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1 **Spatial memory predicts home range size and predation risk in pheasants**

2

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20

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22

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 range¹⁻⁴. The patterns and dynamics of animal home ranges have fundamental consequences
44 across biology, from epidemiology^{5,6} to population dynamics and predator-prey interactions⁶⁻⁹, 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 shelter¹¹⁻¹³. Consequently, an

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 risk³⁸. 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 traits³⁹. 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 behaviour⁴⁴, 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 stimuli⁵²), 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 time¹¹; see Methods) calculated from autocorrelated kernel density estimates (AKDEs,
174 which control for temporal autocorrelation in location data⁶⁴) (-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 species⁶⁷).

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: $\chi^2 = 242.61$, $df = 70$,
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 ($89.1\% \pm 22.2$ (mean \pm 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 ($65\% \pm 34\%$ (mean \pm 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 \pm 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 \pm
245 SE); Table S13), although there was no important effect of working memory as a main effect (Cph: -
246 0.45 ± 0.59 (coefficient \pm 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 component⁷¹, 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 \pm 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 predators⁷³⁻⁷⁵, 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*

302 On the 24th May 2018 we hatched 126 pheasant chicks from eggs obtained from commercial breeders
303 (which sell large numbers of pheasant eggs each year) and allocated these approximately equally
304 across four indoor enclosures (each 2m x 2m). Chicks were provided water and fed commercial chick
305 crumbs (Sportsman© Game Feed) *ad libitum*, provided a brooder heat lamp for thermoregulation, and
306 given various perches. At eight days old, we tagged all birds with small patagial wing tags (Roxan
307 Ltd, Selkirk, UK) to allow individual identification. Chicks were given access to a sheltered outdoor
308 enclosure (1.5 x 2.4m) at two weeks old and an outdoor run (4m x 12m) at four weeks old. At 10
309 weeks old, we weighed and measured the tarsus length of all individuals (a common proxy for
310 skeletal body size in birds⁷⁶) before releasing all birds into a large outdoor pen allowing them to
311 disperse into the surrounding rural landscape (mixed farmland and woodland; North Wyke Farm,
312 Okehampton, Devon, UK). Prior to the release of our study birds, all wild pheasants were captured for
313 a captive breeding programme. Pre-release visual surveys, as well as ongoing observations during the
314 study, confirmed that less than 10 wild birds were ever present in the entire field site during the study.

315

316 *Cognitive testing*

317 All cognitive tasks took place within the same 75cm x 75cm testing chamber adjacent to their indoor
318 enclosure. For the first three weeks we trained chicks to enter this chamber via a remotely controlled
319 sliding door using live mealworms as rewards. An additional remotely controlled door with access to
320 the outdoor enclosure enabled us to ensure birds entered and were tested within the testing chamber
321 individually. Trial and session number represent a compromise between maximising the collection of
322 cognitive data that our and previous work has suggested should allow the collection of learning slopes
323 (e.g. ^{57,71}) against the time and logistical constraints of running this multi-stage study.

324

325 *Colour discrimination task*

326 At 25 days old, we tested the chick's associative learning ability on a binary-choice colour
327 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 inverted 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 ($\sim 4000 \text{ m}^2$ 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 measurements⁶³, 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 Lavielle⁷⁷, 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* package⁶⁴ in R (version 3.5.3)⁸¹. Parameters for our
465 ctmmms 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 patterns¹¹. 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.

486

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).

499

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

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 $\Delta\text{AICc} \leq 2$ 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 per⁸⁷) 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

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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

662 **Competing interests**

663 The authors declare that they have no competing interests

664

665

666 **Figure legends**

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

673

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

685

686

687 **References**

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