



LJMU Research Online

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

Is habitat selection in the wild shaped by individual-level cognitive biases in orientation strategy?

<https://researchonline.ljmu.ac.uk/id/eprint/19005/>

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Beardsworth, CE ORCID logoORCID: <https://orcid.org/0000-0003-1308-1455>,
Whiteside, MA ORCID logoORCID: <https://orcid.org/0000-0001-7212-7279>,
Laker, PR ORCID logoORCID: <https://orcid.org/0000-0002-3214-4098>,
Nathan. R ORCID logoORCID: <https://orcid.org/0000-0002-5733-6715>.**

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.








The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

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

<http://researchonline.ljmu.ac.uk/>

LETTER

Is habitat selection in the wild shaped by individual-level cognitive biases in orientation strategy?

Christine E. Beardsworth,^{1*} 
 Mark A. Whiteside,¹ 
 Philippa R. Laker,¹ 
 Ran Nathan,² 
 Yotam Orchan,² Sivan Toledo,³ 
 Jayden O.van Horik  and
 Joah R. Madden¹ 

Abstract

Cognitive biases for encoding spatial information (orientation strategies) in relation to self (egocentric) or landmarks (allocentric) differ between species or populations according to the habitats they occupy. Whether biases in orientation strategy determine early habitat selection or if individuals adapt their biases following experience is unknown. We determined orientation strategies of pheasants, *Phasianus colchicus*, using a dual-strategy maze with an allocentric probe trial, before releasing them ($n = 20$) into a novel landscape, where we monitored their movement and habitat selection. In general, pheasants selected for woodland over non-woodland habitat, but allocentric-biased individuals exhibited weaker avoidance of non-woodland habitat, where we expected allocentric navigation to be more effective. Sex did not influence selection but was associated with speed and directional persistence in non-woodland habitat. Our results suggest that an individual's habitat selection is associated with inherent cognitive bias in early life, but it is not yet clear what advantages this may offer.

Keywords

Allocentric, cognition, egocentric, habitat, movement ecology, navigation, orientation strategies, spatial memory.

Ecology Letters (2021) 24: 751–760

INTRODUCTION

Animals often use information about their environment to efficiently navigate between places of refuge and resources and so reduce energetic costs and risk (Fagan *et al.* 2013). However, differences in habitat type can strongly influence the availability of cues that assist navigation. Animals navigate in a range of environments using two different spatial reference systems, termed here orientation strategies (O'Keefe & Nadel 1978; Burgess 2006). Spatial information can be encoded relative to the position of environmental features (allocentric strategy) (Normand & Boesch 2009) or the animal themselves (egocentric strategy) by monitoring direction and distance travelled (Wittlinger *et al.* 2006; Huber & Knaden 2015) or learning a sequence of turns (Bisch-Knaden & Wehner 2001). Combinations of these strategies can also be used in parallel (Rodriguez *et al.* 1994; Müller & Wehner 2010). Importantly, reliance on allocentric or egocentric strategies is not independent from the availability of cues within their habitat.

In habitats where landmarks are conspicuous, easy to distinguish and/or consistent and hence reliable, an allocentric orientation strategy permits robust and efficient route choice. Such habitats may be relatively open and contain distal landmarks such as unique horizons (Huber & Knaden 2015) or anthropogenic structures (Mora *et al.* 2012). By contrast, in habitats where landmarks are obscured, hard to distinguish and/or ephemeral and hence unreliable, an egocentric

orientation strategy can be more effective. These habitats may contain short fields of view such as found in woodlands or dense foliage and may be devoid of landmarks entirely such as featureless deserts (Buhlmann *et al.* 2011) or contain few stable landmarks such as in fast flowing rivers (Odling-Smee & Braithwaite 2003). Biased use of orientation strategy has been previously linked to the availability of cues in an animal's habitat. Populations of three-spined sticklebacks, *Gasterosteus aculeatus*, from fast-flowing rivers, where landmarks are ephemeral and frequently move with water flow, rely on egocentric strategies whereas those from stable pond habitats, where landmarks persist, rely on allocentric strategies (Odling-Smee & Braithwaite 2003). What is not yet established is whether dominant orientation strategies are a consequence of experience within a particular habitat or whether animals have an inherent cognitive bias for a certain strategy. A laboratory-based study of performance on an egocentric-only maze task showed that mound-building mice, *Mus spicilegus*, which naturally rely on egocentric cues to navigate burrows during the winter, outperform open-living eastern house mice, *Mus musculus musculus*, which can use both strategies year-round (Bruck *et al.* 2017). Tested mice were bred in the laboratory and therefore never directly experienced these habitats themselves, indicating that an innate component to this cognitive trait may exist. It is unknown whether any innate biases persist within populations and whether individuals that use one strategy preferentially may also select more strongly for

¹Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter EX4 4QG, UK

²Movement Ecology Laboratory, Department of Ecology, Evolution and Behaviour, Edmond J. Safra Campus, The Hebrew University of Jerusalem, Jerusalem 9190401, Israel

³Blavatnik School of Computer Science, Tel-Aviv University, Tel Aviv 67798, Israel

*Correspondence: E-mail: c.e.beardsworth@gmail.com

habitats, relative to conspecifics, that are more easily navigated using their preferred orientation strategy.

While interspecific differences in spatial cognitive ecology are not new (Pravosudov & Roth II 2013), intraspecific differences in cognitive traits have only recently been investigated (Boogert *et al.* 2018) and linked to elements of spatial ecology (Bessa Ferreira *et al.* 2019; Shaw *et al.* 2019). The clearest link between orientation strategy and spatial ecology is in habitat selection, since habitats can differ markedly in their salience of cues. Various non-cognitive explanations for habitat selection range from landscape structure (Morellet *et al.* 2011), natal habitat experience (Davis & Stamps 2004; Nielsen *et al.* 2013), risk (Loveridge *et al.* 2017) or prey density (Bijleveld *et al.* 2016). In general, individuals within a population or species will select similar habitats, but evidence is emerging that some individuals may select or avoid habitats more strongly than others within the same population (Leclerc *et al.* 2016). To link spatial ecology to cognition via orientation strategy, it is necessary to assess an individual's preferred orientation strategy early in life in a standardised environment, before entry into a more complex, natural habitat. We can then ask if their preferred strategy can explain differences in subsequent habitat selection and movement within it.

Identifying biases in orientation strategy can be achieved using maze tasks, typically where the goal location is baited with food or provides an escape (Grech *et al.* 2018). The type of cues used to successfully complete the maze can be assessed in two ways. First, performance in single-strategy mazes that either provide stable allocentric or egocentric cue use (but not both) gives an indication of the proficiency of an individual with a particular strategy (Rodriguez *et al.* 1994; Bruck *et al.* 2017). Second, dual-strategy mazes (that allow consistent use of egocentric and/or allocentric cues) allow an animal to learn to navigate a maze using their preferred strategy, before presenting the animal with a single-strategy probe trial. Good performance on the probe trial suggests that the animal used the same strategy to learn the task as was tested, and poor performance suggests use of the other strategy or a mix (Alves *et al.* 2007; Tierney & Andrews 2013; Ferguson *et al.* 2019). These tasks should be completed in early life before entry into a novel environment to assess associations between orientation strategy and habitat selection. Consequently, testing whether spatial cognition biases habitat selection is not trivial, and requires a study system permitting controlled cognitive assessments and movement monitoring in the wild.

Pheasants, *Phasianus colchicus*, provide a useful system to investigate links between orientation strategies and spatial ecology. Chicks can be reared under controlled conditions, accounting for potential effects of experience during early life and maternal influences. Furthermore, variation between individuals in their spatial cognition is well documented (Whiteside *et al.* 2016; Langley *et al.* 2018a, 2018b), although inherent differences in orientation strategy use are unstudied. In the UK, juvenile pheasants are released annually in large groups into the wild to supplement hunting stock. This provides a unique opportunity to measure the cognitive biases of young individuals reared under controlled conditions, before releasing birds into the same initial habitat and monitoring their movements. In the wild, pheasants occupy a range of habitats, including

complex and cluttered woodland environments, open farmland and rural agricultural yards. Habitat selection has previously been suggested to differ by sex, with females feeding more often in woodland than males (Hill & Ridley 1987), so we may expect sex differences in orientation strategy.

In this study, we first established whether individuals differed in their orientation strategy, despite homogeneity of rearing environment. We then released these birds into the same environment and used a novel, high temporal (1/8 Hz) and spatial resolution (~5–10 m) tracking system (Weiser *et al.* 2016; Toledo *et al.* 2020) to monitor their movements. Based on previous habitat selection work in pheasants, we expected that woodland would be selected for (Aebischer *et al.* 1993), with stronger selection by females (Hill & Ridley 1987). We investigated whether individual differences in orientation strategies influenced patterns of habitat selection in free-roaming birds. We expected that animals with an allocentric bias as juveniles would select habitats containing conspicuous, distinct and stable landmarks. In the context of this study, open and urban habitats offer vistas that include large and stable landmarks such as buildings, roads, telegraph posts and hedgerows. Open habitat was predominantly large grass fields where landmarks could be seen on distant horizons, but there were few distinct features within the fields themselves. Urban habitat comprised farmyards, buildings and gardens containing plentiful distinct anthropogenic items that could serve as landmarks, visible over moderate distances. In contrast, woodland was densely vegetated, reducing visual fields and making distal landmarks difficult to detect. We predicted that, if habitat selection was driven by inherent biases in orientation strategies, then individuals that exhibited an allocentric bias would select more strongly for open and urban habitats, relative to other birds. Furthermore, if matching strategy preference to availability of cues is useful, we may also expect differences in movement that could be advantageous, such as increased speed or directedness of movement.

METHODS

Subjects and housing

One hundred and twenty-six pheasant chicks were habituated to human experimenters from one day old (24 May 2018) and housed in four groups ($3 \times n = 32$, $1 \times n = 30$) with *ad libitum* access to age appropriate food (Keeper's Choice, Norfolk, UK) and water. They were trained to voluntarily enter a 75 cm \times 75 cm testing chamber following positive reinforcement (mealworm rewards) during their first 3 weeks of life. Birds entered the testing chamber from their holding pen (1 m \times 2 m) through a sliding door and exited through a pulley-assisted door to a separate pen (0.75 m \times 1.25 m) with further access to an outdoor shelter (1.5 m \times 2.4 m) and an outdoor enclosure (4 m \times 12 m). All birds were individually identifiable using numbered patagial tags.

Maze task

The testing chamber was converted into a 3 \times 3 cell maze using 35 cm high walls of opaque black plastic (Fig. 1a). At

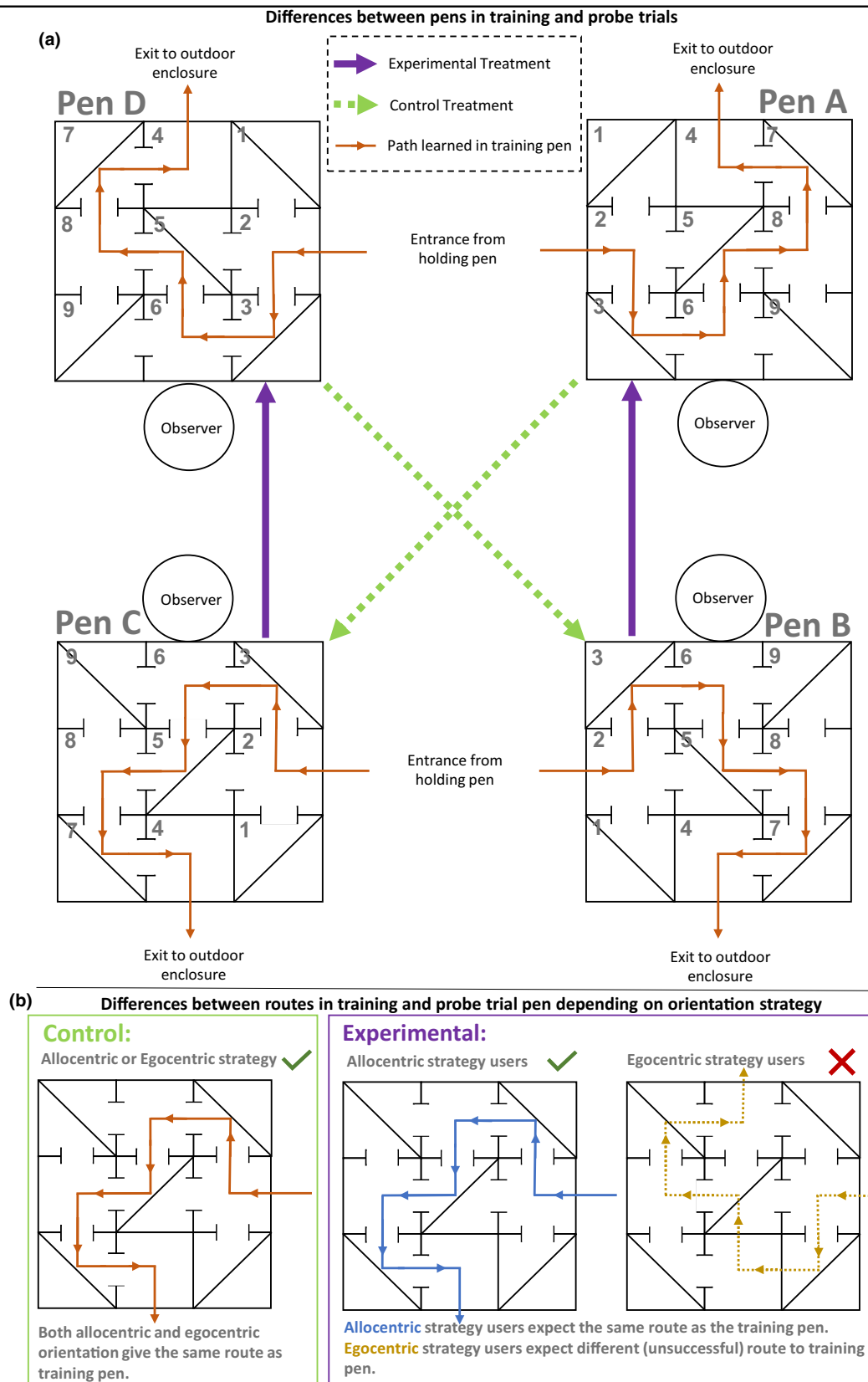


Figure 1 (a) Maze task schematic for each pen. Orange line indicates the most efficient route for pheasants to reach rewarded/exit cell (cell 4). Each pen consists of a holding area, maze and outdoor enclosure. Birds are swapped between pens (following the direction of the arrow) after the final training trial to a pen with the same allocentric cues but where egocentric cues are either the same (control treatment: green dashed arrow) or different (experimental treatment: purple solid arrow). (b) Example of expected routes that pheasants would attempt based on their memories of the training trial, taking into account the location of allocentric cues and direction of turns on entrance into the chamber (egocentric). Both allocentric and egocentric strategies are successful in the control treatment but only allocentric strategy is successful in the experimental treatment.

5 weeks old (3–5 July 2018), birds were habituated to the maze using mealworm rewards scattered throughout the cells, with all walls between cells having 10 cm wide openings giving access to all neighbouring cells. Once birds were voluntarily entering the chamber alone with no obvious signs of stress, we added four extra walls to create a maze structure. To solve the task as bird would enter the chamber and make a minimum of seven orientation decisions to reach to the exit cell where they were rewarded with three mealworms and could exit the maze (Fig. 1a). We assessed maze performance by subtracting 7 (the minimum cells to complete the maze) from the total number of cells entered (defined by the bird's head entering the cell). Birds completed eight training trials. Extra-maze (allocentric) cues such as the experimenter's location or the pulley system for the exit door (which ran from the experimenter to the opposite wall of the testing chamber) were the same across pens.

After the eighth training trial, birds in two of the pens were swapped to pens where the maze had undergone a 180-degree rotation (Fig. 1a) so that egocentric cues, but not allocentric cues were disrupted. As a control, birds in the other two enclosures were moved to pens containing an identical maze to their previous pen and surrounded by the same extra-maze cues so birds could successfully use the same strategy to complete the maze. The birds were left overnight to habituate to their new pen, although separated from the novel mazes. The following day (6 July 2018), chicks were given a probe trial on the new maze task. To determine which orientation strategy an individual used, we made explicit predictions about how they would move when in the new maze. In the experimental treatment, birds that used an egocentric strategy were expected to attempt to use a route that was no longer possible since the learned turning pattern of the maze was reversed throughout (Fig. 1b). We therefore expected them to make more errors (perhaps many more, since the memory of the route is totally disrupted). Even if birds did not solely rely on an egocentric strategy and instead used a mixed strategy, they would make more errors since the disassociation of the cues causes confusion. Alternatively, birds that use primarily allocentric cues (such as observer location) to navigate the maze would have access to the same cues that they used in the training trials and therefore we expected them either make the same number or fewer errors (Fig. 1b). In essence, any reliance on an egocentric orientation strategy should lead to more errors overall. We predicted a bimodal distribution in the difference in errors between the final training trial and the probe trial, demonstrating the two different strategies within the experimental treatment. Seventy-eight birds (control = 24 (F), 20 (M), experimental = 17 (F), 17 (M)) completed all eight training trials and the probe trial.

Maze task analysis

All statistical analysis was performed in R (v.3.5.3) (R Core Team 2019) using the R Studio wrapper (v.1.2.1335) (RStudio Team 2018). To investigate whether the birds learned the maze task at a population level, we fitted a generalized linear mixed model (*lme4* v1.1-21 (Bates *et al.* 2015)) with a Poisson error structure and log-link function to assess whether number

of errors decreased with trial number. We controlled for potential differences between sex and treatment group by including these as fixed effects and Bird ID as a random effect in the model.

We assessed an individual's orientation strategy use by measuring the difference in errors between the final training trial and the probe trial. Individuals in the experimental treatment that maintained or improved performance in the trials after their switch to a new pen were considered to be using an allocentric strategy, which remained efficient in the new pen. Birds that made more errors after their switch were considered to have used either a mixed strategy or egocentric strategy to learn the maze. To assess what factors explained individual differences in their orientation strategy, we fitted a binomial GLM where improved performance (0) and worsened performance (1) was used as the response variable. Sex and treatment were included as fixed effects to test whether differences in strategy existed between sexes and to test whether the control treatment outperformed the experimental treatment. Differences between treatments were expected if some or all learners attended to egocentric cues in the learning phase and no difference was expected if pheasants used allocentric cues. We fitted both sex and treatment as fixed effects, and their interaction to identify whether sexes responded differently between treatments. For all model selection, we used the *MuMIn* package (v1.43.17) to identify and average the top candidate models ($\Delta AIC_{\min} \leq 2$). We present the weighted averaged coefficients and standard errors.

We investigated within-treatment differences in improvement score using chi-square tests. This first confirmed that birds within the control treatment were improving in performance between the final learning trial and probe trial, indicating that the birds solved the training and probe mazes in the same way. Second, for the experimental treatment, we expected more birds to 'improve' if they followed an allocentric strategy and make more errors in the probe trial than in the final learning trial if they followed an egocentric or mixed strategy.

Release of birds

At 9 weeks old, birds were sexed (via plumage) and tagged with ATLAS radio tags (see below). We monitored birds for one week in captivity to assess tag effects, before releasing them into an open topped woodland pen of $\sim 4000 \text{ m}^2$ in which they were protected from terrestrial predators. Birds could disperse by flying over the fence and could re-enter through one-way tunnels. We provided supplementary food (wheat) at 43 feeders situated throughout our field site.

Tracking birds after release

We tracked the birds using the ATLAS reverse-GPS system (Toledo *et al.* 2020) from 26 July 2018 to 10 February 2019. This system uses fixed position receiver stations to detect and collect the time of arrival data from tag-derived radio-signal which were then filtered and smoothed (Appendix S1) to reveal locations of each bird at 5-min resolution. We only analysed data from birds in the experimental treatment

($n = 34$), since these were the only ones for which we could assign strategy use. To ensure that the locations that we assessed were of live birds, we rigorously searched the field site, guided by the ATLAS system. We confirmed the date of death for 16 experimental birds (nine allocentric, seven ego-centric/mixed) by finding corpses and assessing trajectories of their ATLAS data until natural movement ceased. Five birds were removed from the analysis as their trajectories did not indicate natural movement patterns, but we did not find their corpses. We restricted analysis to data collected at least three weeks after the birds had been released into the pen (17 August 2018), by which time they had begun to explore the surrounding habitat. Since some birds had much shorter sampling durations than others (due to tag failure, death or dispersal from the study area (Appendix S3)), we only used data up to 31 October to maintain comparability between individuals. Twenty birds from the experimental treatment (6 females, 14 males) had movement data that matched these criteria.

Habitat selection and movement of free-living birds

We created a habitat map for our field site consisting of three habitat types: woodland, open and urban. We used the *National Forest Inventory Woodland GB 2017* shapefile (accessed 21 February 2019: <http://data.gov.uk>) as a base for our habitat map. Definitions of woodland for the national forest inventory is a minimum area of 0.5 ha with a minimum width of 20 m unless a narrow corridor connects two or more woodland areas. This did not include most hedgerows, but we felt that hedgerows likely gave similar visibility to open habitat and these were therefore classified as such. We manually digitised urban habitats, classified as farm yards, gardens, buildings and rural homes and gardens using a Bing satellite layer (print rights under the Microsoft® Bing™ Maps Platform API's Terms of Use, April 2019) for reference in QGIS (QGIS Development Team 2017). Areas that were not designated as woodland or urban habitats were classified as open habitat. This included grazing grassland, hedgerows and a small wetland. The final habitat map covered a 3 km × 3 km area and encompassed all detected movement of the 20 experimental birds (see Appendix S2).

Habitat selection and movement are interlinked and failure to account for movement can bias habitat selection estimates (Forester *et al.* 2009; Avgar *et al.* 2016). Using the *amt* R package (Signer *et al.* 2019), we evaluated habitat selection using integrated step selection analysis (iSSA), which allows for the simultaneous inference of both habitat and movement processes (Avgar *et al.* 2016). In all iSSA models, for every 5-min relocation (step), we simulated 10 random steps, where step length was sampled from a gamma distribution and turn angles from a von Mises distribution (Duchesne *et al.* 2015). We only analysed temporally regular trajectories of at least three location estimates and that were collected during the day (from civil dawn to civil dusk), since pheasants roost in trees overnight. Habitat covariates were extracted at start and the end point of each step, enabling us to investigate both selection and movement (Dickie *et al.* 2020).

We tested the fit of four initial iSSA models to explain habitat selection. We found the availability (number of random

steps in particular habitat) in urban habitat to be < 1% for some birds and generally low in all birds. Since the urban environments in this study were agricultural standings and yards where stable distal landmarks could still be viewed, much like open habitat, we combined open and urban habitats into a 'non-woodland' category and simply compared woodland (the reference category, where we expect allocentric navigation to be less effective) to non-woodland habitat (a relatively open habitat where we expect allocentric navigation to be more effective). We included step length and the natural logarithm (\ln) of step length as covariates in each iSSA model. Resulting coefficients of step length and \ln step length can be used to modify the shape and scale of the initial gamma distribution. The product of these parameters gives the mean displacement distance per step (speed) while controlling for habitat selection. We also included the cosine of turning angles as a covariate to give an indication of directional persistence, whereby positive β -coefficients indicate forward movement and negative values indicate reversals. Our final covariate was the distance to the nearest feeder. We may expect feeders to act as attractors, thus influencing movement choices. Incorporating this as a log-transformed variable allows the spatial effects to decay exponentially with distance and is commonly used for continuous spatial variables in iSSAs (Prokopenko *et al.* 2017). However, in our small study area, we may not expect such decays as birds are rarely far from a feeder, therefore we tested the fit of both distance and log-transformed distance. Overall, we tested the fit of 8 candidate models by calculating a bootstrapped ($n = 1000$) AIC per individual and chose the model that was the most supported (Table 1). To calculate log relative selection strength (log-RSS, Avgar *et al.* 2017), we compared differences in habitat type at the step end points and set all continuous covariates to the median values from the observed population and the starting step as woodland.

To assess differences in habitat selection, speed, and directional persistence, we fitted three gaussian GLMs using the bootstrapped log-RSS, mean speed and mean of the cos(turning angle) iSSA coefficients as response variables respectively.

Table 1 Set of candidate models to test hypotheses relating to selection and movement of pheasants. After bootstrapping (1000 iterations), nAIC represents the number of individuals for which the model had the lowest AIC

Selection: How likely is an individual to select non-woodland over woodland habitat?		nAIC _{best}
Base (M1)	Habitat(end) + stepLength + \ln stepLength + \cos TurnAngle	1
M2	Base + distFeeder	1
M3	Base + \ln distFeeder	0
Movement: Does an individual move faster or more directly in different habitats types?		
Base (M4)	Habitat(start) × (stepLength + \ln stepLength + \cos TurnAngle)	0
M5	Base + distFeeder	0
M6	Base + \ln distFeeder	0
Selection + Movement		
Base (M7)	Habitat(end) + Habitat(start) × (stepLength + \ln stepLength + \cos TurnAngle)	0
M8	Base + distFeeder	13
M9	Base + \ln distFeeder	3

In the habitat selection model, we included sex, strategy, their interaction and the availability (n random steps in non-woodland habitats) as covariates. For each of the movement GLMs we included strategy, sex, habitat type and their interactions. We also included the inverse variance of the response variable ($1/SE^2$) as a weight in all models to reduce the contribution of less certain values. We identified and averaged the top candidate models ($\Delta AIC_{\min} \leq 2$) and present the weighted average coefficients and standard errors.

RESULTS

Did the pheasants learn the maze task?

Pheasants made fewer errors as the trials progressed (Trial 1 mean = 5.09, SD = 6.23; Trial 8 mean = 3.84, SD = 5.68). The top model included only trial number ($w_i = 0.51$) indicating that they were learning, although learning was slow ($\beta = -0.05$, SE = 0.01, Appendix S4). Models with either sex ($\Delta AIC_c = 1.82$, Male: $\beta = -0.01$, SE = 0.07) or treatment ($\Delta AIC_c = 1.82$, Experimental: $\beta = 0.01$, SE = 0.07) in addition to trial number were indistinguishable from the top model but the estimate and weights of these models were small (Table 2).

Did birds vary in chosen orientation strategy?

Treatment best explained the number of errors made in the probe trail ($w_i = 0.68$, Table 2). Birds from the experimental treatment were more likely to make more errors in the probe trial than in the final learning trial than birds from the control treatment ($\beta = 1.78$, SE = 0.54, Fig. 2a). Sex was not included in the top model and the closest ΔAIC_c that included sex was 2.16.

Within the control treatment, 84% of birds (37/44) continued to improve their performance between the final training trial and the probe trial ($\chi^2 = 20.455$, d.f. = 1, $P < 0.001$, Fig. 2a). In contrast, in the experimental treatment 47% of

birds (16/34) continued to show an improvement between the final learning trial and the probe trial while 53% (18/34) showed no such improvement or got worse ($\chi^2 = 0.118$, d.f. = 1, $P = 0.732$, Fig. 2a). Within the experimental treatment, there was a bimodal distribution of errors, indicating two distinct strategies (Fig. 2b). We classified birds in the experimental treatment that maintained their performance or improved in the rotated (probe) maze to be relying on an allocentric orientation strategy and classified birds that performed worse to be relying on an egocentric or mixed orientation strategy.

Habitat selection

Pheasants selected for woodland habitat (19/20 birds) over non-woodland habitats. While the top log-RSS GLM candidate model was the null model, a second model incorporating strategy was indistinguishable from the best model ($\Delta AIC_c = 1.70$, Table 3). Full averaging of the two top models indicated that birds with an allocentric bias had a slightly lower aversion to non-woodland habitat than egocentric/mixed strategy birds (Fig. 3a). Sex was not present in any of the top models for habitat selection (closest model $\Delta AIC_c = 3.00$). We note that there was one potential outlier that selected for non-woodland habitat over woodland (Fig. 3a), but even with this outlier removed the results did not change.

Movement

The top GLM composition for speed included an interaction between sex and habitat and no other models had $\Delta AIC_c < 2$ (Table 3). While both males and females moved faster in non-woodland habitat, males had a higher mean speed than females (Fig. 3b). For directional persistence, the top model included sex and habitat, but a second model was indistinguishable ($\Delta AIC_c = 1.36$) and also included an interaction between sex and habitat (Table 3). The mean β coefficients for the cosine of the turning angle for all birds was negative, indicating that pheasants made many reversals, regardless of habitat (Fig. 3c). However, while females did not change their directional persistence between habitats, males had higher coefficients in general and this was more pronounced in non-woodland habitat (Fig. 3c). Orientation strategy was not included in any of the top models therefore we found no evidence to suggest that orientation strategy is associated with movement in this study.

DISCUSSION

Individual pheasants use different orientation strategies to learn a maze task early in life with about half of our experimental group exhibiting an allocentric bias and the other half preferring either an egocentric or mixture of strategies. Males and females did not differ in their biases for orientation strategies. In the wild, pheasants selected for woodland over non-woodland habitats, matching previous findings (Lachlan & Bray 1976; Hill & Ridley 1987), although individuals that had an allocentric bias also exhibited a slightly lower

Table 2 Top models for the two cognition GLMs with corresponding AICc, weights and their full averages where covariates that are not included in the model have a β of zero

		AICc	Weight
Reduction of errors over trials			
Top models:	Trial number	0	0.51
	Trial number + Sex	1.82	0.21
	Trial number	1.85	0.20
	+ Treatment		
Full average (β (SE)):			
Intercept	1.48 (0.09)		
	Trial number	-0.05 (0.01)	
	Sex (male)	-0.01 (0.07)	
	Treatment (experimental)	0.01 (0.07)	
Difference in scores (final trial – probe trial)			
Top models:	Treatment	0	0.68
	β (SE):		
	Intercept	-1.67 (0.41)	
	Treatment	1.78 (0.54)	

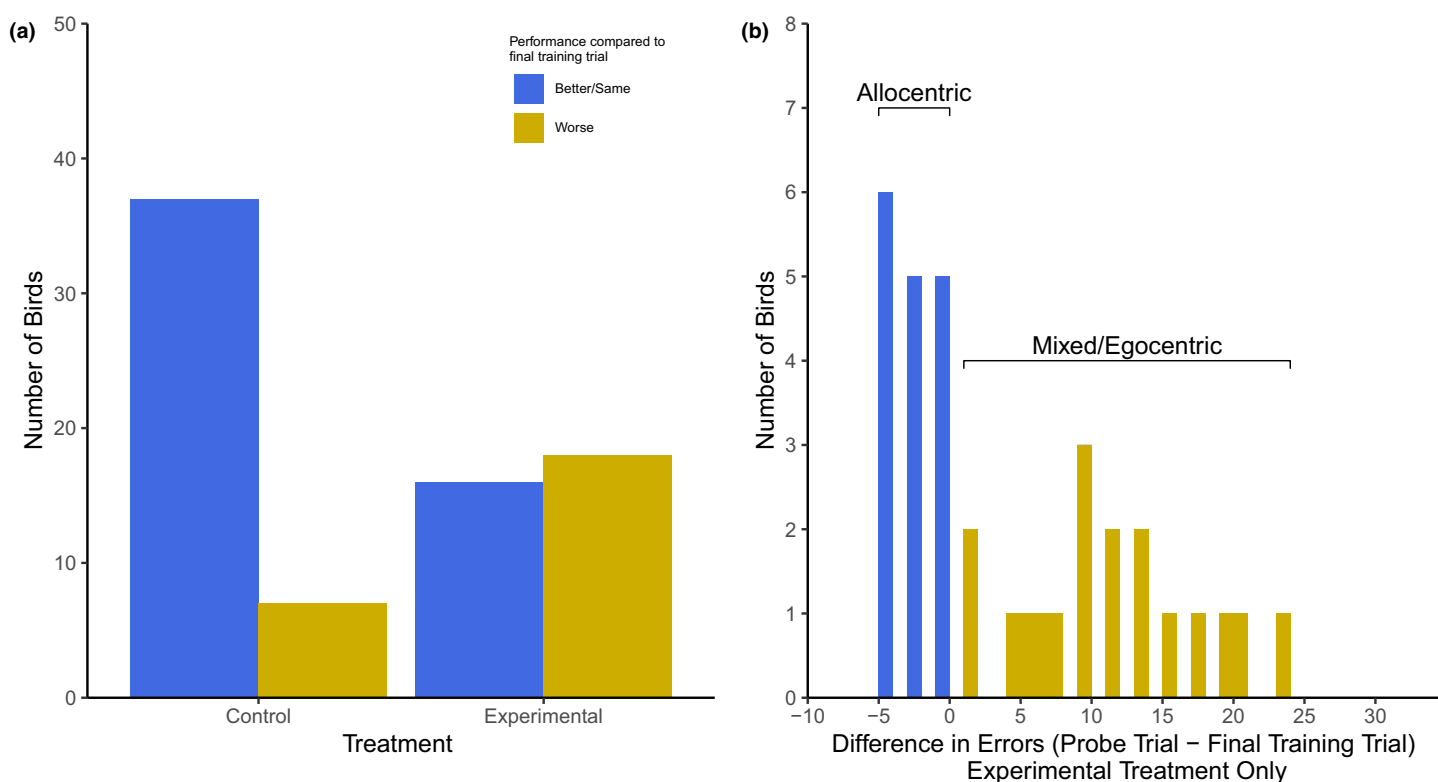


Figure 2 (a) Differences in performance between birds in the control and experimental treatments where blue indicates improvement or the same score on the probe trial when compared to the final training trial and yellow indicates a worse score. (b) Distribution of birds classified as allocentric (blue) or mixed/egocentric strategy users (yellow) in a rotated maze (experimental treatment birds only).

Table 3 Top models for the three habitat selection and movement GLMs with corresponding AICc, weights and their full averages where covariates that are not included in the model have a β of zero

		AICc	Weight
Log-RSS			
Top models:	Availability	0	0.55
	Strategy + Availability	1.70	0.28
Full average (β (SE)):			
Intercept	-5.66 (0.05)		
Availability	0.00 (0.00)		
Strategy (allocentric)	0.02 (0.04)		
Speed			
Top models:	Habitat + Sex + Habitat:Sex	0	0.67
β (SE):			
Intercept	20.91 (0.27)		
Habitat (non-woodland)	4.19 (0.61)		
Sex (male)	1.22 (0.38)		
Sex: Habitat	2.32 (0.75)		
Directional persistence			
Top models:	Habitat + Sex	0	0.43
	Habitat + Sex + Habitat:Sex	1.36	0.22
Full average (β (SE)):			
Intercept	-0.81 (0.04)		
Habitat (non-woodland)	0.12 (0.06)		
Sex (male)	0.19 (0.05)		
Habitat: Sex	0.03 (0.07)		

avoidance of non-woodland habitats. We did not detect any obvious movement advantages to the matching of cognitive bias to habitat selection. The preferred strategy an individual

used did not predict either speed or directional persistence in either habitat type. Instead, we found these descriptors of movement to be linked to sex.

In contrast with other studies where almost all individuals followed one particular strategy (Alves *et al.* 2007), we found that pheasants reared in intentionally controlled and standardised environments prior to their testing, exhibited differences in their preferred orientation strategies. We therefore suggest that individuals of the same species may exhibit differing cognitive biases in the way that they acquire and process spatial information, differentially relying more or less on cues relative to the environment or themselves, at least in early life. While we cannot exclude the explanation that very subtle differences in experience may have led to the differential use of spatial cues in pheasant chicks, our efforts to ensure uniform rearing conditions from hatching make it likely that other factors, for example genetic differences, may influence attention to cue types. These early-life differences in orientation strategy were not explained by sex, which others observed to be linked to habitat selection in the wild (Hill & Ridley 1987). However, we did not find evidence for these sex differences in habitat selection. Instead, we found an interaction between habitat type and sex when considering how an animal moves (speed and directional persistence). While both sexes seemed to move faster though non-woodland compared to woodland habitat, males moved faster than females. We did not investigate the cause of this sex difference but suggest that it could be due to differences in body size (Whiteside *et al.* 2016). The

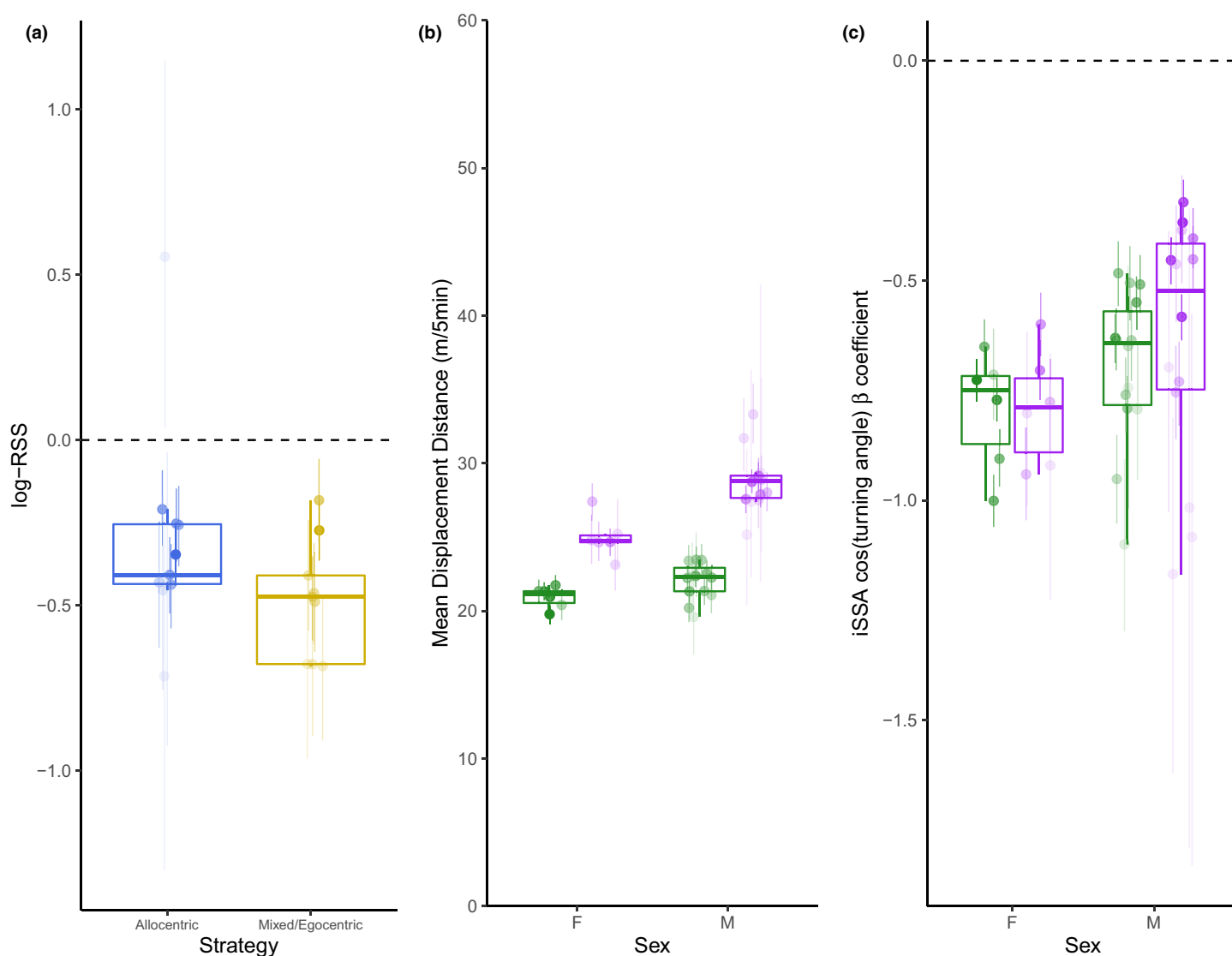


Figure 3 Boxplots with individual points overlaid showing 95% confidence intervals for: (a) log relative selection strength (log-RSS) of non-woodland habitats with woodland as the reference habitat for allocentric (blue) and mixed/egocentric (yellow) strategy users; (b) Mean displacement distance (speed) of female and male birds in woodland (green) or non-woodland (purple) habitat; and (c) the directionality of females and males in woodland (green) and non-woodland habitat (purple), determined by the bootstrapped beta-coefficient from the individual iSSA for cosine of the turning angle. Since models were weighted by inverse variance, transparency of the individual points indicates inverse variance values with less transparent points indicating higher (more certain) inverse variance.

interaction that we found between sex and habitat in describing directional persistence is more difficult to explain. We suggest that high rates of foraging behaviour, which is related to tortuous movements as animals exploit their landscape (Bracis *et al.* 2015), could lead to negative directionality estimates. If males move faster than females in non-woodland habitat, they may also be foraging less within these habitats leading to directional persistence values that are closer to zero. Accounting for these differences in movement allows us to make robust inferences about habitat selection.

Differences in an individual's orientation strategy preferences early in life helped to explain differences in their habitat selection when in the wild, although this effect was small, but robust to the removal of an outlier. Specifically, and as we predicted, individuals that were biased towards an allocentric

orientation strategy either selected non-woodland habitats or avoided them to a lesser extent than other birds, perhaps because they were more competent at orientating effectively using prolific, stable and conspicuous landmarks (Mora *et al.* 2012; Ferguson *et al.* 2019). While the effect was small, we suggest that this may not necessarily be due to a weak relationship between habitat selection and orientation strategy, but to our ability to detect bias towards each strategy. Our probe trial was biased towards allocentric individuals and so we were unable to distinguish between individuals that used an egocentric strategy and those that used a mixed strategy (Etienne *et al.* 1996, 1998; Marchette *et al.* 2011). Future studies could attempt to tease apart biases towards allocentric or egocentric cues, or a mixed strategy to obtain a clearer estimate of how these biases influence habitat selection. However,

we note that incorporating multiple mazes and probe tasks to assay relative use of both strategies is not trivial. It was not logistically possible in this study due to time constraints around the release of pheasants.

Our work demonstrates that the spatial ecology of individuals, long assumed to have an important but rather complex cognitive dimension (Nathan *et al.* 2008; Fagan *et al.* 2013), may be shaped by cognitive biases for particular orientation strategies that determine critical aspects of their landscape use. Here, we offer an alternative hypothesis to explain disproportionate usage of particular orientation strategies between populations that occupy different habitats, which has previously been suggested to have developed following occupancy (Odling-Smee & Braithwaite 2003; Bruck *et al.* 2017). Differences in cognitive biases towards using allocentric or mixed/egocentric orientation strategies early in life, determined before occupancy of a natural habitat, was related to differences in habitat selection in the wild, later in life. This finding has important consequences for our understanding of home range occupancy (Börger *et al.* 2008), migration patterns (Phillips *et al.* 2009) and predicted responses to conservation challenges (Greggor *et al.* 2014) as individuals could be drawn to areas and routes that best suit their cognitive biases.

ACKNOWLEDGEMENTS

The authors thank Rothamsted Research North Wyke for accommodating the rearing and release of the pheasants and various landowners in Mid Devon for hosting our tracking equipment. The authors also thank the Minerva Center for movement ecology for their persistence in developing ATLAS. Additionally, the authors thank Kandace Griffin and Anna Morris for their help with data collection and animal husbandry. This work was funded by an ERC Consolidator award (616474) to JRM. Finally, the authors thank Tal Avgar and two anonymous reviewers for their thoughtful comments on the manuscript.

AUTHORSHIP

CEB, MAW and JRM conceived the idea for the manuscript. CEB conducted the analyses and led the writing of the manuscript. CEB, PRL, MAW, JOvH and JRM collected the cognition data. CEB, MAW and JRM collected the movement data. RN, YO and ST developed the reverse-GPS system and provided support throughout data collection. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13694>.

DATA AVAILABILITY STATEMENT

Data and R code relevant to this article are available at Zenodo: <https://doi.org/10.5281/zenodo.4428265>

REFERENCES

- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74, 1313–1325.
- Alves, C., Chichery, R., Boal, J.G. & Dickel, L. (2007). Orientation in the cuttlefish *Sepia officinalis*: response versus place learning. *Anim. Cogn.*, 10, 29–36.
- Avgar, T., Lele, S.R., Keim, J.L. & Boyce, M.S. (2017). Relative selection strength: quantifying effect size in habitat- and step-selection inference. *Ecol. Evol.*, 7, 5322–5330.
- Avgar, T., Potts, J.R., Lewis, M.A. & Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods Ecol. Evol.*, 7, 619–630.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, 1–48.
- Bessa Ferreira, V.H., Peuteman, B., Lormant, F., Valenchon, M., Germain, K., Brachet, M. *et al.* (2019). Relationship between ranging behavior and spatial memory of free-range chickens. *Behav. Process.*, 166, 103888.
- Bijleveld, A.I., MacCurdy, R.B., Chan, Y.C., Penning, E., Gabrielson, R.M., Cluderay, J. *et al.* (2016). Understanding spatial distributions: negative density-dependence in prey causes predators to trade-off prey quantity with quality. *Proc. R. Soc. B Biol. Sci.*, 283(1828), 20151557.
- Bisch-Knaden, S. & Wehner, R. (2001). Egocentric information helps desert ants to navigate around familiar obstacles. *J. Exp. Biol.*, 204, 4177–4184.
- Boogert, N.J., Madden, J.R., Morand-Ferron, J. & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Phil. Trans. R. Soc. B*, 373, 20170280.
- Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.*, 11, 637–650.
- Bracis, C., Gurarie, E., Van Moorter, B. & Goodwin, R.A. (2015). Memory effects on movement behavior in animal foraging. *PLoS ONE*, 10, 1–21.
- Bruck, J.N., Allen, N.A., Brass, K.E., Horn, B.A. & Campbell, P. (2017). Species differences in egocentric navigation: the effect of burrowing ecology on a spatial cognitive trait in mice. *Anim. Behav.*, 127, 67–73.
- Buhlmann, C., Cheng, K. & Wehner, R. (2011). Vector-based and landmark-guided navigation in desert ants inhabiting landmark-free and landmark-rich environments. *J. Exp. Biol.*, 214, 2845–2853.
- Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends Cogn. Sci.*, 10, 551–557.
- Davis, J.M. & Stamps, J.A. (2004). The effect of natal experience on habitat preferences. *Trends Ecol. Evol.*, 19, 411–416.
- Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M. & Avgar, T. (2020). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *J. Anim. Ecol.*, 89, 623–634.
- Duchesne, T., Fortin, D. & Rivest, L.P. (2015). Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. *PLoS ONE*, 10, 1–12.
- Etienne, A.S., Maurer, R. & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *J. Exp. Biol.*, 199, 201–209.
- Etienne, A.S., Maurer, R., Derivaz, V., Georgakopoulos, J., Griffin, A., Rowe, T. *et al.* (1998). Cooperation between dead reckoning and external position cues. *J. Navig.*, 51, 23–34.
- Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G. *et al.* (2013). Spatial memory and animal movement. *Ecol. Lett.*, 16, 1316–1329.
- Ferguson, T.D., Livingstone-Lee, S.A. & Skelton, R.W. (2019). Incidental learning of allocentric and egocentric strategies by both men and women in a dual-strategy virtual Morris Water Maze. *Behav. Brain Res.*, 364, 281–295.
- Forester, J.D., Im, H.K. & Rathouz, P.J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, 90, 3554–3565.

- Grech, A.M., Nakamura, J.P. & Hill, R.A. (2018). The importance of distinguishing allocentric and egocentric search strategies in rodent hippocampal-dependent spatial memory paradigms: getting more out of your data. In: *The Hippocampus - Plasticity and Functions* (ed Stuchlik, A.). IntechOpen. Available at: <https://www.intechopen.com/books/the-hippocampus-plasticity-and-functions/the-importance-of-distinguishing-allocentric-and-egocentric-search-strategies-in-rodent-hippocampal->. Last accessed 19 October 2019.
- Greggor, A.L., Clayton, N.S., Phalan, B. & Thornton, A. (2014). Comparative cognition for conservationists. *Trends Ecol. Evol.*, 29, 489–495.
- Hill, D.A. & Ridley, M.W. (1987). Sexual selection in winter, spring dispersal and habitat use in the pheasant (*Phasianus colchicus*). *J. Zool. London.*, 212, 657–668.
- Huber, R. & Knaden, M. (2015). Egocentric and geocentric navigation during extremely long foraging paths of desert ants. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.*, 201, 609–616.
- Lachlan, C. & Bray, R.P. (1976). Habitat selection by cock pheasants in Spring. *J. Appl. Ecol.*, 13, 691–704.
- Langley, E.J.G., van Horik, J.O., Whiteside, M.A., Beardsworth, C.E. & Madden, J.R. (2018a). The relationship between social rank and spatial learning in pheasants, *Phasianus colchicus*: cause or consequence? *PeerJ*, 6, e5738.
- Langley, E.J.G., van Horik, J.O., Whiteside, M.A. & Madden, J.R. (2018b). Individuals in larger groups are more successful on spatial discrimination tasks. *Anim. Behav.*, 142, 87–93.
- Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J. & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, 180, 697–705.
- Loveridge, A.J., Valeix, M., Elliot, N.B. & Macdonald, D.W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *J. Appl. Ecol.*, 54, 815–825.
- Marchette, S.A., Bakker, A. & Shelton, A.L. (2011). Cognitive mappers to creatures of habit: differential engagement of place and response learning mechanisms predicts human navigational behavior. *J. Neurosci.*, 31, 15264–15268.
- Mora, C.V., Ross, J.D., Gorsevski, P.V., Chowdhury, B. & Bingman, V.P. (2012). Evidence for discrete landmark use by pigeons during homing. *J. Exp. Biol.*, 215, 3379–3387.
- Morellet, N., Van Moorter, B., Cargnelutti, B., Angibault, J.M., Lourtet, B., Merlet, J. et al. (2011). Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landsc. Ecol.*, 26, 999–1010.
- Müller, M. & Wehner, R. (2010). Path integration provides a scaffold for landmark learning in desert ants. *Curr. Biol.*, 20, 1368–1371.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci.*, 105, 19052–19059.
- Nielsen, S.E., Shafer, A.B.A., Boyce, M.S. & Stenhouse, G.B. (2013). Does learning or instinct shape habitat selection? *PLoS ONE*, 8, 1–5.
- Normand, E. & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Anim. Behav.*, 77, 1195–1201.
- Odling-Smee, L. & Braithwaite, V.A. (2003). The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Anim. Behav.*, 65, 701–707.
- O'Keefe, J. & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford University Press, Oxford.
- Phillips, R.A., Bearhop, S., McGill, R.A.R. & Dawson, D.A. (2009). Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia*, 160, 795–806.
- Pravosudov, V.V. & Roth II, T.C. (2013). Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annu. Rev. Ecol. Evol. Syst.*, 44, 173–193.
- Prokopenko, C.M., Boyce, M.S. & Avgar, T. (2017). Extent-dependent habitat selection in a migratory large herbivore: road avoidance across scales. *Landsc. Ecol.*, 32, 313–325.
- QGIS Development Team. (2017). QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org>.
- Rodriguez, F., Duran, E., Vargas, J.P., Torres, B. & Salas, C. (1994). Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Anim. Learn. Behav.*, 22, 409–420.
- RStudio Team. (2018). RStudio: Integrated Development for R.
- Shaw, R.C., MacKinlay, R.D., Clayton, N.S. & Burns, K.C. (2019). Memory performance influences male reproductive success in a wild bird. *Curr. Biol.*, 29, 1498–1502.e3.
- Signer, J., Fieberg, J. & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.*, 9, 880–890.
- Tierney, A.J. & Andrews, K. (2013). Spatial behavior in male and female crayfish (*Orconectes rusticus*): Learning strategies and memory duration. *Anim. Cogn.*, 16, 23–34.
- Toledo, S., Shohami, D., Schiffner, I., Orchan, Y., Bartan, Y. & Nathan, R. (2020). Cognitive map-based navigation in wild bats revealed by a new high-throughput wildlife tracking system. *Science (80-)*, 369, 188–193.
- Weiser, A.W., Orchan, Y., Nathan, R., Charter, M., Weiss, A.J. & Toledo, S. (2016). Characterizing the accuracy of a self-synchronized reverse-GPS wildlife localization system. In: *15th ACM/IEEE International Conference on Information Processing in Sensor Networks*. Vienna, Austria.
- Whiteside, M.A., Sage, R. & Madden, J.R. (2016). Multiple behavioural, morphological and cognitive developmental changes arise from a single alteration to early life spatial environment, resulting in fitness consequences for released pheasants. *R. Soc. Open Sci.*, 3, 160008.
- Wittlinger, M., Wehner, R. & Wolf, H. (2006). The ant odometer: stepping on stilts and stumps. *Science (80-)*, 312, 1965–1967.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Joshua Lawler

Manuscript received 28 November 2019

First decision made 26 October 2020

Manuscript accepted 16 December 2020