the development of home range size.

95

96 The degree to which individuals can learn and process spatial information, particularly in relation to

97 resources, should assumedly affect fitness, with potential consequences on selection depending on the

98 heritability of these traits [39]. Indeed, a limited number of studies have uncovered fitness benefits

99 associated with variation in cognitive ability [40,41], and some have suggested that spatially-explicit

100 processes are critical in driving the association [42,43]. Nevertheless, the pathway by which spatial

101 memory and other cognitive modalities drive variation in the movement of individuals, and how this

102   in turn affects how individuals interact with their environment to ultimately generate selection on

103   spatial memory, is still unclear. Whilst most studies addressing the formation and benefits of home

104   ranges have focused on the importance of exploiting patchily distributed resources (or restrictions in

105   movement caused by aggressive defence by territorial neighbours [7,10,27]), another critical factor that

106   shapes natural selection and varies non-randomly across the landscape, is predation. Many predators,

107   particularly ambush hunters, display fine-scale temporal and spatial patterning in their hunting

108   behaviour [44], which prey can potentially learn and mitigate through strategies such as increased

109   vigilance, avoidance of high risk areas, or exploiting memorised escape routes [38,44–47]. As such, there

110   is growing evidence that predation risk may be particularly high in regions that prey are less familiar

111   [44,48,49]. An intuitively appealing, but so far untested, pathway by which selection may operate on

112   spatial memory ability is therefore via variation in predation risk mediated by an individual's

113   familiarity (i.e. degree of prior experience) with high-risk areas as determined by the location and

114   structure of its home range.

115

116   The high spatial and temporal resolution of our tracking data allowed us to identify the precise

117   location and timing of predation events during our study (n=45), as well as identify the predator

118   species responsible (all caused by red foxes (*Vulpes vulpes*), an ambush hunter). These death locations

119   were non-randomly distributed across the landscape, constituting regions of high predation risk. By

120   coupling cognition, movement, and predation data, we were therefore able to test whether individuals

121   are more likely to be killed outside their core home range in regions they have less knowledge

122   regarding predation risk, the degree to which this is predicted by different cognitive abilities, and

123   whether this 'experience-dependent' predation risk has the potential to generate selection on cognition

124   and home range variation. A likely consequence of the hypothesised relationship between spatial

125   memory and home range size we detail above is that predation will also be higher in less familiar

126   parts of the landscape (as found previously in deer [44,49]), a phenomenon we predict to be particularly

127   exaggerated in individuals with poor spatial memory since these would be less capable of memorising

128   the locations of non-lethal predator encounters and thus optimising antipredator behaviours across

129   varying regions of predation risk (e.g. [38]). Whilst prior work on the antipredator benefit of different

130   cognitive modalities is scarce, we predict that all three types of cognition we measured can affect

131   predation risk; reference memory for learning landscape features and specific locations associated

132   with regions of high risk; working memory in memorising and exploiting the locations of recently

133   visited refuges and escape routes when predators are encountered; and general associative memory

134   via the learning of non-spatial components associated with predation (e.g. heterospecific alarm calls [50]

135   and search images of camouflaged predators [51]).

136

137   We hatched and reared 126 pheasants and assayed their performance on three well-established

138   cognitive tasks between the ages of four and seven weeks old. The first cognitive assay, a binary

139   colour discrimination task, tested the ability of individuals to associate a particular colour with a food

140   reward, a proxy for general associative learning ability (i.e. the ability to learn simple associations

141   between stimuli[52]), and was explicitly designed to not be solved using spatial cues (Fig. 1C). The

142   second, a radial arm maze task, was intended to test an individual's ability to use spatial cues to orient

143   around a maze and optimally exploit multiple food resources as they were depleted, a common

144   paradigm for testing spatial working memory [53] and one that is particularly ecologically relevant to

145   species such as pheasants that feed on patchily-distributed resources (e.g. [54]). The third, a task similar

146   to the classic 'Lashley maze' [55], was intended to test the ability of an individual to learn to navigate

147   through a complex maze ('complex maze task' from hereon; Fig. 1A). Previous studies have shown

148   that the Lashley maze can be solved using allocentric-based visual spatial cues, and/or varying

149   degrees of egocentric-based learned turn sequences when these are absent or insufficient [56]. We have

150   previously shown that pheasants show individual-level variation in their preference for using

151   allocentric and egocentric processes when solving this same complex maze task [57], suggesting that

152   performance in this maze reflects at least some degree of spatial reference memory ability in this

153   species, regardless of navigation strategy deployed. Indeed, whilst multiple cognitive modalities can

154   be used to solve even explicitly domain-targeted tasks (e.g. [58]), we chose these three tasks due to their

155 extensive prior validation from classical cognition testing, their suitability for testing with pheasants,

156 and specifically for their likely relevance to processes important in animal movement ecology [21].

157

158 After the completion of their cognitive tests, we simultaneously released the juvenile pheasants into a

159 heterogeneous rural landscape (mixture of agricultural, grassland and woodland habitats) at 10 weeks

160 old (the age wild birds start independence from their mother [59]). We followed their movements and

161 fate using ATLAS, a recently-developed reverse-GPS automated radio-tracking system with high

162 spatial and temporal resolution [60–63], detecting locations at up to eight times per minute, for up to 120

163 days as birds acquired their home ranges. This design ensured that all birds were equally naïve to a

164 shared landscape, allowing us to test whether the stabilized size of an individual's home range was

165 predicted by their earlier performance in our three cognitive tests (accounting for prior experience;

166 difficult with studies of adult animals but critical when comparing developmental patterns of

167 behaviour between individuals [14]).

168

169 *Results and Discussion*

170 We found that pheasants exhibiting superior performance in the complex maze task (designed to test

171 navigation-related spatial cognition, including spatial reference memory) subsequently developed

172 larger core home ranges (i.e. the area of the home range that birds spend a disproportionately large

173 amount of time[11]; see Methods) calculated from autocorrelated kernel density estimates (AKDEs,

174 which control for temporal autocorrelation in location data[64]) (-0.52 ± 0.24 (coefficient $\pm$ standard

175 error); Fig. 1D; Table S1 and Table S3). This positive relationship provides direct empirical support

176 for the long-standing implicit home range hypothesis suggesting that greater cognitive ability,

177 particularly spatial memory, allows an individual to form a larger core home range [15,65,66]. In contrast,

178 we found no evidence that spatial working memory or associative learning ability predicted core

179 home range size, or that any cognitive metrics predicted the size of the peripheral home range (area of

180 the 85% AKDE isopleth subtracted from the area of the 99% AKDE isopleth; Table S2 – Table S6).

181   Comparison of our results to two previous mechanistic studies that incorporated multiple spatial

182   memory systems show interesting discrepancies. Studies by both Van Moorter et al, and Riotte-

183   Lambert et al suggest that home range size should strongly covary with working memory, and in the

184   former study, be largely insensitive to variation in reference memory [21,22], with both memory systems

185   working synergistically to result in the optimal exploitation of resources that causes the emergence of

186   realistic home range patterns. Our study suggests that variation in spatial reference memory,

187   independent of working memory, predicts the development of differing home range sizes (also

188   suggested by Riotte-Lambert et al. [22]), with no evidence for an interaction between these two spatial

189   cognitive processes or any effect of working memory variation on home range size at all. We note that

190   comparisons between theoretical and empirically-derived measures of cognition should be made with

191   caution, but nonetheless a fascinating avenue for future mechanistic studies would be to investigate

192   the relative importance played by predators and resource utilisation, and how these in turn place

193   differing priorities on different memory systems, in driving home range development, particularly in

194   systems that suffer high predation rates such as ours (as has been done in more nomadic species [67]).

195

196   We recorded 45 separate predation events during our study, for which we could identify the precise

197   timing, location and predator species responsible due to the high temporal and spatial accuracy of our

198   ATLAS data. All predation events were caused by red foxes (see Methods for a separate validation

199   experiment that characterised untagged-predator and tagged-prey movement patterns). By comparing

200   the whereabouts within the predated bird's home range of these real death locations to a null

201   distribution of simulated death locations, we find that pheasants were disproportionately likely to be

202   predated on the periphery of their core home range, the area with which they had least experience

203   (deaths occurring on 85% $\pm$ 25% (mean $\pm$ SD) isopleth of AKDE; Omnibus test: χ= 242.61, df= 70,

204   P<0.001; Fig. 2A and Fig. 2B). This suggests that familiarity with the landscape was an important

205   determinant of an individual's predation risk, supporting previous work in deer [44,49]. However, a

206   potential alternative (but not mutually exclusive) explanation for this spatial distribution of predation,

207   not discounted in previous studies, is that prey individuals may simply establish their home ranges

208   outside of high-risk areas - mortality might be particularly high outside of the core home range simply

209   because this is the area with highest intrinsic risk. Indeed, many prey species are known to form a

210   'landscape of fear' by learning the temporal and spatial patterns of predation risk in their habitat [47,68],

211   providing a possible avenue by which cognitive ability may facilitate predator avoidance. We directly

212   tested for this possibility by calculating areas of high predation risk based on the predation events we

213   recorded during our study. Whilst these were non-randomly distributed across the landscape, we

214   found no indication that cognitive ability played a role in pheasants' ability to avoid these high-

215   mortality areas (Tables S7 – S10), or indeed any evidence that pheasants avoided these areas at all

216   (Extended Data Figure 1). Instead, the home ranges of surviving birds overlapped substantially more

217   with the high-mortality regions than we would expect by chance (89.1% ± 22.2 (mean ± standard

218   deviation) of a bird's core home range; Permutation test: P=0.010; Extended Data Figure 1), possibly

219   due to predators being attracted to areas of high prey abundance [69]. Crucially, the locations of each

220   death commonly fell within the home ranges of multiple individuals. We were therefore able to test, at

221   a fine scale, whether it was an individual's own experience (as determined by the percentage kernel

222   isopleth of their home range) of the location that predicted their death rather than the intrinsic risk of

223   the location itself. For the bird killed at a particular location, this was situated more peripherally

224   within their home ranges compared to the other birds whose home ranges encompassed the location

225   yet were not killed by predators during the study (65% ± 34% (mean ± SD) isopleth of AKDE;

226   Kolmogorov-Smirnov test; D=0.32, P=0.001; Extended Data Figure 2). Taken together, these results

227   suggest that predation risk is not simply a product of the probability of interacting with predators, but

228   rather the level of experience an individual has with the landscape when it encounters those predators.

229   Ignorance of local risk at the home range edge may manifest as a failure to optimally resolve the

230   trade-off between vigilance and resource use, which may develop with age and experience as

231   individuals obtain knowledge about the spatial and temporal patterns of predation risk, refuges and

232   escape routes within their environment [47,68,70], rendering juveniles (or otherwise naïve individuals) in

233   rarely visited areas at greatest risk of predation.

234

235 Further corroborating the antipredatory importance of spatial knowledge, the familiarity-dependent

236 patterning of predation risk we found also created differential survival in pheasants contingent on

237 their spatial memory. Survival was highest in pheasants whose performance in the complex maze task

238 (assessing spatial reference memory) was correlated with their performance in the working memory

239 task; birds had the highest survival if they combined good spatial working memory abilities with good

240 spatial reference memory, and the lowest survival was found in birds with mismatching spatial

241 abilities (i.e. they performed well in one but not the other) (Cox proportional hazards (Cph) model;

242 reference memory x working memory interaction: -2.98 ± 0.90 (coefficient ± SE); Fig. 2C; Table

243 S11- Table S13). When controlling for this interaction, birds with better performance in the complex

244 maze task also had an overall lower probability of being predated (Cph: -1.02 ± 0.44 (coefficient ±

245 SE); Table S13), although there was no important effect of working memory as a main effect (Cph: -

246 0.45 ± 0.59 (coefficient ± SE); Table S13). We found no support for an effect of general associative

247 learning on survival, where our two best models included only sex or an intercept-only model (Table

248 S14). Given that spatial cognition in pheasants has a (albeit low) heritable component [71], the

249 familiarity-dependent spatial variation in predation risk we detail here has potential to generate

250 selection on these two forms of spatial memory. An important prediction from our results is that, since

251 spatial memory positively predicts home range size, with predation risk being highest just outside the

252 core home range, and that this predation risk in turn generates selection on spatial memory, then core

253 home range itself should be expected to be under directional, positive selection. Confirming this, we

254 find that indeed the size of the core home range itself also predicted mortality, with predation risk

255 being lowest in the birds with the largest home ranges (Cph: 0.12 ± 0.07 (coefficient ± SE); Fig. 2D).

256

257 A small number of previous studies have demonstrated survival or mate choice benefits that are

258 associated with cognitive abilities [40,42,43,72]. However, the process by which cognition actually conveys

259 these benefits by mediating how animals interact with their environment is unclear. Our results reveal

260 that spatial variation in predation risk, arising from a prey individual's own familiarity within its

261 home range, may generate selection on spatial cognitive abilities that in turn predict home range size.

262   An intriguing result from our data is that survival was also relatively high in birds that performed

263   poorly in the tasks that test both spatial working memory as well as navigational-based spatial

264   cognition (spatial reference memory) (Fig. 2C). This result requires further exploration to determine

265   the overall effect on selection experienced across multiple generations, although the overall effect of

266   highest survival being found in the birds that performed best in both, in combination with the highest

267   mortality being found in birds with mismatching performance, should result in overall positive

268   selection in both cognitive abilities (as suggested by our result showing that birds with the largest

269   home ranges also had highest survival). Previous modelling work has highlighted the importance of a

270   synergistic mechanistic role of working and reference memory for an animal to create a home range

271   that optimises foraging efficiency [21,22]; our results suggest that a mismatch between these two facets

272   of spatial memory may also have ultimate consequences in terms of survival. Whilst spatial reference

273   memory is known to be important in allowing prey to efficiently exploit safe refuges, particularly

274   when encountering predators [73–75], the role of working memory in relation to predation risk is poorly

275   known so we can only speculate on this intriguing result. Perhaps birds with greater reference but

276   poor working memory traverse larger home ranges, with correspondingly greater exposure to high-

277   risk areas, but their poor working memory means they are less capable of exploiting recently visited

278   escape routes should they encounter a predator. Regardless of the explanatory factor for this result, it

279   suggests that interactions between complementary modalities may be required for selection on some

280   cognitive abilities to arise. The nature of our study site, with the simultaneous introduction of same-

281   aged, equally naïve birds at a single location, in the virtual absence of resident competitors and

282   abundant natural and provisioned food mean that we cannot explore the role of resource distribution

283   on home range development, maintenance and benefits in this analysis. Fluctuations or heterogeneity

284   in resources or competition likely affect home ranges with larger ranges expected in low-productivity

285   areas with patchily distributed resources. Under such circumstances, the relative values of working

286   and reference memories may differ. Thus, we encourage future studies to explore the interplay

287   between risk or resource distributions and spatial memory ability to better understand how selection

288   may act more generally on cognition under varying ecological conditions.

289

290 Our findings provide empirical support for the long-assumed links proposed between movement

291 ecology and spatial cognition as revealed in abstract cognitive tasks dependent on cues of space and

292 movement. They suggest that spatially-contingent predation risk arises through familiarity and

293 experience with the landscape, a potentially critical factor with important implications for how

294 cognition shapes movement and space use. Importantly, they provide a plausible pathway by which

295 selection acts on spatial learning and memory through an individual's acquisition of, and familiarity

296 with, their home range, and their life or death within it.

297

298

299 **Methods**

300

301 *Housing and rearing conditions*

On the 24th May 2018 we hatched 126 pheasant chicks from eggs obtained from commercial breeders

(which sell large numbers of pheasant eggs each year) and allocated these approximately equally

across four indoor enclosures (each 2m x 2m). Chicks were provided water and fed commercial chick

crumbs (Sportsman© Game Feed) *ad libitum*, provided a brooder heat lamp for thermoregulation, and

given various perches. At eight days old, we tagged all birds with small patagial wing tags (Roxan

Ltd, Selkirk, UK) to allow individual identification. Chicks were given access to a sheltered outdoor

enclosure (1.5 x 2.4m) at two weeks old and an outdoor run (4m x 12m) at four weeks old. At 10

weeks old, we weighed and measured the tarsus length of all individuals (a common proxy for

skeletal body size in birds[76]) before releasing all birds into a large outdoor pen allowing them to

disperse into the surrounding rural landscape (mixed farmland and woodland; North Wyke Farm,

Okehampton, Devon, UK). Prior to the release of our study birds, all wild pheasants were captured for

a captive breeding programme. Pre-release visual surveys, as well as ongoing observations during the

study, confirmed that less than 10 wild birds were ever present in the entire field site during the study.

Cognitive testing

All cognitive tasks took place within the same 75cm x 75cm testing chamber adjacent to their indoor

enclosure. For the first three weeks we trained chicks to enter this chamber via a remotely controlled

sliding door using live mealworms as rewards. An additional remotely controlled door with access to

the outdoor enclosure enabled us to ensure birds entered and were tested within the testing chamber

individually. Trial and session number represent a compromise between maximising the collection of

cognitive data that our and previous work has suggested should allow the collection of learning slopes

(e.g. [57,71]) against the time and logistical constraints of running this multi-stage study.

Colour discrimination task

At 25 days old, we tested the chick's associative learning ability on a binary-choice colour

discrimination task that required birds to pierce tissue paper-covered wells to reach a mealworm food

328   reward (Fig. 1C). One week prior to testing, birds were trained to peck through the tissue paper via

329   repeated exposure to the apparatus in the testing chamber in small groups until all birds could

330   consistently perform this behaviour. Each bird completed 10 trials within each of eight sessions (80

331   binary choices) between the 19th and 22nd June. In each session, a bird would enter the testing

332   chamber where they then completed a total of 10 trials. Each 2cm diameter well was encircled with

333   either a blue or green coloured ring; wells encircled with a blue ring contained three mealworms,

334   while those encircled with a green ring could not be pierced due to a layer of undetectable cardboard

335   immediately underneath the tissue. The two wells were oriented vertically in relation to the pheasant's

336   perspective, with a 1cm gap between them. We placed a dead mealworm between the two wells to

337   attract birds to the apparatus and ensure they had a standardised orientation for each set of trials. Birds

338   were only allowed to make one choice per trial. After each choice, the apparatus was replaced before

339   starting the next trial. The location of the rewarded well was pseudorandomised so that it did not

340   appear on the top or bottom more than 3 times in a row and thus removing any spatial associations

341   that may form.

342

343   *Complex maze task*

344   Between 3rd – 5th July 2018 (once the birds reached five weeks old), the testing chamber was

345   converted into a 3 x 3 chambered maze using 35cm walls of opaque black plastic to test the

346   pheasants' reference learning ability, recalling a route after an interval of several hours (Fig. 1A). We

347   first habituated birds to this arena by repeatedly feeding them within the maze when all the doors to

348   each chamber were open. During the complex maze task, birds were required to make at least seven

349   turns to navigate to the exit, at which point they would receive a mealworm reward and could exit to

350   the outdoor enclosure. We ensured that all cues external to the maze (e.g. observer position) were

351   identical in all trials. Each bird first underwent a total of eight trials. In each trial, we counted the

352   number of chambers that a bird entered erroneously, with an error being defined as a chamber that did

353   not lie on the most direct route to the exit. A bird was considered to have entered a chamber if their

354   head passed over the chamber threshold. A bird could repeatedly re-enter a wrong chamber so the

355 number of (potential) errors was not capped. In a perfect performance with no errors, the bird would

356 progress directly through the maze via seven chambers to the exit.

357

358 *Radial arm maze*

359 Once chicks had reached seven weeks old, we tested their working memory based on spatial cues over

360 a period of a couple of minutes, by converting the testing chamber into a radial arm-style maze with

361 four arms rewarded with a single large mealworm (Fig. 1B). The reward was concealed at the end of

362 each arm by an opaque black plastic wall which the birds had to navigate around. On entry to the

363 testing chamber, birds were lured to approach a central platform using a single mealworm as bait,

364 after which they could enter one of the arms and so make their decision. In each trial, we recorded the

365 number of errors a bird made (number of times a bird stepped off the central platform into an arm

366 they had already depleted the reward from) and a trial continued until a bird found all the mealworm

367 rewards, at which point it was released into the outdoor enclosure. All birds received a total of 12

368 trials. A perfect performance would see a bird visiting and depleting each location just once, with no

369 visits to previously visited locations.

370

371 *Cognitive performance analyses*

372 We quantified an individual's learning performance in the radial arm and complex maze tasks by

373 using the slope that describes their reduction in numbers of errors across trials, and for the colour

374 discrimination task by using the slope that describes the number of correct choices out of the 10 trials

375 across the eight sessions. For the colour discrimination task, we obtained the slope from running a

376 Poisson regression between the number of correct choices out of the 10 trials across the eight sessions

377 of the task. For the complex maze and radial arm maze tasks, we fitted a linear relationship to the

378 pattern of errors across the 8 and 12 trials respectively. We derived the equation for the relationship

379 and used the coefficient slope value. Steeper negative slopes for the radial arm and complex mazes,

380 and steeper positive slopes for the colour discrimination task, indicate that their learning of the task

381 was faster (although these are inversed in our figures to aid interpretation; Fig. 1D and Fig. 2C).

382 We only included birds that had completed at least eight of the ten trials in the radial arm maze and

383 colour discrimination tasks, and seven of the eight trials in the complex maze for further analysis.

384 Different birds reached criterion on different tests, which is why sample sizes for relationships with

385 particular tests vary, and also why not all birds that contributed death location data also contributed

386 spatial ability data (and vice-versa if birds did not establish a stable home range; see below). None of

387 our cognitive variables were significantly correlated (linear model (lm) of spatial reference memory

388 predicted by spatial reference memory: -0.01 ± 0.26 (coefficient $\pm$ standard error), $F_{1,42} = <0.01$,

389 P=0.999; lm of spatial reference memory predicted by colour discrimination: -0.08 ± 3.91 (coefficient

390 $\pm$ standard error), $F_{1,31}=<0.01$, P=0.983; lm of spatial working memory predicted by colour

391 discrimination: 2.66 ± 2.18 (coefficient $\pm$ standard error), $F_{1,31}=1.49$, P=0.232.

392

393 *Release into the wild and ATLAS system*

394 All birds were allowed to naturally disperse into the wild by being first released into an outdoor

395 release pen (~4000 m^2 in area) within woodland at North Wyke Farm, North Wyke, UK, once they

396 reached ten weeks old. Before release, they were fitted with radio tags, sexed, and their mass was

397 recorded. Within the pen, birds could enter and leave as necessary by flying or via a system of wire

398 tunnels that were too small to admit terrestrial predators. We provided birds with supplementary food

399 supplied in 43 artificial feeders situated inside and within 2 km of the release pen (see Fig. 2A for

400 map of the release site). To ensure the attached radio tags had no adverse effects, tagged birds were

401 monitored in captivity for seven days before being released. Specifically, we monitored behavioural

402 (lethargy, isolation) and physiological (breathing, vocalisation) indicators of welfare as well as

403 visually monitoring the pheasants for sites on the body that could be susceptible to abrasion. We

404 tracked birds using a recently developed reverse-GPS system (ATLAS) [60,61,63]. This system uses

405 fixed-position receiver stations to detect and collect the time of arrival data from tag-derived radio-

406   signals. These data are then collated at a database on a central server where location is calculated.

407   Location data, accurate to ~4-6m relative to GPS measurements [63], can be accessed in real-time

408   through an internet connection which allows for continuous monitoring.

409

410   *Determination of death locations*

411   Because the major predator of pheasants in our field sites, red foxes (*Vulpes vulpes*), will frequently

412   transport their captured prey before eating or caching them, we combined three methods to determine

413   the exact death location of each of our predated pheasants. Firstly, we ran an observational study

414   using ATLAS-tagged fresh pheasant carcasses to determine the range of movement patterns displayed

415   by predators carrying a dead pheasant (details of experiment below). Secondly, informed by the

416   filtered movement tracks of scavenged dead pheasants, we visually assessed movement patterns of

417   our live birds to subjectively determine putative kill sites where the bird's movement path underwent

418   an unusual substantial change (e.g. when the bird rapidly covered a large distance in an

419   uncharacteristically straight line before suddenly stopping) and matched those displayed by the

420   movement patterns of scavenged carcasses. Thirdly, we confirmed our putative kill sites by running a

421   state change analysis on the tracked paths of each predated bird to determine whether locations that

422   immediately preceded a substantial change in movement highlighted by our subjective assessment

423   matched those determined using our state change analysis. Specifically, we used the segmentation

424   approach by Lavielle[77], where segment numbers (allowing us to identify change-points) were

425   identified based on graphically examining the relationship between segment number and the

426   decreasing contrast function, produced using the '*lavielle*' function in the '*adehabitatLT*' R package

427   (version 0.3.25)[78].

428   In our carcass tracking study, we placed 44 carcasses of ATLAS tagged adult pheasants (22 male and

429   22 female) on 5th February 2019 in locations around the field site frequented by our live tracked birds.

430   Two camera traps (Bushnell Trophy) were setup at each location to identify the predator that moved

431   the carcass. After eight days (once all carcasses had been moved), we then located carcasses based on

432   their ATLAS coordinates. Camera trap footage confirmed that all carcasses moved from the

433   introduction site were caused by red foxes. ATLAS coordinates for each bird were then filtered using

434   the same method for our real birds, and the resulting movement patterns were used to help denote

435   death locations as described above.

436   In all instances of predation from our main release experiment, the paths of live birds that were

437   predated were typified by regular movement patterns before a sudden and uncharacteristically long-

438   distance and rapid movement in a straight line before immediately becoming stationary. This rapid,

439   single straight-line movement was recorded for all red fox scavenging instances we recorded in the

440   carcass tracking study above, representing a fox moving its prey a long distance from the site it was

441   captured to a new location to process and cache. This first 'stop' location was usually the spot where

442   we recovered the predated bird via radio tracking, and the location immediately preceding the first

443   long-distance movement (i.e. the last point of normal pheasant movement) was denoted as the

444   location the bird was predated. We confirmed the species of predator using field signs around

445   carcasses such as whether the carcass was buried, teeth marks on the radio-tags, and feather remains

446   (e.g. characteristic field signs of a fox kill are large wing and tail feathers cleanly severed close to the

447   base of the feather shaft, whereas raptors pluck feathers by grasping the feather further up the shaft,

448   leaving a characteristic V-shaped kink). All the birds killed outside their pens in this study were

449   predated by red foxes.

450

451   *Location data filtering*

452   All ATLAS coordinates were first filtered to increase the accuracy of locations used to calculate the

453   home ranges. We first removed all coordinates where the variance in signal strength between base

454   stations was greater than 75%. Each day was then split into five-minute blocks, and the median

455   location during each five-minute block was calculated (so that every bird in the study had one location

456   assigned within the same time periods within each day). This filtering process excluded anomalous

457   locations caused by standard issues with radiotracking such as reflection [79,80]. Because the release

458   pens which birds were kept in before dispersing effectively excluded foxes, we only included the

459   coordinates of birds that were outside the pen in our home range estimations.

460

461   *Home range estimation*

462   To estimate home ranges of each pheasant we fitted a continuous-time stochastic movement model

463   (ctmm) followed by AIC-based model selection to calculate autocorrelated kernel density estimates

464   (AKDEs) for each of our birds using the *ctmm* package [64] in R (version 3.5.3) [81]. Parameters for our

465   ctmms were chosen based on visually assessing variograms of time-series movement patterns for each

466   individual bird. The variograms also allowed us to identify and discard from the analysis a further 39

467   birds who had not formed a stable home range because of either predation or death soon after release,

468   tracker malfunction, or because they quickly dispersed from the study site. Core home ranges were

469   estimated as the 85% AKDE isopleth based on the mean point of asymptote between the home range

470   size and AKDE isopleth, indicating the region within which birds were concentrating their movement

471   patterns [11]. To determine the region of the home range where birds were killed, we then calculated the

472   minimum AKDE isopleth that encompassed the coordinates of the bird's predation location.

473

474   *Do pheasants avoid high-risk areas?*

475   One explanation for why pheasants are killed more frequently on the outskirts of their home range is

476   because they avoid riskier areas - death locations on the home range periphery may simply reflect

477   cases where pheasants ventured into high-risk areas instead of occurring due to a lack of intrinsic

478   knowledge about local predation risk. To test whether our mortality patterns could therefore be driven

479   by birds avoiding areas of high risk, we quantified the home ranges of non-predated pheasants and

480   determined the proportion of their core home range (85% AKDE) that overlapped with a kernel

481   density estimate (80% kernel estimate with no autocorrelated time estimate) created from the death

482   locations of our predated birds. The 80% kernel density estimate from the actual death locations was

483   chosen as a suitable 'high risk zone' as it represented the start of the plateau between the kernel

484   density percentage and size (surface area) of the home range, thus representing an area of

485   concentrated predation risk.

487   To determine whether the home range-risk area overlap differed from what we would expect by

488   chance, based on the null hypothesis that pheasants can be predated with equal probability at any

489   previously visited location within their home range, we compared the overlaps of our real birds to

490   5000 simulated high-risk zones. Each simulated high-risk zone was created by selecting a single

491   relocation coordinate (randomly selected from any of the coordinates recorded during a bird's

492   lifetime) from each of our predated birds and using this as a simulated predation location, before re-

493   calculating a new high-risk zone and subsequently calculating how much this overlapped with the real

494   core home range of the surviving birds. Only those surviving birds that overlapped with some part of

495   the home range of at least one of the predated birds were included in this analysis. The proportion of

496   randomised survivor-predation home range overlaps that were lower or higher than the real survivor-

497   predation home range overlaps was used as our two-tailed statistical significance value (Extended

498   Data Figure 2).

500   In addition to the above, we also ran an analysis to determine whether the AKDE isopleth containing

501   a death location was higher in the bird that actually died compared to the same death location of a

502   neighbouring bird that did not die. This is directly testing whether the actual death location itself was

503   avoided at a more fine-scale level than can be determined by comparing home range overlaps with

504   regions of high risk. We therefore calculated the minimum AKDE isopleth that contained a death

505   location for birds that were killed and birds that were not recorded as being killed (surviving birds;

506   n=67). Surviving birds were only included if the 100% minimum convex polygon of their home range

507   encompassed the death location of the killed bird (to avoid including birds that never encountered the

508   death location). We then compared the distribution of minimum isopleths that contained death

509 locations between killed and surviving birds using a Kolmogorov-Smirnov test (Extended Data Figure

510 2).

511

512 *Statistical analysis*

513 To determine the drivers of home range variation, we ran linear models (LMs) with core and

514 peripheral home range size in hectares of the eventual stable home range of each pheasant as the

515 response variables. We define the peripheral home range as the area covered by the core (85% kernel

516 isopleth) subtracted from the area of the total (99% kernel isopleth) home range. We used this

517 measure rather than the 99% kernel to detect any effects of total home range size exclusive of the role

518 played by the underlying core home range (which is of course a composite of the total home range).

519 Both core home range size and peripheral home range size were strongly left skewed and so were log-

520 transformed to obtain normally-distributed residuals from our models. To test the effect of different

521 cognitive modalities on these home range parameters we created a model to test performance in the

522 colour discrimination task, and a model that tested for the role of performance in both the spatial

523 cognition tasks, across both of the response variables detailed above. To be included in any analysis,

524 pheasants of course had to reach criterion in the relative cognitive tests (two tests in the case of the

525 spatial analyses), as well as form a stable home range before dying/suffering a transmitter

526 malfunction/dispersing out of the field site. For the survival analysis, we also only include birds

527 where the known cause of death was predation (as determined from above), or to include birds that

528 'survived', we only included their location data up to the point that they were still moving freely and

529 were producing high-accuracy data (i.e. hadn't dispersed outside of the range of the ATLAS

530 receivers). As such, there was rather extensive data loss from our original 126 birds (see specific

531 numbers in each statistical section below).

532

533 In the spatial cognition models, performance in the radial arm maze and complex maze were included

534 as main effects to test for the general hypothesis that spatial reference memory is important in the

21

535   development and utilisation of a home range (e.g. [25,26]), as well as in a two-way interaction to

536   explicitly test the hypothesis that home range development and size arise and vary due to the

537   synergistic effect of working and reference memory [21]. To control for the amount of time that a bird

538   could familiarise itself with the landscape, we also included a bird's lifespan (in days) as a covariate

539   in all models. In addition, pheasants show sex differences in home range size, with females having

540   larger home ranges than males when the latter become territorial during the breeding season (although

541   our study did not encompass this period), and so we therefore include sex in our models as a fixed

542   term [82,83]. Our code syntax for the structure of our starting maximal model for the core home range

543   spatial analysis (n=44) was therefore: '*lm(log(Core_HR_hr) ~ Slope_LM * Slope_RAM + Sex +*

544   *Lifespan, data= akde_data_main)*', and we returned support for a single model in our model selection

545   procedure (Table S1). To test whether body mass is a confound in this analysis (since home range is

546   known to scale with body mass at the intraspecific level in some species [84], although see [36]), we also

547   ran a final model that included only lifespan and mass as predictors. Model comparison using AICc

548   (154.1 for the reference memory model and 156.3 for the mass model) confirmed that mass is not a

549   confound. We intentionally excluded mass in our starting model to avoid issues with collinearity since

550   it is strongly correlated with sex (female mass: 575g ± 65; male mass: 717g ± 100 (mean ± standard

551   deviation); t-test: $t = -5.65$, $df = 37.2$, $P<0.001$).

552

553   Our code syntax for the structure of the starting maximal model for the peripheral home range spatial

554   analysis (n=44) was: '*lm(log(Peripheral_HR_H) ~ Slope_LM * Slope_RAM + Sex + Lifespan, data=*

555   *akde_data_main)*'. Our model selection procedure produced two minimum adequate models (Table

556   S4). As with the core home range model above, we also tested for any confounding effect of mass by

557   comparing our two final model AICcs with a model that only contained mass and lifespan as

558   predictors, confirming again that it is not a confound.

559

560   For the associative learning analyses based on the colour discrimination task, we included sex, colour

561   discrimination performance and lifespan as the fixed effects. The syntax for our starting maximal

562   model for the core home range colour discrimination analysis (n=55) was therefore:

563   '*lm(log(core_HR_hr) ~ CD_Slope + Sex + Lifespan, data = akde_CD)*', returning a single model

564   with only sex and lifespan as covariates. The syntax for our starting maximal model for the peripheral

565   home range colour discrimination analysis (n=55) was: '*lm(log(Peripheral_HR_hr) ~ CD_Slope +*

566   *Sex + Lifespan, data = akde_CD)*'. This produced three separate minimum adequate models (Table

567   S5).

568

569   A central question in this study was to test whether animals were more likely to be predated on the

570   outskirts of their home range, in areas they were less familiar. However, the null expectation of where

571   predation locations should occur across a home range density estimate such as AKDE are unclear. As

572   such, we took a simulation approach, comparing the AKDE isopleth that a real death occurred on to a

573   null distribution of 'simulated death isopleths', where every location a bird was recorded was

574   assigned as a simulated death location and the accompanying minimum AKDE isopleth that

575   encompassed it. To calculate our total P value for each bird, we then calculated the proportion of

576   simulated death isopleths that were higher or lower than the observed death isopleth, and tested for

577   overall significance of all birds by combining the P values using Fisher's combination (omnibus) test

578   [85].

579

580   We also ran two binomial regression analyses investigating whether cognitive ability predicted the

581   proportion of a pheasant's core home range that overlapped with the region of high predation risk. We

582   again separated spatial memory and associative learning into separate models to maximise our sample

583   sizes and statistical power, using a conditional log-link function in our models to control for the

584   unequal distribution of our proportion data. We controlled for the size of the core home range in

585   driving these patterns by including this variable as a covariate in all models. The syntax for our

586   maximal starting model for spatial memory (n=29) was: '*glm(HR_death_overlap_prop ~ Slope_LM **

587   *Slope_RAM + core_HR + Sex, family= binomial(link= "cloglog"), data=*

588   *akde_cognition_HR_overlap)*' and for associative learning (n=29): '*glm(HR_death_overlap_prop ~*

589   *core_HR + CD_Slope + Sex, family= binomial, data= HR_overlap_CD)*'. We identified three

590   candidate models for the spatial memory analysis and a single model for associative learning (Table

591   S7 and Table S8).

592

593   To determine how spatial cognitive performance and home range size affected a pheasant's

594   probability of being predated, we ran three Cox-proportional hazards models to determine the effect

595   on lifespan and general probability of death. In the first survival model we included performance in

596   the complex and radial arm maze tasks as covariates, sex, and the size of the core home range

597   (hectares) as predictors. We also directly test whether an interaction between working and reference

598   spatial memory are important for the ultimate consequences of forming a home range, as suggested by

599   mechanistic models (e.g. [21]) by including an interaction between performance in our complex maze

600   and in our radial arm maze tasks. We also included sex within a three-way interaction that also

601   includes working and reference memory. Our model syntax for this starting model (n=51) was

602   therefore: *coxph(Surv(Lifespan, State_bin) ~ Sex + Slope_LM*Slope_RAM, data=spatial_data)*. Our

603   AICc based model selection returned support for a single model (Table S11). As with our home range

604   models, we also investigated whether body size was a confound by adding it to our final model

605   (where sex and was not included and could therefore not cause any collinearity issues).

606

607   To test for the importance of associative learning performance on survival, our second model included

608   performance in the colour discrimination task, sex, and tarsus size, with a single two-way interaction

609   between colour discrimination and sex. Our syntax for this starting model (n=61) was therefore:

610   *coxph(Surv(Lifespan, State_bin) ~ CD_Slope*Sex+Tarsus, data=CD_data)*). Our AICc based model

611   selection returned support for a single, intercept-only model (Table S12). Because different birds did

612 not reach criterion in the different cognitive tests and were thus removed (see above), we also ran a

613 third survival model that included all birds for which we had stable home range sizes to maximise

614 statistical power (resulting in n=68) to test if core home range size itself, independent of cognitive

615 variables, affected survival. In this model, we included three predictors: core home range size in

616 hectares, sex, and a two-way interaction between these variables. Our model syntax for this starting

617 model (n=68) was therefore: *coxph(formula = Surv(Lifespan, State_bin) ~ core_HR_H*Sex, data =*

618 *HR_surv_data)*, and our our AICc based model selection returned support for a single model with

619 core home range size as the sole term (see main text).

620

621 Diagnostics were performed on all models to check they met assumptions. We used a stepwise AICc

622 (AIC corrected for small sample size) model selection approach to find our best models. Specifically,

623 after constructing our starting model that allowed us to test our most complex hypotheses, we

624 performed a stepwise simplification procedure based on the "AICc" function from the R package

625 'MuMin' [86] to compare nested models until a best set of plausible models were obtained (minimum

626 adequate models), where models with ΔAICc ≤ 2 were deemed more plausible. If this process created

627 more than a single best model, we used the *model.avg* function in the 'MuMin' package to average

628 the model estimates and standard errors. In addition, we present P values, uncorrected for multiple

629 testing (as per [87]) for each of our best models in the supplementary material, which were obtained

630 using likelihood-ratio tests for change in deviance between nested models with and without the term

631 of interest.

632

633 All animal work in this study was conducted under Home Office license PPL 30/3204 and approved

634 by the University of Exeter Animal Welfare Ethical Review Board.

635

636 **Data availability**

637 Data required to rerun the statistical analyses of this study are available online

638 (https://data.mendeley.com/datasets/m89226xg6p)[88]. Animal AKDE models and GPS coordinates are

639 available from the corresponding author upon request.

640

641 **Code availability**

642 R code used to run the simulation analyses of this study are available online

643 (https://data.mendeley.com/datasets/m89226xg6p)[88].

644

645 **Acknowledgements**

654

655 **Author contributions**

656 RJPH and JRM conceived the idea for the manuscript. CEB, PRL, MAW, JOvH and JRM collected

657 the cognition data. MAW, CEB and JRM collected the movement data. RJPH and MAW carried out

658 the carcass tracking study. RJPH conducted the analyses and led the writing. RN, YO and ST

659 developed the reverse-GPS system and provided support throughout data collection. All authors

660 contributed critically to the drafts.

661

Competing interests

663   The authors declare that they have no competing interests

664

665

Figure legends

Fig. 1. Cognitive predictors of home range size in pheasants. A: The complex maze task (A) radial arm maze task (B) and colour discrimination tasks (C) used to assess spatial memory (A & B) and associative learning (C), respectively, in juvenile pheasants. D: Performance in the complex maze task positively predicted the size of the core home range in pheasants. Error bars denote the 95% CI. X-axis in D represents the inverted coefficients taken from a regression between number of trial errors over time for ease of interpretation, i.e. a positive slope equals increased learning rates.

 Fig. 2. Spatial patterns of pheasant mortality and consequences for selection on spatial memory and home range. A. Map of the release site showing an example pheasant home range showing 85% (dark blue) and 99% (pale blue) kernel estimates in relation to where a bird was predated (red dot). B. Histograms showing the percentage kernel isopleths that contained the observed death locations (left) compared to the kernel isopleths that contained simulated death locations (right) taken from the same killed individuals. C. Mortality risk from predators depends on the interaction between working and reference memory. Complex maze and radial arm maze performance measures represent inverted coefficients taken from a regression between trial errors over time for ease of interpretation. D. Predation risk in pheasants is predicted by core home range size. Error bars denote the 95% CI. Map layer Imagery ©2022 Google Maps, CNES / Airbus, Getmapping pic, Infoterra Ltd & Bluesky, Maxar Technologies, Map data @2022.

References

1. Börger, L., Dalziel, B. D. & Fryxell, J. M. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters* **11**, 637–650 (2008).

692 2. Burt, W. H. Territoriality and Home Range Concepts as Applied to Mammals. *Journal of*

693   *Mammalogy* **24**, 346 (1943).

694 3. Darwin, C. *On the Origin of Species by Means of Natural Selection*. *D. Appleton and*

695   *Company* (1859). doi:10.1007/s11664-006-0098-9.

696 4. Merkle, J., Fortin, D. & Morales, J. M. A memory-based foraging tactic reveals an

697   adaptive mechanism for restricted space use. *Ecology letters* **17**, 924–931 (2014).

698 5. Bordes, F., Morand, S., Kelt, D. A. & Van Vuren, D. H. Home range and parasite diversity

699   in mammals. *American Naturalist* **173**, 467–474 (2009).

700 6. Morales, J. M. *et al.* Building the bridge between animal movement and population

701   dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**,

702   2289–2301 (2010).

703 7. Lewis, M. A. & Murray, J. D. Modelling territoriality and wolf-deer interactions. *Nature*

704   **366**, 738–740 (1993).

705 8. Kelt, D. A. & Van Vuren, D. H. The ecology and macroecology of mammalian home range

706   area. *American Naturalist* **157**, 637–645 (2001).

707 9. Wang, M. & Grimm, V. Home range dynamics and population regulation: An individual-

708   based model of the common shrew Sorex araneus. *Ecological Modelling* **205**, 397–409

709   (2007).

710 10. Moorcroft, P. R., Lewis, M. A. & Crabtree, R. L. Mechanistic home range models capture

711   spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the*

712   *Royal Society B: Biological Sciences* **273**, 1651–1659 (2006).

713 11. Powell, R. A. Animal Home Ranges and Territories and Home Range Estimators. in

714   *Research Techniques in Animal Ecology* (eds. Boitani, L. & Fuller, T. K.) vol. 65 599

715   (Columbia University Press, 2000).

716   12. Spencer, W. D. Home ranges and the value of spatial information. *Journal of*

717   *Mammalogy* **93**, 929–947 (2012).

718   13. Bracis, C., Gurarie, E., Van Moorter, B. & Goodwin, R. A. Memory effects on movement

719   behavior in animal foraging. *PLoS ONE* **10**, e0136057 (2015).

720   14. Fagan, W. F. *et al.* Spatial memory and animal movement. *Ecology Letters* **16**, 1316–

721   1329 (2013).

722   15. Powell, R. A. & Mitchell, M. S. What is a home range? *Journal of Mammalogy* **93**, 948–

723   958 (2012).

724   16. Stamps, J. Motor learning and the value of familiar space. *American Naturalist* **146**, 41–

725   58 (1995).

726   17. Gautestad, A. O. & Mysterud, I. Spatial memory, habitat auto-facilitation and the

727   emergence of fractal home range patterns. *Ecological Modelling* **221**, 2741–2750 (2010).

728   18. Gautestad, A. O. & Mysterud, I. Intrinsic scaling complexity in animal dispersion and

729   abundance. *American Naturalist* **165**, 44–55 (2005).

730   19. Merkle, J. A., Potts, J. R. & Fortin, D. Energy benefits and emergent space use patterns of

731   an empirically parameterized model of memory-based patch selection. *Oikos* **126**,

732   (2017).

733   20. Schlägel, U. E. & Lewis, M. A. Detecting effects of spatial memory and dynamic

734   information on animal movement decisions. *Methods in Ecology and Evolution* **5**, 1236–

735   1246 (2014).

736   21. Van Moorter, B. *et al.* Memory keeps you at home: A mechanistic model for home range

737   emergence. *Oikos* **118**, 641–652 (2009).

738   22. Riotte-Lambert, L., Benhamou, S. & Chamaillé-Jammes, S. How memory-based

739   movement leads to nonterritorial spatial segregation. *The American Naturalist* **185**,

740   E103–E116 (2015).

741   23. Marchand, P. *et al.* Combining familiarity and landscape features helps break down the

742   barriers between movements and home ranges in a non-territorial large herbivore.

743   *Journal of Animal Ecology* **86**, 371–383 (2017).

744   24. Gautestad, A. O., Loe, L. E. & Mysterud, A. Inferring spatial memory and spatiotemporal

745   scaling from GPS data: comparing red deer Cervus elaphus movements with simulation

746   models. *Journal of animal Ecology* **82**, 572–586 (2013).

747   25. Ranc, N., Cagnacci, F. & Moorcroft, P. R. Memory drives the formation of animal home

748   ranges: evidence from a reintroduction. *Ecology Letters* **25**, 716–728 (2022).

749   26. Ranc, N., Moorcroft, P. R., Ossi, F. & Cagnacci, F. Experimental evidence of memory-

750   based foraging decisions in a large wild mammal. *Proc Natl Acad Sci USA* **118**,

751   e2014856118 (2021).

752   27. Potts, J. R. & Lewis, M. A. A mathematical approach to territorial pattern formation. *The*

753   *American Mathematical Monthly* **121**, 754–770 (2014).

754   28. Shettleworth, S. J. *Cognition, evolution, and behavior*. (Oxford University Press UK,

755   2009).

756   29. van Asselen, M. *et al.* Brain areas involved in spatial working memory. *Neuropsychologia*

757   **44**, 1185–1194 (2006).

758   30. Paul, C., Magda, G. & Abel, S. Spatial memory: Theoretical basis and comparative review

759   on experimental methods in rodents. *BEHAVIOURAL BRAIN RESEARCH* **203**, 151–164

760   (2009).

761   31. Boratyński, Z. Energetic constraints on mammalian home-range size. *Functional Ecology*

762   **34**, 468–474 (2020).

763   32. Tamburello, N., Côté, I. M. & Dulvy, N. K. Energy and the Scaling of Animal Space Use.

764   *The American Naturalist* **186**, 196–211 (2015).

765   33. McNab, B. K. Bioenergetics and the Determination of Home Range Size. *The American*

766   *Naturalist* **97**, 133–140 (1963).

767   34. McNab, B. K. Food habits, energetics, and the population biology of mammals. *The*

768   *American Naturalist* **116**, 106–124 (1980).

769   35. Fokidis, H. B., Risch, T. S. & Glenn, T. C. Reproductive and resource benefits to large

770   female body size in a mammal with female-biased sexual size dimorphism. *Animal*

771   *Behaviour* **73**, 479–488 (2007).

772   36. Saïd, S. *et al.* What shapes intra-specific variation in home range size? A case study of

773   female roe deer. *Oikos* **118**, 1299–1306 (2009).

774   37. Schradin, C. *et al.* Female home range size is regulated by resource distribution and

775   intraspecific competition: a long-term field study. *Animal Behaviour* **79**, 195–203 (2010).

776   38. Dröge, E., Creel, S., Becker, M. S. & M'soka, J. Risky times and risky places interact to

777   affect prey behaviour. *Nature Ecology & Evolution* **1**, 1123–1128 (2017).

778   39. Croston, R., Branch, C., Kozlovsky, D., Dukas, R. & Pravosudov, V. Heritability and the

779   evolution of cognitive traits. *Behavioral Ecology* **26**, 1447–1459 (2015).

780   40. Ashton, B. J., Ridley, A. R., Edwards, E. K. & Thornton, A. Cognitive performance is linked

781   to group size and affects fitness in Australian magpies. *Nature* **554**, 364–367 (2018).

782   41. Madden, J. R., Langley, E. J. G., Whiteside, M. A., Beardsworth, C. E. & Van Horik, J. O.

783   The quick are the dead: Pheasants that are slow to reverse a learned association survive

784 for longer in the wild. *Philosophical Transactions of the Royal Society B: Biological*

785 *Sciences* **373**, (2018).

786 42. Sonnenberg, B. R., Branch, C. L., Pitera, A. M., Bridge, E. & Pravosudov, V. V. Natural

787 selection and spatial cognition in wild food-caching mountain chickadees. *Current*

788 *Biology* **29**, 670–676 (2019).

789 43. Shaw, R. C., MacKinlay, R. D., Clayton, N. S. & Burns, K. C. Memory Performance

790 Influences Male Reproductive Success in a Wild Bird. *Current Biology* **29**, 1498-1502.e3

791 (2019).

792 44. Gehr, B. *et al.* Stay home, stay safe—Site familiarity reduces predation risk in a large

793 herbivore in two contrasting study sites. *Journal of Animal Ecology* **89**, 1329–1339

794 (2020).

795 45. Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M. & Packer, C. A 'dynamic' landscape

796 of fear: prey responses to spatiotemporal variations in predation risk across the lunar

797 cycle. *Ecology Letters* **20**, 1364–1373 (2017).

798 46. Willems, E. P. & Hill, R. A. Predator-specific landscapes of fear and resource distribution:

799 effects on spatial range use. *Ecology* **90**, 546–555 (2009).

800 47. Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. & Brashares, J. S. Landscapes

801 of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology and*

802 *Evolution* **34**, 355–368 (2019).

803 48. Bose, S. *et al.* Implications of fidelity and philopatry for the population structure of

804 female black-tailed deer. *Behavioral Ecology* **28**, 983–990 (2017).

805 49. Forrester, T. D., Casady, D. S. & Wittmer, H. U. Home sweet home: fitness consequences

806 of site familiarity in female black-tailed deer. *Behavioral Ecology and Sociobiology* **69**,

807 603–612 (2015).

808   50. Magrath, R. D., Haff, T. M., Fallow, P. M. & Radford, A. N. Eavesdropping on

809   heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews* **90**,

810   560–586 (2015).

811   51. Skelhorn, J. & Rowe, C. Cognition and the evolution of camouflage. *Proceedings of the*

812   *Royal Society B: Biological Sciences* **283**, 20152890 (2016).

813   52. Dickinson, A. Associative learning and animal cognition. *Philosophical Transactions of*

814   *the Royal Society B: Biological Sciences* **367**, 2733–2742 (2012).

815   53. Baddeley, A. D. & Lieberman, K. Spatial working memory. in *Exploring working memory*

816   206–223 (Routledge, 2017).

817   54. Olton, D. S. & Samuelson, R. J. Remembrance of places passed: Spatial memory in rats.

818   *Journal of Experimental Psychology: Animal Behavior Processes* **2**, 97–116 (1976).

819   55. Lashley, K. S. *Brain mechanisms and intelligence: A quantitative study of injuries to the*

820   *brain.* (University of Chicago Press, 1929).

821   56. O'keefe, J. & Nadel, L. *The hippocampus as a cognitive map*. (Oxford university press,

822   1978).

823   57. Beardsworth, C. E. *et al.* Is habitat selection in the wild shaped by individual-level

824   cognitive biases in orientation strategy? *Ecology Letters* **24**, 751–760 (2021).

825   58. Rowe, C. & Healy, S. D. Measuring variation in cognition. *Behavioral Ecology* **25**, 1287–

826   1292 (2014).

827   59. Warner, R. E. Use of cover by pheasant broods in east-central Illinois. *The Journal of*

828   *Wildlife Management* **43**, 334 (1979).

829   60. Toledo, S. *et al.* Cognitive map-based navigation in wild bats revealed by a new high-

830   throughput tracking system. *Science (New York, N.Y.)* **369**, 188–193 (2020).

831   61. Weiser, A. W. *et al.* Characterizing the Accuracy of a Self-Synchronized Reverse-GPS

832   Wildlife Localization System. in *2016 15th ACM/IEEE International Conference on*

833   *Information Processing in Sensor Networks, IPSN 2016 - Proceedings* 1–12 (IEEE, 2016).

834   doi:10.1109/IPSN.2016.7460662.

835   62. Nathan, R. *et al.* Big-data approaches lead to an increased understanding of the ecology

836   of animal movement. *Science* **375**, eabg1780 (2022).

837   63. Beardsworth, C. E. *et al.* Validating ATLAS: A regional-scale high-throughput tracking

838   system. *Methods in Ecology and Evolution* **13**, 1990–2004 (2022).

839   64. Calabrese, J. M., Fleming, C. H. & Gurarie, E. ctmm: an r package for analyzing animal

840   relocation data as a continuous-time stochastic process. *Methods in Ecology and*

841   *Evolution* **7**, 1124–1132 (2016).

842   65. Van Moorter, B. *et al.* Memory keeps you at home: A mechanistic model for home range

843   emergence. *Oikos* **118**, 641–652 (2009).

844   66. Clutton-Brock, T. H. & Harvey, P. H. Primates, brains and ecology. *Journal of Zoology*

845   **190**, 309–323 (1980).

846   67. Avgar, T. *et al.* Space-use behaviour of woodland caribou based on a cognitive

847   movement model. *Journal of Animal Ecology* **84**, 1059–1070 (2015).

848   68. Laundré, J. W., Hernández, L. & Ripple, W. J. The landscape of fear: ecological

849   implications of being afraid. *Open Ecology Journal* **3**, 1–7 (2010).

850   69. Stephens, D. W. & Krebs, J. R. *Foraging theory*. (Princeton University Press, 2019).

851   70. Beauchamp, G. *Animal Vigilance: Monitoring Predators and Competitors*. *Animal*

852   *Vigilance: Monitoring Predators and Competitors* (2015). doi:10.1016/C2014-0-01423-2.

853   71. Langley, E. J. G. *et al.* Heritability and correlations among learning and inhibitory control

854   traits. *Behavioral Ecology* **31**, 798–806 (2020).

855   72. Chen, J., Zou, Y., Sun, Y.-H. & Ten Cate, C. Problem-solving males become more

856   attractive to female budgerigars. *Science* **363**, 166–167 (2019).

857   73. Vale, R., Evans, D. A. & Branco, T. Rapid spatial learning controls instinctive defensive

858   behavior in mice. *Current Biology* **27**, 1342–1349 (2017).

859   74. Burt de Perera, T. & Guilford, T. Rapid learning of shelter position in an intertidal fish,

860   the shanny Lipophrys pholis L. *Journal of Fish biology* **72**, 1386–1392 (2008).

861   75. Font, E. Rapid learning of a spatial memory task in a lacertid lizard (Podarcis liolepis).

862   *Behavioural Processes* **169**, 103963 (2019).

863   76. Senar, J. & Pascual, J. Keel and tarsus length may provide a good predictor of avian body

864   size. *ARDEA-WAGENINGEN-* **85**, 269–274 (1997).

865   77. Lavielle, M. Detection of multiple changes in a sequence of dependent variables.

866   *Stochastic Processes and their applications* **83**, 79–102 (1999).

867   78. Calenge, C. The package "adehabitat" for the R software: a tool for the analysis of space

868   and habitat use by animals. *Ecological modelling* **197**, 516–519 (2006).

869   79. Millspaugh, J. J. *A Manual for Wildlife Radio Tagging Robert E. Kenward. The Auk* vol.

870   118 (Academic press, 2001).

871   80. Gupte, P. R. *et al.* A Guide to Pre-Processing High-Throughput Animal Tracking Data 1

872   Introduction. *bioRxiv* 1–27 (2020).

873   81. R Development Core Team. R: A language and environment for statistical computing.

874   *Vienna, Austria* Preprint at https://doi.org/R Foundation for Statistical Computing,

875   Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org. (2018).

876   82. Grahn, M., Göransson, G. & Von Schantz, T. Territory acquisition and mating success in

877   pheasants, Phasianus colchicus: An experiment. *Animal Behaviour* **46**, 721–730 (1993).

878   83. RIDLEY, M. W. & HILL, D. A. Social organization in the pheasant (Phasianus colchicus):

879   harem formation, mate selection and the role of mate guarding. *Journal of Zoology* **211**,

880   619–630 (1987).

881   84. Gompper, M. E. & Gittleman, J. L. Home range scaling: intraspecific and comparative

882   trends. *Oecologia* **87**, 343–348 (1991).

883   85. Fisher, R. A. Statistical methods for research workers. in *Breakthroughs in statistics* 66–

884   70 (Springer, 1992).

885   86. Barton, Kamil. MuMIn: Multi-Model Inference. (2022).

886   87. Nakagawa, S. A farewell to Bonferroni: The problems of low statistical power and

887   publication bias. *Behavioral Ecology* **15**, 1044–1045 (2004).

888   88. Heathcote, Robert. J. P. Data for 'Spatial memory predicts home range size and

889   predation risk in pheasants' Nature Ecology and Evolution. doi:10.17632/m89226xg6p.1.

890