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Spatial memory predicts home range size and predation risk in pheasants

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Abstract

Most animals confine their activities to a discrete home range, long assumed to reflect the fitness benefits of obtaining spatial knowledge about the landscape. However, few empirical studies have linked spatial memory to home range development, or determined how selection operates on spatial memory via the latter's role in mediating space use. We assayed the cognitive ability of juvenile pheasants (*Phasianus colchicus*) reared under identical conditions before releasing them into a novel landscape and used high-throughput tracking to record their movements as they developed their home ranges, and determine the location, timing and cause of any mortality events. Individuals with greater spatial reference memory developed larger home ranges. Mortality risk from predators was highest at the periphery of an individual's home range, in areas they had less experience and opportunity to obtain spatial information. Importantly, predation risk was lower in individuals with greater spatial memory and larger core home ranges, suggesting selection may operate on spatial memory by increasing the ability to learn about predation risk across the landscape. Our results reveal that spatial memory, determined from abstract cognitive assays, shapes home range development and variation, and suggests predation risk selects for spatial memory via experience-dependent spatial variation in mortality.

Main text

Introduction

Most animals confine the majority of their activities to a relatively restricted spatial region: their home range [1–4]. The patterns and dynamics of animal home ranges have fundamental consequences across biology, from epidemiology [5,6] to population dynamics and predator-prey interactions [6–9], yet surprisingly little work demonstrates the processes by which selection can emerge and shape home range variation. A long-standing explanation for why many animals form home ranges, supported by a wealth of mechanistic modelling studies (e.g. [1,10]), is that it allows a resident to learn the location of, and optimally exploit, patchily distributed resources such as food and shelter [11–13]. Consequently, an animal's ability to learn, retain and update information on the spatial location of resources within its home range is assumed to be of great benefit [12,14], and is a central tenet to many definitions of the home range [15,16]. Decades of work incorporating proxies of resource-based spatial memory into mechanistic random-walk models of home range development results in the emergence of more realistic home ranges, or better statistical power in predicting the development of real animal home ranges, compared to alternative processes such as sensory detection of resources [4,17–27]. Whilst these prior studies have produced convincing conclusions when incorporating artificial analogues of spatial memory, they still require empirical validation in light of the extensive work from comparative and classical psychology demonstrating animals often make use of multiple and distinct cognitive modalities that work synergistically to process different types of information during daily life [28]. Indeed, the few studies that incorporate different types of spatial memory such as 'working memory' (short-term memory of recently visited locations [29]) and 'reference memory' (longer-term memory of landmarks [30]) suggest they work in concert to maximise the efficiency of movement patterns within a home range (e.g. [21,22]), and that working memory itself may be a particularly important determinant of home range size [21]. However, we still lack empirical studies that test the predictions made by these simulation studies to establish the role of cognitive ability (and specifically various types of spatial memory) in real home range formation and size variation.

Whilst a great deal of work has focused on the drivers of interspecific variation in home range size, for instance showing that it scales as a function of body size, metabolic rate and forage type [31] as well as being heavily influenced by locomotion and foraging strategies [32–34], less is known about the causes and consequences of home range size at the intraspecific level, particularly with regards to how these are affected by individual-level variation in different traits. Larger home ranges may infer a range of benefits such as increased access to mates, refuges and resources [35], although the factors constraining size are less well established empirically, particularly in species that do not suffer economic costs of aggressively defending spatially distributed and non-divisible resources [22,36,37]. Spatial memory ability, as a major factor enabling animals to form stable home ranges in the first place, could be a potential mechanistic component limiting home range size. If animals form home ranges to exploit spatial knowledge about important resources or local variation in predation risk, then all else being equal, better spatial memory should translate to animals being able to utilise larger home ranges without suffering associated costs caused by poor knowledge about the landscape such as inefficient travel between resources [21,22] or suboptimal vigilance whilst travelling across regions of varying predation risk [38]. Whilst some biologically-plausible mechanistic models incorporating multiple cognitive modalities have indeed suggested that better spatial memory can translate into the emergence of larger home ranges [21,22], this needs validation from field-based studies of real animals.

Here, we use a unique system in common pheasants (*Phasianus colchicus*) where we can rear large numbers of individuals under standardised conditions, assay them across a battery of cognitive tasks, tag all individuals with high spatial and temporal resolution radio tags, and release them into a novel wild landscape to track their movements as they develop their home ranges. This approach reduces variation in early life environmental effects on subsequent behavioural traits, allowing us to test key predictions about the causes and consequences of movement ecology (although, as with any experimental control, this comes at the potential expense of reducing ecological realism). Specifically, we aimed to test how individual-level variation in three cognitive modalities (associative learning, spatial working memory, and development of a spatial reference memory) obtained from psychometric assays predict variation in the development of home range size.

The degree to which individuals can learn and process spatial information, particularly in relation to resources, should assumedly affect fitness, with potential consequences on selection depending on the heritability of these traits [39]. Indeed, a limited number of studies have uncovered fitness benefits associated with variation in cognitive ability [40,41], and some have suggested that spatially-explicit processes are critical in driving the association [42,43]. Nevertheless, the pathway by which spatial memory and other cognitive modalities drive variation in the movement of individuals, and how this in turn affects how individuals interact with their environment to ultimately generate selection on spatial memory, is still unclear. Whilst most studies addressing the formation and benefits of home ranges have focused on the importance of exploiting patchily distributed resources (or restrictions in movement caused by aggressive defence by territorial neighbours [7,10,27]), another critical factor that shapes natural selection and varies non-randomly across the landscape, is predation. Many predators, particularly ambush hunters, display fine-scale temporal and spatial patterning in their hunting behaviour [44], which prey can potentially learn and mitigate through strategies such as increased vigilance, avoidance of high risk areas, or exploiting memorised escape routes [38,44–47]. As such, there is growing evidence that predation risk may be particularly high in regions that prey are less familiar [44,48,49]. An intuitively appealing, but so far untested, pathway by which selection may operate on spatial memory ability is therefore via variation in predation risk mediated by an individual's familiarity (i.e. degree of prior experience) with high-risk areas as determined by the location and structure of its home range.

The high spatial and temporal resolution of our tracking data allowed us to identify the precise location and timing of predation events during our study (n=45), as well as identify the predator species responsible (all caused by red foxes (*Vulpes vulpes*), an ambush hunter). These death locations were non-randomly distributed across the landscape, constituting regions of high predation risk. By coupling cognition, movement, and predation data, we were therefore able to test whether individuals are more likely to be killed outside their core home range in regions they have less knowledge regarding predation risk, the degree to which this is predicted by different cognitive abilities, and whether this 'experience-dependent' predation risk has the potential to generate selection on cognition and home range variation. A likely consequence of the hypothesised relationship between spatial memory and home range size we detail above is that predation will also be higher in less familiar parts of the landscape (as found previously in deer [44,49]), a phenomenon we predict to be particularly exaggerated in individuals with poor spatial memory since these would be less capable of memorising the locations of non-lethal predator encounters and thus optimising antipredator behaviours across varying regions of predation risk (e.g. [38]). Whilst prior work on the antipredator benefit of different cognitive modalities is scarce, we predict that all three types of cognition we measured can affect predation risk; reference memory for learning landscape features and specific locations associated with regions of high risk; working memory in memorising and exploiting the locations of recently visited refuges and escape routes when predators are encountered; and general associative memory via the learning of non-spatial components associated with predation (e.g. heterospecific alarm calls [50] and search images of camouflaged predators [51]).

We hatched and reared 126 pheasants and assayed their performance on three well-established cognitive tasks between the ages of four and seven weeks old. The first cognitive assay, a binary colour discrimination task, tested the ability of individuals to associate a particular colour with a food reward, a proxy for general associative learning ability (i.e. the ability to learn simple associations between stimuli[52]), and was explicitly designed to not be solved using spatial cues (Fig. 1C). The second, a radial arm maze task, was intended to test an individual's ability to use spatial cues to orient around a maze and optimally exploit multiple food resources as they were depleted, a common paradigm for testing spatial working memory [53] and one that is particularly ecologically relevant to species such as pheasants that feed on patchily-distributed resources (e.g. [54]). The third, a task similar to the classic 'Lashley maze' [55], was intended to test the ability of an individual to learn to navigate through a complex maze ('complex maze task' from hereon; Fig. 1A). Previous studies have shown that the Lashley maze can be solved using allocentric-based visual spatial cues, and/or varying degrees of egocentric-based learned turn sequences when these are absent or insufficient [56]. We have previously shown that pheasants show individual-level variation in their preference for using allocentric and egocentric processes when solving this same complex maze task [57], suggesting that performance in this maze reflects at least some degree of spatial reference memory ability in this species, regardless of navigation strategy deployed. Indeed, whilst multiple cognitive modalities can be used to solve even explicitly domain-targeted tasks (e.g. [58]), we chose these three tasks due to their extensive prior validation from classical cognition testing, their suitability for testing with pheasants, and specifically for their likely relevance to processes important in animal movement ecology [21].

After the completion of their cognitive tests, we simultaneously released the juvenile pheasants into a heterogeneous rural landscape (mixture of agricultural, grassland and woodland habitats) at 10 weeks old (the age wild birds start independence from their mother [59]). We followed their movements and fate using ATLAS, a recently-developed reverse-GPS automated radio-tracking system with high spatial and temporal resolution [60–63], detecting locations at up to eight times per minute, for up to 120 days as birds acquired their home ranges. This design ensured that all birds were equally naïve to a shared landscape, allowing us to test whether the stabilized size of an individual's home range was predicted by their earlier performance in our three cognitive tests (accounting for prior experience; difficult with studies of adult animals but critical when comparing developmental patterns of behaviour between individuals [14]).

Results and Discussion

We found that pheasants exhibiting superior performance in the complex maze task (designed to test navigation-related spatial cognition, including spatial reference memory) subsequently developed larger core home ranges (i.e. the area of the home range that birds spend a disproportionately large amount of time[11]; see Methods) calculated from autocorrelated kernel density estimates (AKDEs, which control for temporal autocorrelation in location data[64]) (-0.52 ± 0.24 (coefficient ± standard error); Fig. 1D; Table S1 and Table S3). This positive relationship provides direct empirical support for the long-standing implicit home range hypothesis suggesting that greater cognitive ability, particularly spatial memory, allows an individual to form a larger core home range [15,65,66]. In contrast, we found no evidence that spatial working memory or associative learning ability predicted core home range size, or that any cognitive metrics predicted the size of the peripheral home range (area of the 85% AKDE isopleth subtracted from the area of the 99% AKDE isopleth; Table S2 – Table S6).

Comparison of our results to two previous mechanistic studies that incorporated multiple spatial memory systems show interesting discrepancies. Studies by both Van Moorter et al, and Riotte-Lambert et al suggest that home range size should strongly covary with working memory, and in the former study, be largely insensitive to variation in reference memory [21,22], with both memory systems working synergistically to result in the optimal exploitation of resources that causes the emergence of realistic home range patterns. Our study suggests that variation in spatial reference memory, independent of working memory, predicts the development of differing home range sizes (also suggested by Riotte-Lambert et al. [22]), with no evidence for an interaction between these two spatial cognitive processes or any effect of working memory variation on home range size at all. We note that comparisons between theoretical and empirically-derived measures of cognition should be made with caution, but nonetheless a fascinating avenue for future mechanistic studies would be to investigate the relative importance played by predators and resource utilisation, and how these in turn place differing priorities on different memory systems, in driving home range development, particularly in systems that suffer high predation rates such as ours (as has been done in more nomadic species [67]).

We recorded 45 separate predation events during our study, for which we could identify the precise timing, location and predator species responsible due to the high temporal and spatial accuracy of our ATLAS data. All predation events were caused by red foxes (see Methods for a separate validation experiment that characterised untagged-predator and tagged-prey movement patterns). By comparing the whereabouts within the predated bird's home range of these real death locations to a null distribution of simulated death locations, we find that pheasants were disproportionately likely to be predated on the periphery of their core home range, the area with which they had least experience (deaths occurring on 85% ± 25% (mean ± SD) isopleth of AKDE; Omnibus test: $\chi= 242.61$, df= 70, $P<0.001$; Fig. 2A and Fig. 2B). This suggests that familiarity with the landscape was an important determinant of an individual's predation risk, supporting previous work in deer [44,49]. However, a potential alternative (but not mutually exclusive) explanation for this spatial distribution of predation, not discounted in previous studies, is that prey individuals may simply establish their home ranges outside of high-risk areas - mortality might be particularly high outside of the core home range simply because this is the area with highest intrinsic risk. Indeed, many prey species are known to form a 'landscape of fear' by learning the temporal and spatial patterns of predation risk in their habitat [47,68], providing a possible avenue by which cognitive ability may facilitate predator avoidance. We directly tested for this possibility by calculating areas of high predation risk based on the predation events we recorded during our study. Whilst these were non-randomly distributed across the landscape, we found no indication that cognitive ability played a role in pheasants' ability to avoid these high-mortality areas (Tables S7 – S10), or indeed any evidence that pheasants avoided these areas at all (Extended Data Figure 1). Instead, the home ranges of surviving birds overlapped substantially more with the high-mortality regions than we would expect by chance (89.1% ± 22.2 (mean ± standard deviation) of a bird's core home range; Permutation test: P=0.010; Extended Data Figure 1), possibly due to predators being attracted to areas of high prey abundance [69]. Crucially, the locations of each death commonly fell within the home ranges of multiple individuals. We were therefore able to test, at a fine scale, whether it was an individual's own experience (as determined by the percentage kernel isopleth of their home range) of the location that predicted their death rather than the intrinsic risk of the location itself. For the bird killed at a particular location, this was situated more peripherally within their home ranges compared to the other birds whose home ranges encompassed the location yet were not killed by predators during the study (65% ± 34% (mean ± SD) isopleth of AKDE; Kolmogorov-Smirnov test; D=0.32, P=0.001; Extended Data Figure 2). Taken together, these results suggest that predation risk is not simply a product of the probability of interacting with predators, but rather the level of experience an individual has with the landscape when it encounters those predators. Ignorance of local risk at the home range edge may manifest as a failure to optimally resolve the trade-off between vigilance and resource use, which may develop with age and experience as individuals obtain knowledge about the spatial and temporal patterns of predation risk, refuges and escape routes within their environment [47,68,70], rendering juveniles (or otherwise naïve individuals) in rarely visited areas at greatest risk of predation.

Further corroborating the antipredatory importance of spatial knowledge, the familiarity-dependent patterning of predation risk we found also created differential survival in pheasants contingent on their spatial memory. Survival was highest in pheasants whose performance in the complex maze task (assessing spatial reference memory) was correlated with their performance in the working memory task; birds had the highest survival if they combined good spatial working memory abilities with good spatial reference memory, and the lowest survival was found in birds with mismatching spatial abilities (i.e. they performed well in one but not the other) (Cox proportional hazards (Cph) model; reference memory x working memory interaction: -2.98 ± 0.90 (coefficient ± SE); Fig. 2C; Table S11- Table S13). When controlling for this interaction, birds with better performance in the complex maze task also had an overall lower probability of being predated (Cph: -1.02 ± 0.44 (coefficient ± SE); Table S13), although there was no important effect of working memory as a main effect (Cph: -0.45 ± 0.59 (coefficient ± SE); Table S13). We found no support for an effect of general associative learning on survival, where our two best models included only sex or an intercept-only model (Table S14). Given that spatial cognition in pheasants has a (albeit low) heritable component [71], the familiarity-dependent spatial variation in predation risk we detail here has potential to generate selection on these two forms of spatial memory. An important prediction from our results is that, since spatial memory positively predicts home range size, with predation risk being highest just outside the core home range, and that this predation risk in turn generates selection on spatial memory, then core home range itself should be expected to be under directional, positive selection. Confirming this, we find that indeed the size of the core home range itself also predicted mortality, with predation risk being lowest in the birds with the largest home ranges (Cph: 0.12 ± 0.07 (coefficient ± SE); Fig. 2D).

A small number of previous studies have demonstrated survival or mate choice benefits that are associated with cognitive abilities [40,42,43,72]. However, the process by which cognition actually conveys these benefits by mediating how animals interact with their environment is unclear. Our results reveal that spatial variation in predation risk, arising from a prey individual's own familiarity within its home range, may generate selection on spatial cognitive abilities that in turn predict home range size.

An intriguing result from our data is that survival was also relatively high in birds that performed poorly in the tasks that test both spatial working memory as well as navigational-based spatial cognition (spatial reference memory) (Fig. 2C). This result requires further exploration to determine the overall effect on selection experienced across multiple generations, although the overall effect of highest survival being found in the birds that performed best in both, in combination with the highest mortality being found in birds with mismatching performance, should result in overall positive selection in both cognitive abilities (as suggested by our result showing that birds with the largest home ranges also had highest survival). Previous modelling work has highlighted the importance of a synergistic mechanistic role of working and reference memory for an animal to create a home range that optimises foraging efficiency [21,22]; our results suggest that a mismatch between these two facets of spatial memory may also have ultimate consequences in terms of survival. Whilst spatial reference memory is known to be important in allowing prey to efficiently exploit safe refuges, particularly when encountering predators [73–75], the role of working memory in relation to predation risk is poorly known so we can only speculate on this intriguing result. Perhaps birds with greater reference but poor working memory traverse larger home ranges, with correspondingly greater exposure to high-risk areas, but their poor working memory means they are less capable of exploiting recently visited escape routes should they encounter a predator. Regardless of the explanatory factor for this result, it suggests that interactions between complementary modalities may be required for selection on some cognitive abilities to arise. The nature of our study site, with the simultaneous introduction of same-aged, equally naïve birds at a single location, in the virtual absence of resident competitors and abundant natural and provisioned food mean that we cannot explore the role of resource distribution on home range development, maintenance and benefits in this analysis. Fluctuations or heterogeneity in resources or competition likely affect home ranges with larger ranges expected in low-productivity areas with patchily distributed resources. Under such circumstances, the relative values of working and reference memories may differ. Thus, we encourage future studies to explore the interplay between risk or resource distributions and spatial memory ability to better understand how selection may act more generally on cognition under varying ecological conditions.

Our findings provide empirical support for the long-assumed links proposed between movement ecology and spatial cognition as revealed in abstract cognitive tasks dependent on cues of space and movement. They suggest that spatially-contingent predation risk arises through familiarity and experience with the landscape, a potentially critical factor with important implications for how cognition shapes movement and space use. Importantly, they provide a plausible pathway by which selection acts on spatial learning and memory through an individual's acquisition of, and familiarity with, their home range, and their life or death within it.

Methods

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 reward (Fig. 1C). One week prior to testing, birds were trained to peck through the tissue paper via repeated exposure to the apparatus in the testing chamber in small groups until all birds could consistently perform this behaviour. Each bird completed 10 trials within each of eight sessions (80 binary choices) between the 19th and 22nd June. In each session, a bird would enter the testing chamber where they then completed a total of 10 trials. Each 2cm diameter well was encircled with either a blue or green coloured ring; wells encircled with a blue ring contained three mealworms, while those encircled with a green ring could not be pierced due to a layer of undetectable cardboard immediately underneath the tissue. The two wells were oriented vertically in relation to the pheasant's perspective, with a 1cm gap between them. We placed a dead mealworm between the two wells to attract birds to the apparatus and ensure they had a standardised orientation for each set of trials. Birds were only allowed to make one choice per trial. After each choice, the apparatus was replaced before starting the next trial. The location of the rewarded well was pseudorandomised so that it did not appear on the top or bottom more than 3 times in a row and thus removing any spatial associations that may form.

Complex maze task

Between 3rd – 5th July 2018 (once the birds reached five weeks old), the testing chamber was converted into a 3 x 3 chambered maze using 35cm walls of opaque black plastic to test the pheasants' reference learning ability, recalling a route after an interval of several hours (Fig. 1A). We first habituated birds to this arena by repeatedly feeding them within the maze when all the doors to each chamber were open. During the complex maze task, birds were required to make at least seven turns to navigate to the exit, at which point they would receive a mealworm reward and could exit to the outdoor enclosure. We ensured that all cues external to the maze (e.g. observer position) were identical in all trials. Each bird first underwent a total of eight trials. In each trial, we counted the number of chambers that a bird entered erroneously, with an error being defined as a chamber that did not lie on the most direct route to the exit. A bird was considered to have entered a chamber if their head passed over the chamber threshold. A bird could repeatedly re-enter a wrong chamber so the number of (potential) errors was not capped. In a perfect performance with no errors, the bird would progress directly through the maze via seven chambers to the exit.

Radial arm maze

Once chicks had reached seven weeks old, we tested their working memory based on spatial cues over a period of a couple of minutes, by converting the testing chamber into a radial arm-style maze with four arms rewarded with a single large mealworm (Fig. 1B). The reward was concealed at the end of each arm by an opaque black plastic wall which the birds had to navigate around. On entry to the testing chamber, birds were lured to approach a central platform using a single mealworm as bait, after which they could enter one of the arms and so make their decision. In each trial, we recorded the number of errors a bird made (number of times a bird stepped off the central platform into an arm they had already depleted the reward from) and a trial continued until a bird found all the mealworm rewards, at which point it was released into the outdoor enclosure. All birds received a total of 12 trials. A perfect performance would see a bird visiting and depleting each location just once, with no visits to previously visited locations.

Cognitive performance analyses

We quantified an individual's learning performance in the radial arm and complex maze tasks by using the slope that describes their reduction in numbers of errors across trials, and for the colour discrimination task by using the slope that describes the number of correct choices out of the 10 trials across the eight sessions. For the colour discrimination task, we obtained the slope from running a Poisson regression between the number of correct choices out of the 10 trials across the eight sessions of the task. For the complex maze and radial arm maze tasks, we fitted a linear relationship to the pattern of errors across the 8 and 12 trials respectively. We derived the equation for the relationship and used the coefficient slope value. Steeper negative slopes for the radial arm and complex mazes, and steeper positive slopes for the colour discrimination task, indicate that their learning of the task was faster (although these are inversed in our figures to aid interpretation; Fig. 1D and Fig. 2C).

We only included birds that had completed at least eight of the ten trials in the radial arm maze and colour discrimination tasks, and seven of the eight trials in the complex maze for further analysis. Different birds reached criterion on different tests, which is why sample sizes for relationships with particular tests vary, and also why not all birds that contributed death location data also contributed spatial ability data (and vice-versa if birds did not establish a stable home range; see below). None of our cognitive variables were significantly correlated (linear model (lm) of spatial reference memory predicted by spatial reference memory: -0.01 ± 0.26 (coefficient ± standard error), $F_{1,42} = <0.01$, P=0.999; lm of spatial reference memory predicted by colour discrimination: -0.08 ± 3.91 (coefficient ± standard error), $F_{1,31}=<0.01$, P=0.983; lm of spatial working memory predicted by colour discrimination: 2.66 ± 2.18 (coefficient ± standard error), $F_{1,31}=1.49$, P=0.232.

Release into the wild and ATLAS system

All birds were allowed to naturally disperse into the wild by being first released into an outdoor release pen (~4000 m^2 in area) within woodland at North Wyke Farm, North Wyke, UK, once they reached ten weeks old. Before release, they were fitted with radio tags, sexed, and their mass was recorded. Within the pen, birds could enter and leave as necessary by flying or via a system of wire tunnels that were too small to admit terrestrial predators. We provided birds with supplementary food supplied in 43 artificial feeders situated inside and within 2 km of the release pen (see Fig. 2A for map of the release site). To ensure the attached radio tags had no adverse effects, tagged birds were monitored in captivity for seven days before being released. Specifically, we monitored behavioural (lethargy, isolation) and physiological (breathing, vocalisation) indicators of welfare as well as visually monitoring the pheasants for sites on the body that could be susceptible to abrasion. We tracked birds using a recently developed reverse-GPS system (ATLAS) [60,61,63]. This system uses fixed-position receiver stations to detect and collect the time of arrival data from tag-derived radiosignals. These data are then collated at a database on a central server where location is calculated. Location data, accurate to ~4-6m relative to GPS measurements [63], can be accessed in real-time through an internet connection which allows for continuous monitoring.

Determination of death locations

Because the major predator of pheasants in our field sites, red foxes (*Vulpes vulpes*), will frequently transport their captured prey before eating or caching them, we combined three methods to determine the exact death location of each of our predated pheasants. Firstly, we ran an observational study using ATLAS-tagged fresh pheasant carcasses to determine the range of movement patterns displayed by predators carrying a dead pheasant (details of experiment below). Secondly, informed by the filtered movement tracks of scavenged dead pheasants, we visually assessed movement patterns of our live birds to subjectively determine putative kill sites where the bird's movement path underwent an unusual substantial change (e.g. when the bird rapidly covered a large distance in an uncharacteristically straight line before suddenly stopping) and matched those displayed by the movement patterns of scavenged carcasses. Thirdly, we confirmed our putative kill sites by running a state change analysis on the tracked paths of each predated bird to determine whether locations that immediately preceded a substantial change in movement highlighted by our subjective assessment matched those determined using our state change analysis. Specifically, we used the segmentation approach by Lavielle[77], where segment numbers (allowing us to identify change-points) were identified based on graphically examining the relationship between segment number and the decreasing contrast function, produced using the '*lavielle*' function in the '*adehabitatLT*' R package (version 0.3.25)[78].

In our carcass tracking study, we placed 44 carcasses of ATLAS tagged adult pheasants (22 male and 22 female) on 5th February 2019 in locations around the field site frequented by our live tracked birds. Two camera traps (Bushnell Trophy) were setup at each location to identify the predator that moved the carcass. After eight days (once all carcasses had been moved), we then located carcasses based on their ATLAS coordinates. Camera trap footage confirmed that all carcasses moved from the introduction site were caused by red foxes. ATLAS coordinates for each bird were then filtered using the same method for our real birds, and the resulting movement patterns were used to help denote death locations as described above.

In all instances of predation from our main release experiment, the paths of live birds that were predated were typified by regular movement patterns before a sudden and uncharacteristically long-distance and rapid movement in a straight line before immediately becoming stationary. This rapid, single straight-line movement was recorded for all red fox scavenging instances we recorded in the carcass tracking study above, representing a fox moving its prey a long distance from the site it was captured to a new location to process and cache. This first 'stop' location was usually the spot where we recovered the predated bird via radio tracking, and the location immediately preceding the first long-distance movement (i.e. the last point of normal pheasant movement) was denoted as the location the bird was predated. We confirmed the species of predator using field signs around carcasses such as whether the carcass was buried, teeth marks on the radio-tags, and feather remains (e.g. characteristic field signs of a fox kill are large wing and tail feathers cleanly severed close to the base of the feather shaft, whereas raptors pluck feathers by grasping the feather further up the shaft, leaving a characteristic V-shaped kink). All the birds killed outside their pens in this study were predated by red foxes.

Location data filtering

All ATLAS coordinates were first filtered to increase the accuracy of locations used to calculate the home ranges. We first removed all coordinates where the variance in signal strength between base stations was greater than 75%. Each day was then split into five-minute blocks, and the median location during each five-minute block was calculated (so that every bird in the study had one location assigned within the same time periods within each day). This filtering process excluded anomalous locations caused by standard issues with radiotracking such as reflection [79,80]. Because the release pens which birds were kept in before dispersing effectively excluded foxes, we only included the coordinates of birds that were outside the pen in our home range estimations.

Home range estimation

To estimate home ranges of each pheasant we fitted a continuous-time stochastic movement model (ctmm) followed by AIC-based model selection to calculate autocorrelated kernel density estimates (AKDEs) for each of our birds using the *ctmm* package [64] in R (version 3.5.3) [81]. Parameters for our ctmms were chosen based on visually assessing variograms of time-series movement patterns for each individual bird. The variograms also allowed us to identify and discard from the analysis a further 39 birds who had not formed a stable home range because of either predation or death soon after release, tracker malfunction, or because they quickly dispersed from the study site. Core home ranges were estimated as the 85% AKDE isopleth based on the mean point of asymptote between the home range size and AKDE isopleth, indicating the region within which birds were concentrating their movement patterns [11]. To determine the region of the home range where birds were killed, we then calculated the minimum AKDE isopleth that encompassed the coordinates of the bird's predation location.

Do pheasants avoid high-risk areas?

One explanation for why pheasants are killed more frequently on the outskirts of their home range is because they avoid riskier areas - death locations on the home range periphery may simply reflect cases where pheasants ventured into high-risk areas instead of occurring due to a lack of intrinsic knowledge about local predation risk. To test whether our mortality patterns could therefore be driven by birds avoiding areas of high risk, we quantified the home ranges of non-predated pheasants and determined the proportion of their core home range (85% AKDE) that overlapped with a kernel density estimate (80% kernel estimate with no autocorrelated time estimate) created from the death locations of our predated birds. The 80% kernel density estimate from the actual death locations was chosen as a suitable 'high risk zone' as it represented the start of the plateau between the kernel density percentage and size (surface area) of the home range, thus representing an area of concentrated predation risk.

To determine whether the home range-risk area overlap differed from what we would expect by chance, based on the null hypothesis that pheasants can be predated with equal probability at any previously visited location within their home range, we compared the overlaps of our real birds to 5000 simulated high-risk zones. Each simulated high-risk zone was created by selecting a single relocation coordinate (randomly selected from any of the coordinates recorded during a bird's lifetime) from each of our predated birds and using this as a simulated predation location, before re-calculating a new high-risk zone and subsequently calculating how much this overlapped with the real core home range of the surviving birds. Only those surviving birds that overlapped with some part of the home range of at least one of the predated birds were included in this analysis. The proportion of randomised survivor-predation home range overlaps that were lower or higher than the real survivor-predation home range overlaps was used as our two-tailed statistical significance value (Extended Data Figure 2).

In addition to the above, we also ran an analysis to determine whether the AKDE isopleth containing a death location was higher in the bird that actually died compared to the same death location of a neighbouring bird that did not die. This is directly testing whether the actual death location itself was avoided at a more fine-scale level than can be determined by comparing home range overlaps with regions of high risk. We therefore calculated the minimum AKDE isopleth that contained a death location for birds that were killed and birds that were not recorded as being killed (surviving birds; n=67). Surviving birds were only included if the 100% minimum convex polygon of their home range encompassed the death location of the killed bird (to avoid including birds that never encountered the death location). We then compared the distribution of minimum isopleths that contained death locations between killed and surviving birds using a Kolmogorov-Smirnov test (Extended Data Figure 2).

Statistical analysis

To determine the drivers of home range variation, we ran linear models (LMs) with core and peripheral home range size in hectares of the eventual stable home range of each pheasant as the response variables. We define the peripheral home range as the area covered by the core (85% kernel isopleth) subtracted from the area of the total (99% kernel isopleth) home range. We used this measure rather than the 99% kernel to detect any effects of total home range size exclusive of the role played by the underlying core home range (which is of course a composite of the total home range). Both core home range size and peripheral home range size were strongly left skewed and so were log-transformed to obtain normally-distributed residuals from our models. To test the effect of different cognitive modalities on these home range parameters we created a model to test performance in the colour discrimination task, and a model that tested for the role of performance in both the spatial cognition tasks, across both of the response variables detailed above. To be included in any analysis, pheasants of course had to reach criterion in the relative cognitive tests (two tests in the case of the spatial analyses), as well as form a stable home range before dying/suffering a transmitter malfunction/dispersing out of the field site. For the survival analysis, we also only include birds where the known cause of death was predation (as determined from above), or to include birds that ‘survived’, we only included their location data up to the point that they were still moving freely and were producing high-accuracy data (i.e. hadn’t dispersed outside of the range of the ATLAS receivers). As such, there was rather extensive data loss from our original 126 birds (see specific numbers in each statistical section below).

In the spatial cognition models, performance in the radial arm maze and complex maze were included as main effects to test for the general hypothesis that spatial reference memory is important in the development and utilisation of a home range (e.g. [25,26]), as well as in a two-way interaction to explicitly test the hypothesis that home range development and size arise and vary due to the synergistic effect of working and reference memory [21]. To control for the amount of time that a bird could familiarise itself with the landscape, we also included a bird's lifespan (in days) as a covariate in all models. In addition, pheasants show sex differences in home range size, with females having larger home ranges than males when the latter become territorial during the breeding season (although our study did not encompass this period), and so we therefore include sex in our models as a fixed term [82,83]. Our code syntax for the structure of our starting maximal model for the core home range spatial analysis (n=44) was therefore: '*lm(log(Core_HR_hr) ~ Slope_LM * Slope_RAM + Sex + Lifespan, data= akde_data_main)*', and we returned support for a single model in our model selection procedure (Table S1). To test whether body mass is a confound in this analysis (since home range is known to scale with body mass at the intraspecific level in some species [84], although see [36]), we also ran a final model that included only lifespan and mass as predictors. Model comparison using AICc (154.1 for the reference memory model and 156.3 for the mass model) confirmed that mass is not a confound. We intentionally excluded mass in our starting model to avoid issues with collinearity since it is strongly correlated with sex (female mass: 575g ± 65; male mass: 717g ± 100 (mean ± standard deviation); t-test: t = -5.65, df = 37.2, P<0.001).

Our code syntax for the structure of the starting maximal model for the peripheral home range spatial analysis (n=44) was: '*lm(log(Peripheral_HR_H) ~ Slope_LM * Slope_RAM + Sex + Lifespan, data= akde_data_main)*'. Our model selection procedure produced two minimum adequate models (Table S4). As with the core home range model above, we also tested for any confounding effect of mass by comparing our two final model AICcs with a model that only contained mass and lifespan as predictors, confirming again that it is not a confound.

For the associative learning analyses based on the colour discrimination task, we included sex, colour discrimination performance and lifespan as the fixed effects. The syntax for our starting maximal model for the core home range colour discrimination analysis (n=55) was therefore: '*lm(log(core_HR_hr) ~ CD_Slope + Sex + Lifespan, data = akde_CD)*', returning a single model with only sex and lifespan as covariates. The syntax for our starting maximal model for the peripheral home range colour discrimination analysis (n=55) was: '*lm(log(Peripheral_HR_hr) ~ CD_Slope + Sex + Lifespan, data = akde_CD)*'. This produced three separate minimum adequate models (Table S5).

A central question in this study was to test whether animals were more likely to be predated on the outskirts of their home range, in areas they were less familiar. However, the null expectation of where predation locations should occur across a home range density estimate such as AKDE are unclear. As such, we took a simulation approach, comparing the AKDE isopleth that a real death occurred on to a null distribution of 'simulated death isopleths', where every location a bird was recorded was assigned as a simulated death location and the accompanying minimum AKDE isopleth that encompassed it. To calculate our total P value for each bird, we then calculated the proportion of simulated death isopleths that were higher or lower than the observed death isopleth, and tested for overall significance of all birds by combining the P values using Fisher's combination (omnibus) test [85].

We also ran two binomial regression analyses investigating whether cognitive ability predicted the proportion of a pheasant's core home range that overlapped with the region of high predation risk. We again separated spatial memory and associative learning into separate models to maximise our sample sizes and statistical power, using a conditional log-link function in our models to control for the unequal distribution of our proportion data. We controlled for the size of the core home range in driving these patterns by including this variable as a covariate in all models. The syntax for our maximal starting model for spatial memory (n=29) was: '*glm(HR_death_overlap_prop ~ Slope_LM * Slope_RAM + core_HR + Sex, family= binomial(link= "cloglog"), data= akde_cognition_HR_overlap)*' and for associative learning (n=29): '*glm(HR_death_overlap_prop ~ core_HR + CD_Slope + Sex, family= binomial, data= HR_overlap_CD)*'. We identified three candidate models for the spatial memory analysis and a single model for associative learning (Table S7 and Table S8).

To determine how spatial cognitive performance and home range size affected a pheasant's probability of being predated, we ran three Cox-proportional hazards models to determine the effect on lifespan and general probability of death. In the first survival model we included performance in the complex and radial arm maze tasks as covariates, sex, and the size of the core home range (hectares) as predictors. We also directly test whether an interaction between working and reference spatial memory are important for the ultimate consequences of forming a home range, as suggested by mechanistic models (e.g. [21]) by including an interaction between performance in our complex maze and in our radial arm maze tasks. We also included sex within a three-way interaction that also includes working and reference memory. Our model syntax for this starting model (n=51) was therefore: *coxph(Surv(Lifespan, State_bin) ~ Sex + Slope_LM*Slope_RAM, data=spatial_data)*. Our AICc based model selection returned support for a single model (Table S11). As with our home range models, we also investigated whether body size was a confound by adding it to our final model (where sex and was not included and could therefore not cause any collinearity issues).

To test for the importance of associative learning performance on survival, our second model included performance in the colour discrimination task, sex, and tarsus size, with a single two-way interaction between colour discrimination and sex. Our syntax for this starting model (n=61) was therefore: *coxph(Surv(Lifespan, State_bin) ~ CD_Slope*Sex+Tarsus, data=CD_data)*). Our AICc based model selection returned support for a single, intercept-only model (Table S12). Because different birds did not reach criterion in the different cognitive tests and were thus removed (see above), we also ran a third survival model that included all birds for which we had stable home range sizes to maximise statistical power (resulting in n=68) to test if core home range size itself, independent of cognitive variables, affected survival. In this model, we included three predictors: core home range size in hectares, sex, and a two-way interaction between these variables. Our model syntax for this starting model (n=68) was therefore: *coxph(formula = Surv(Lifespan, State_bin) ~ core_HR_H*Sex, data = HR_surv_data)*, and our our AICc based model selection returned support for a single model with core home range size as the sole term (see main text).

Diagnostics were performed on all models to check they met assumptions. We used a stepwise AICc (AIC corrected for small sample size) model selection approach to find our best models. Specifically, after constructing our starting model that allowed us to test our most complex hypotheses, we performed a stepwise simplification procedure based on the “AICc” function from the R package ‘MuMin’ [86] to compare nested models until a best set of plausible models were obtained (minimum adequate models), where models with ΔAICc ≤ 2 were deemed more plausible. If this process created more than a single best model, we used the *model.avg* function in the ‘MuMin’ package to average the model estimates and standard errors. In addition, we present P values, uncorrected for multiple testing (as per [87]) for each of our best models in the supplementary material, which were obtained using likelihood-ratio tests for change in deviance between nested models with and without the term of interest.

All animal work in this study was conducted under Home Office license PPL 30/3204 and approved by the University of Exeter Animal Welfare Ethical Review Board.

Data availability

Data required to rerun the statistical analyses of this study are available online (https://data.mendeley.com/datasets/m89226xg6p)[88]. Animal AKDE models and GPS coordinates are available from the corresponding author upon request.

Code availability

R code used to run the simulation analyses of this study are available online (https://data.mendeley.com/datasets/m89226xg6p)[88].

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Author contributions

RJPH and JRM conceived the idea for the manuscript. CEB, PRL, MAW, JOvH and JRM collected the cognition data. MAW, CEB and JRM collected the movement data. RJPH and MAW carried out the carcass tracking study. RJPH conducted the analyses and led the writing. RN, YO and ST developed the reverse-GPS system and provided support throughout data collection. All authors contributed critically to the drafts.

Competing interests

The authors declare that they have no competing interests

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.

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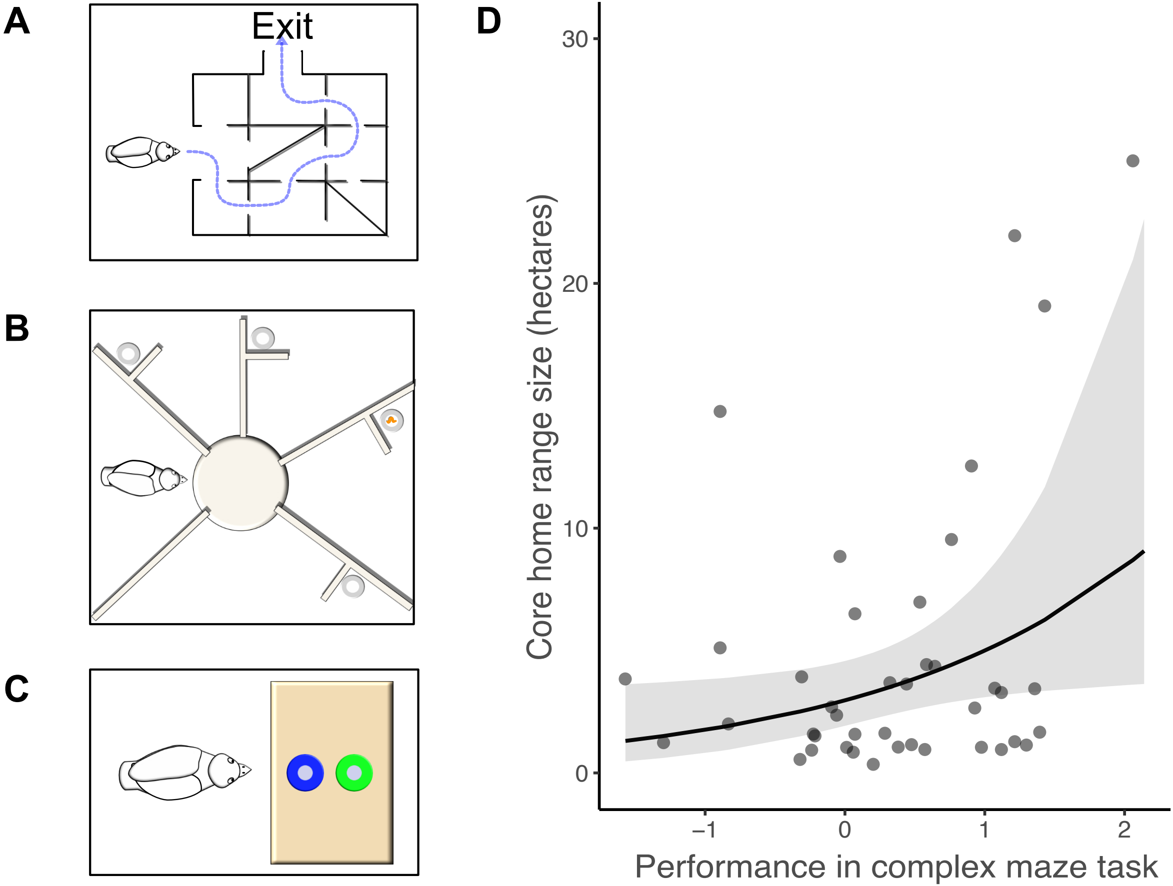
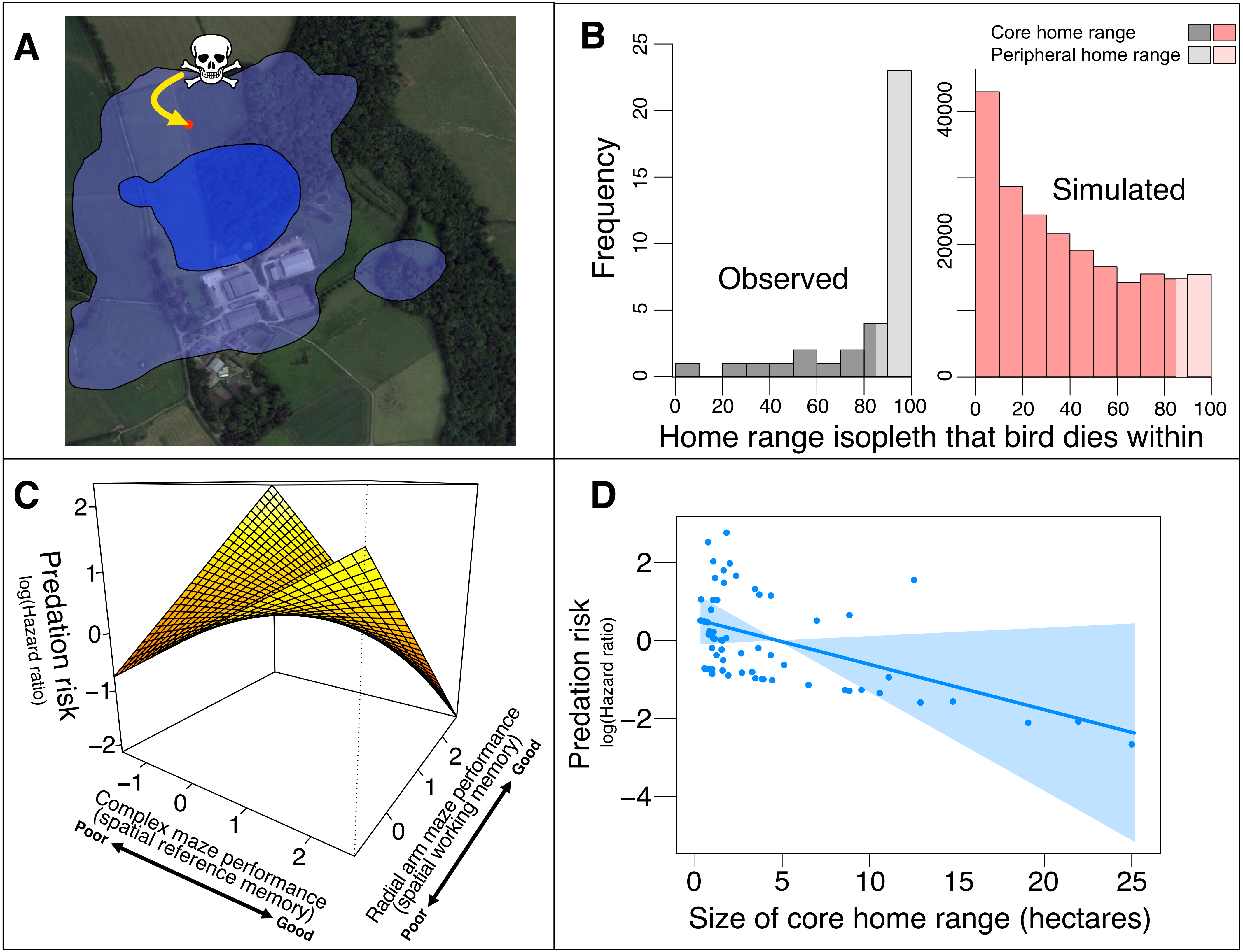
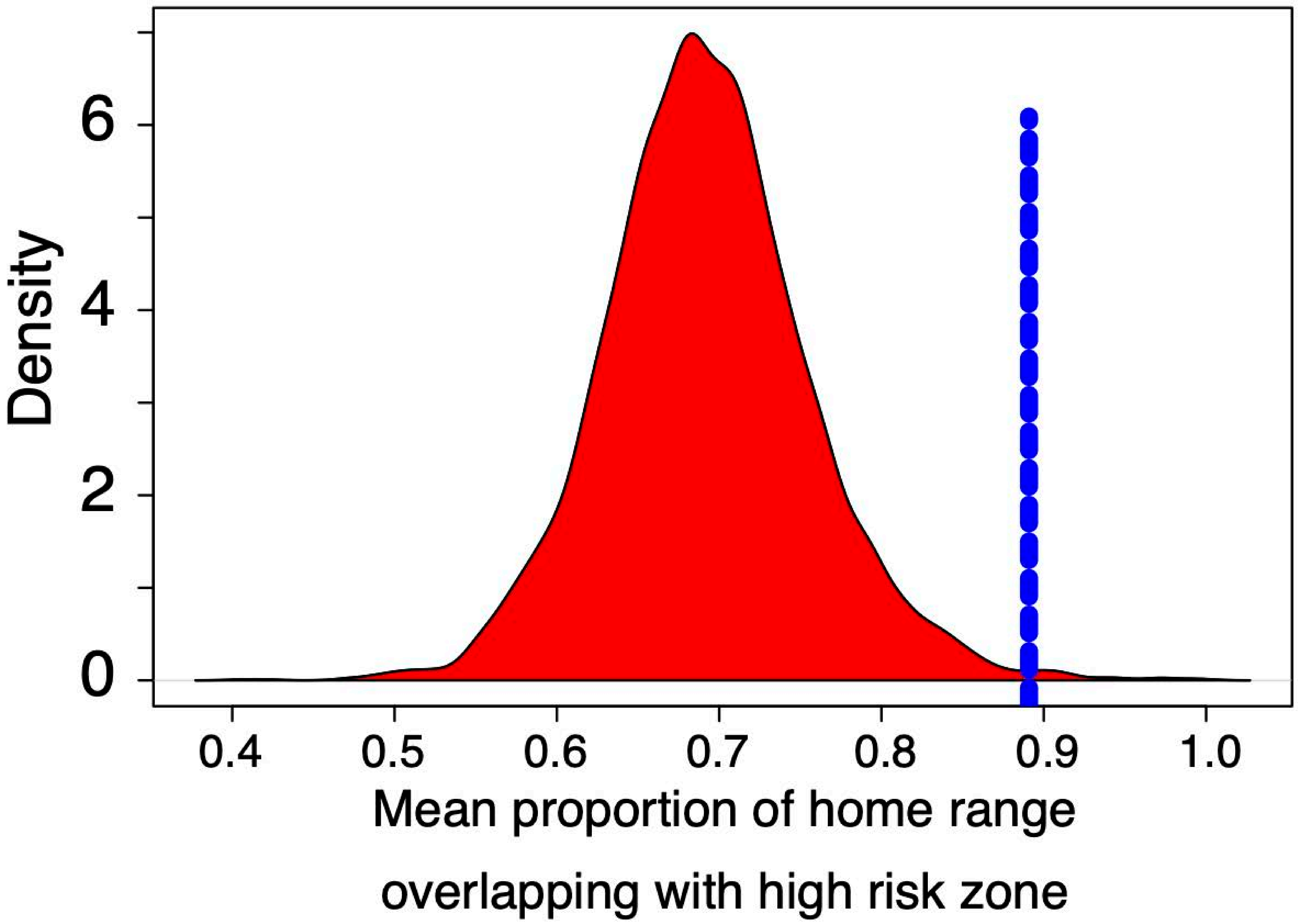

A
Exit
B
C
D
30
20
10
0
Core home range size (hectares)
−1
0
1
2
Performance in complex maze task


A
B
Core home range
Peripheral home range
Frequency
0
5
10
15
20
25
Observed
0
20
40
60
80
100
0
20000
40000
Simulated
0
20
40
60
80
100
Home range isopleth that bird dies within
C
Predation risk
log(Hazard ratio)
2
1
0
−1
−2
−1
0
1
2
Complex maze performance
(spatial reference memory)
Poor
Good
0
1
2
Radial arm maze performance
(spatial working memory)
Poor
Good
D
Predation risk
log(Hazard ratio)
2
0
−2
−4
0
5
10
15
20
25
Size of core home range (hectares)


Density
0
2
4
6
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Mean proportion of home range
overlapping with high risk zone


Frequency
0
100
200
300
400
500
600
700
800
Death location of others
0
20
40
60
80
100
Home range isopleth that bird dies within
0
5
10
15
20
25
Location of own death
0
20
40
60
80
100
Home range isopleth that bird dies within

Supplementary Information

Spatial memory predicts home range size and predation risk in pheasants

Robert J. P. Heathcote; Mark A. Whiteside; Christine E. Beardsworth; Jayden O. Van Horik; Philippa R. Laker; Sivan Toledo, Yotam Orchan, Ran Nathan, and Joah R. Madden.

Supplementary Table 1. Comparison of AICc outputs from linear model selection on spatial memory model of core home range size.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
Lifespan + Ref. memory	4	154.11	0	0.57	0.57	-72.54
Lifespan	3	156.36	2.25	0.19	0.76	-74.88
Lifespan + Ref. memory + Work. memory	5	156.51	2.4	0.17	0.93	-72.47
Lifespan + Ref. memory + Work. memory + Sex	6	158.88	4.76	0.05	0.98	-72.3
Lifespan + Work. memory*Ref. memory + Sex	7	160.96	6.85	0.02	1	-71.93

Supplementary Table 2. Comparison of AICc outputs from linear model selection on associative learning model of core home range size.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
Lifespan + Sex	4	181.98	0	0.66	0.66	-86.59
Lifespan	5	184.24	2.26	0.21	0.87	-86.51
Lifespan + Assoc. learning + Sex	3	185.3	3.32	0.13	1	-89.41

Supplementary Table 3. Summary statistics of final best linear models selected from AICc model selection procedure on cognitive predictors of core home range size. P values are two-tailed and uncorrected for multiple testing.

Model	**Term (contrast)**	**Estimate ± SE**	**SE**	**F**	**df**	**Uncorrected P**
Core HR size ~ Spatial memory ($F_{2,41}$=4.01, R^2adj.=0.123, p=0.026)	Intercept	0.02	0.58	0.00	2,41	0.976
	Reference memory	-0.52	0.24	4.59	2,41	0.038
	Lifespan	0.01	0.01	3.66	2,41	0.063
Core HR size ~ Associative learning ($F_{2,52}$=9.15, R^2=0.232, p=0.001)	Intercept	-0.52	0.40	1.68	2,52	0.200
	Sex (males)	0.79	0.33	5.63	2,52	0.021
	Lifespan	0.02	0.01	10.14	2,52	0.002

Supplementary Table 4. Comparison of AICc outputs from linear model selection on spatial memory model of peripheral home range size.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
Lifespan + Ref. memory	4	156.17	0	0.47	0.47	-73.57
Lifespan	3	156.85	0.68	0.33	0.8	-75.12
Lifespan + Ref. memory + Work. memory	5	158.62	2.45	0.14	0.94	-73.52
Lifespan + Ref. memory*Work. memory	6	160.55	4.39	0.05	0.99	-73.14
Lifespan + Work. memory*Ref. memory + Sex	7	163.4	7.23	0.01	1	-73.14

Supplementary Table 5. Comparison of AICc outputs from linear model selection on associative learning model of peripheral home range size.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
Lifespan + Sex	4	184.57	0	0.52	0.52	-87.89
Lifespan	3	185.92	1.35	0.26	0.78	-89.73
Lifespan + Assoc. learning + Sex	5	186.27	1.7	0.22	1	-87.52

Supplementary Table 6. Summary statistics of cognitive predictors of the size of the peripheral home range. Parentheses under ‘Model’ column denote the number of final models selected by our AICc model selection approach that were used to calculate the averaged outputs reported here. P values are two-tailed and uncorrected for multiple testing.

Model	**Term (contrast)**	**Estimate**	**SE**	**Adj. SE**	**z**	**Uncorrected P**
Peripheral HR size ~ spatial Memory (x2)	Intercept	1.34	0.61	0.62	2.15	0.032
	Ref. memory	-0.25	0.29	0.29	0.87	0.384
	Lifespan	0.01	0.01	0.01	1.89	0.059
Peripheral HR size ~ Assoc. learning (x2)	Intercept	0.65	0.47	0.48	1.35	0.177
	Sex (males)	0.48	0.41	0.41	1.15	0.251
	Lifespan	0.02	0.01	0.01	3.62	<0.001
	Assoc. learning	-0.78	2.50	2.54	0.31	0.759

Supplementary Table 7. Comparison of AICc outputs from generalised linear (binomial) model selection on spatial memory variables predicting overlap of core home range with high predation zone.

Independent variables	k	AICc	ΔAICc	AICc weights	Cumulative AICc weights	Log-likelihood
Core home range	2	6.86	0	0.75	0.75	-1.2
Core home range + Ref. memory	3	9.63	2.77	0.19	0.94	-1.33
Core home range + Ref. memory + Sex	4	12.33	5.46	0.05	0.99	-1.33
Core home range + Ref. memory + Work. Memory + Sex	5	15.23	8.37	0.01	1	-1.31
Core home range + Ref. memory * Work. Memory + Sex	6	18.34	11.48	0	1	-1.26

Supplementary Table 8. Comparison of AICc outputs from generalised linear (binomial) model selection on associative learning variables predicting overlap of core home range with high predation zone.

Independent variables	k	AICc	ΔAICc	AICc weights	Cumulative AICc weights	Log-likelihood
Core HR	2	9.91	0	0.73	0.73	-2.79
Core HR + Sex	3	12.44	2.53	0.21	0.93	-2.89
Core HR + Sex + Assoc. learning	4	15.1	5.19	0.05	0.99	-2.98

Supplementary Table 9. Summary statistics from single best binomial model on spatial memory variables predicting proportion of the core home range that overlapped with the region of high predation risk. P values are two-tailed and uncorrected for multiple testing.

Model	Term	Estimate	SE	z	Uncorrected P
Proportion HR that overlaps	Intercept	1.61	0.43	3.72	<0.001
with high-risk region ~ spatial memory	Core HR size	-0.03	0.02	-1.88	0.060

Supplementary Table 10. Summary statistics from single best binomial model on associative learning predicting proportion of the core home range that overlapped with the region of high predation risk. P values are two-tailed and uncorrected for multiple testing.

Model	Term	Estimate	SE	z	Uncorrected P
Proportion HR that overlaps	Intercept	3.32	0.87	3.82	<0.001
with high-risk region ~ assoc. learning	Core HR size	<0.01	0.00	-2.20	0.028

Supplementary Table 11: Summary statistics of Cox hazards survival models selected from AICc model selection procedure on spatial memory predictors of predation by ambush predators.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
Ref. memory * Work. memory	3	101.66	0	0.76	0.76	-47.55
Sex + Ref. memory * Work. memory	4	104.01	2.36	0.23	1	-47.54
Ref. memory + Work. memory	2	112.95	11.29	0	1	-54.34

Supplementary Table 12: Summary statistics of Cox hazards survival models selected from AICc model selection procedure on associative learning predictors of predation by ambush predators.

Independent variables	**k**	**AICc**	**ΔAICc**	**AICc weights**	**Cumulative AICc weights**	**Log-likelihood**
(Intercept only)	0	96.1	0	0.65	0.65	-48.05
Sex	1	97.95	1.85	0.26	0.9	-47.93
Sex + Assoc. learning	2	99.94	3.84	0.1	1	-47.85

Supplementary Table 13. Summary statistics (Cox proportional hazards models) of single best model of spatial memory predictors of predation by ambush predators. R^2= 0.552. P values are two-tailed and uncorrected for multiple testing.

Model	**Term**	**Estimate**	**SE**	**z**	**Uncorrected P**
Survival analysis on spatial memory	Working memory	-0.45	0.59	-0.77	0.444
	Reference memory	-1.02	0.44	-2.31	0.021
	Reference memory x Working memory	-2.98	0.90	-3.31	<0.001

Supplementary Table 14. Summary statistics (Cox proportional hazards models) of averaged best models of associative learning predictors of predation by ambush predators in pheasants (R^2 of best model= 0.015). Parentheses denote number of final models averaged to obtain summary statistics. P values are two-tailed and uncorrected for multiple testing.

Model	**Term (contrast)**	**Estimate**	**SE**	**Adj. SE**	**z**	**Uncorrected P**
Survival analysis ~ associative learning (x2)	Intercept	1.34	0.61	0.62	2.15	0.032
	Sex	-0.25	0.29	0.29	0.87	0.384

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