

**Exploration behaviour in wild white-footed mice:
relationships with performance, cognition and survival**



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Introduction

Individuals within the same species or population often exhibit variation in various aspects of their morphology, physiology, and phenology. This individual variation also extends to behavioural traits, which are quantifiable patterns in how organisms act or respond to their environment. Indeed, personality differences (i.e., consistent individual differences in activity, exploration, boldness, aggression, and sociability) have been found in many species in which behavioural difference have been shown to remain stable over time and across different contexts (Sih et al. 2004; Réale et al. 2007, 2010). Behavioural traits are of ecological importance because they are subject to natural selection in many circumstances (Dingemanse and Réale 2005). As such, their variability within species and populations is challenging to explain given that selection should erode genetic variance in any trait (Bulmer 1976), unless spatial and temporal variations exists in patterns of selection (Laskowski et al. 2022). Another possible explanation for the maintenance of variation in “adaptive” personality traits is that it results from selection itself (Laskowski et al. 2022). Indeed, correlational selection can act on particular combinations of traits achieving similar fitness (Sinervo and Svensson 2002) and in the long-term should result in trait co-adaptations not only among personality traits, but with other aspects of the phenotype such as energy metabolism (Careau et al. 2008), life-history traits (Biro and Stamps 2008), morphological defences (Dewitt et al. 1999), and locomotor performance.

The focus on among-individual variation stems from the view that any variation occurring within individuals is likely due to measurement error. However, some information might be hidden at the within-individual level, and related to phenotypic plasticity that causes a given individual to differ between different instances. This level of variation is gaining interest in various fields, especially in behavioural ecology because behavioural traits are usually highly labile and thus present a relatively large amount of within-individual variation due to the environment. Integrating this level of variation when looking at trait correlations becomes especially important when: 1) repeatability is low, and 2) trait correlations differ at the among versus within-individual levels (Dingemanse et al. 2012; Brommer 2013). Thus, by partitioning trait correlations at the among- vs within-individual levels, we can improve our understanding of the multi-level variability and (co)evolution of complex organismal traits.

One of the most popular assays to quantify personality differences is the novel environment test, which presumably captures aspects of exploratory behaviours. The open-field test was first used on laboratory rats (Gould et al. 2009), and involves introducing the animal in an open space surrounded by walls to estimate locomotor activity and willingness to explore (Perals et al. 2017). Since then, the open-field test has been used to measure exploration behaviours in several other species of rodents (Dochtermann and Jenkins 2007; Newar and Careau 2018; Mazza et al. 2020; Agnani et al. 2020), including in white-footed mice (Agnani and Careau 2023). Another easy and common test is the “bag test” used to capture docility (Martin and Réale 2008). In many rodent populations studied so far, individuals who struggle more during the bag test (i.e., are less docile) also tend to cover longer distance in the open-field test, for instance in red squirrels (Boon et al. 2007), karoo bush rats (Agnani et al. 2020) and chipmunks (Montiglio et al. 2012 but see Newar and Careau 2018).

The genus *Peromyscus* is a diversified clade of rodents found on the American continent and the white-footed mouse (*Peromyscus leucopus*) is one of the most commonly used in research in this genus (Smith et al. 2012). This species is abundant in southern Ontario, relatively easy

to capture, and short-lived in the wild (1-2 years), making it an interesting model for evolutionary and integrative ecology research. White-footed mice are omnivorous, nocturnal, mainly solitary, and territorial (Vessey and Vessey 2007) with a promiscuous mating system (Xia and Millar 1991). Consequently, as other rodent members of the “mouse” life-history strategy (Koteja and Weiner 1993), white-footed mice presumably need to thoroughly and frequently explore their environment in search for resources (e.g., food, mates) and by doing so they expose themselves to predation. The general objective of my PhD project is to use a wild population of white-footed mice to investigate some potential causes and consequences of variation in exploratory behaviours.

Co-adaptation between exploratory and locomotor performance traits

As many other small rodents, white-footed mice are preyed upon by a variety of species, such as owls, hawks, falcons, foxes, raccoons, coyotes, weasels or snakes. Thus, it should be safe to assume that they are constantly exposed to predation whenever they venture out of their nest. Within a context of anti-predation, I hypothesise that individual differences in exploration behaviour are co-adapted with locomotor performance. I will consider an organisms performance as its ability to perform a task when maximally motivated (Garland and Losos 1994; Careau and Garland 2012). In light of this definition, performance abilities are thought to constitute an envelope constraining the range of behaviours an individual can express (Bennett 1989). I expect locomotion and behavioural traits to co-evolve in prey species. To explain how performance and behaviour might be co-adapted in the context of an anti-predator response, two hypothesis have been developed (Dewitt et al. 1999). The two premisses in both are that (i) high levels of certain behaviours like activity, exploration, and boldness lead to higher predation risk, and that (ii) better performance in traits such as locomotor speed, agility, or strength increase the probability of escaping predators.

The compensation hypothesis predicts that individuals having better locomotor performance should express riskier behaviours (e.g., increased exploration, activity, boldness), because having better chances of escaping predators would enable them to compensate for their greater exposure due to their risk-prone behaviours. Conversely, individuals having weak locomotor performance might be more at risk of being captured when attacked by predators and thus should express risk-averse behaviours that limit their exposure (e.g., shyness, neophobia). This hypothesis predicts a positive correlation between behaviours that increase predation risk and locomotor performance, as observed in different species (Qi et al. 2014; Kern et al. 2016; Reim et al. 2019).

By contrast, the co-specialization hypothesis predicts a negative correlation between risky behaviours and locomotor performance because it stipulates that both phenotypes additively reduce the risk of predation. In other words, individuals that are overall averse to risk are expected to both 1) minimize both their chances to encounter predators and 2) maximise their chances to escape attacks. This hypothesis predicts a negative relationship between activity/exploration and locomotor performance, and there is empirical support for this relation in all six rodents species tested so far (Blumstein et al. 2010; Newar and Careau 2018; Piquet et al. 2018; Agnani et al. 2020; Agnani and Careau 2023).

Empirical evidence indicates that the relationship between locomotor performance and exploratory behaviour differ depending on the species. In others however, no relation was established between these traits (Videlier et al. 2014; Javier Zamora-Camacho 2022) indicating

that exploratory behaviour and locomotor performance traits could also be decoupled in certain cases. The majority of the studies having investigated this relation have considered a single exploration metric (i.e., distance moved in the open-field test) and most have not partitioned the (co)variation at the within-individual level from the among-individual levels. Thus, more studies integrating different behavioural metrics and partitioning the (co)covariation are needed. Ideally, the (co)variance partitioning exercise should continue down to the genetic level, to allow estimating the narrow-sense heritability and genetic correlations of the traits (Wilson et al. 2010). Quantitative genetic studies, however, typically require large sample size of individuals with known relatedness.

Using a large monitoring dataset, I will consider multiple behavioural metrics extracted from an open-field test (e.g., relative area covered, distance from walls) to determine how they relate to exploration and how they covary with locomotor performance. As some studies have shown that the relation between exploration and performance could be different between sexes (Diamond et al. 2014; Qi et al. 2014), I will also investigate the relation between exploration and performance separately between males and females. Finally, ongoing genetic analyses may allow quantification of the relatedness among individuals sampled, which would open the door to the possibility of extending the (co)variance partitioning exercise to quantify trait heritability and genetic correlations.

Individual differences in spatial learning

White-footed mice presumably need to thoroughly explore their environment for resources, and I suppose that they optimise their foraging efforts by learning about their environment. Therefore, I think that cognition and more specifically learning ability may co-evolve with exploratory behaviours. The term “cognition” refers to the mechanisms enabling animals to collect, retain, and use information from their environment (Shettleworth 2010), such as perception, learning, memory, and decision making. Cognitive performances (i.e., measures of behavioural variables used to quantifying cognitive traits (Griffin et al. 2015)) can influence how individuals react to their environment (Mazza et al. 2018) and consequently impact their fitness (Morand-Ferron et al. 2016). Among cognitive traits, learning plays an important role by enabling animals to adjust their behaviour based on past experiences and allowing them to exploit their environment more effectively (Dukas 2013).

Sih and Del Giudice (2012) proposed that a relation between personality and learning could potentially be caused by two trade-offs acting simultaneously. On one hand, a risk-reward trade-off may occur because bolder, more explorative individuals should be risk-prone, enabling them to acquire potentially more resources such as food or mates and conversely, shyer, less explorative individuals should be risk-adverse and collect fewer resources. On the other hand, a speed-accuracy trade-off may occur because fast explorers should not benefit from extensive sampling and make quick decisions based on less accurate information, whereas slower explorers make safer and more accurate decisions based on relatively longer environment sampling (Sih and Del Giudice 2012). Personality could also constrain or promote learning speed because shier/less explorative individual might experience less of their environment, thus learning less rapidly than bolder/more explorative individuals (for which the reverse should be observed) (Carere and Locurto 2011). Thus although the relation between behaviour and cognition can vary depending on several factors, the main paradigm proposed was that

exploratory behaviours and learning speed should covary positively (Dougherty and Guillette 2018).

But empirical evidence is so far not in favor of a positive relation between exploration and learning speed: personality and learning do covary significantly, but there is no evidence for a consistent positive relationship across species (Dougherty and Guillette 2018). For instance, bolder black caped chickadees learned more quickly to complete an associative task (Guillette et al. 2009) whereas learning rate was lower in bolder brook trout (White et al. 2017). Many personality tests are relatively easy to transfer across species (e.g., a novel environment test can capture exploration in a fish and a bird), while cognitive tests must be specifically tailored to the natural history and behaviour of the species. For example, learning speed can be assessed in chickadee by quantifying how fast individuals learn to discriminate between different notes (Guillette et al. 2009), and in trout by measuring in a maze the time individuals take to enter the correct zone and the amount of time spent in it (White et al. 2017). As a consequence, the apparent diversity of cognitive tests may complicate the comparison of cognitive results across species.

Several cognitive tests have historically been developed for laboratory mice and rats, such that it should be relatively straightforward to transpose the test to study the evolution of cognition in wild mice. To my knowledge, however, there have been few applications of cognitive tests in wild rodents. In one such recent application, McKay et al. (2022) successfully conducted a Morris water maze tests to measure associative learning in wild white-footed mice (McKay et al. 2022). Continuing this line of research, I will be conducting repeated Morris water maze tests on wild white-footed mice and estimate individual variation and repeatability in learning abilities. Given that the mice tested will also undergo the docility and open-field tests, I will partition the phenotypic (co)variance and estimate the potential among-individual correlations between cognition and personality traits. My study might help better understand how learning covary with behavioural traits in a wild population of rodents and shed light on how cognition could be selected (or not) in a natural environment.

Relation between exploratory traits and survival

One of the most important challenges in behavioural ecology is to identify sources of adaptive (co)variation in behaviour. Assuming that exploratory behaviours have fitness consequences, two mechanisms have been proposed to explain the variation in behavioural strategies observed in free-living populations: pace of life syndromes and fluctuating/heterogeneous selection pressures. As both predict a relation between exploration and survival, I will test this link in our population of white-footed mice.

According to the pace of life syndrome (POLS) hypothesis, individuals face a trade-off between current and future reproduction. Assuming that riskier behaviours (e.g., high levels of exploration) affect reproduction or resource allocation, we should expect risk-taking individuals to invest more in resource acquisition or reproduction, which can lead to greater short-term reproductive success at the cost of increasing their mortality risk, leading to shorter lifespans. On the other hand, less risk-taking individuals might behave more cautiously, avoiding immediate risks which could extend their lifespan but decrease their rate of reproduction (Réale et al. 2010). Thus, this view predicts that the expression of risky behaviours should be negatively associated with survival.

In a relatively recent meta-analysis, Moiron et al. (2020) did not find strong evidence for a negative relationship between exploratory behaviour and survival. In other words, supposedly risk-prone behaviours (i.e., higher levels of activity, exploration, boldness) were not necessarily associated with a higher mortality. This could indicate that theories explaining the among-individual variation in behaviours may need to be revised, or that measurements of behaviour and survival may have lacked precision (Moiron et al. 2020).

Rather than favouring different strategies with similar overall fitness (as implied in the POLS hypothesis), selection could also be favouring a single strategy whose optimum would change according to spatial and temporal fluctuations in selective agents (e.g., conspecifics, competing or predators density, resource availability and predictability, etc.). Thus, a part of the among-individual variation in exploratory behaviour may be attributed to spatially and temporally heterogeneous environmental characteristics (Laskowski et al. 2022). Few empirical studies have investigated how spatio-temporal variability in selection occurs and can maintain behavioural variation.

Studies investigating fluctuating selection on personality traits need long-term monitoring of wild populations (Laskowski et al. 2022). Using our monitoring that extends over 8 years and includes up to 4 different sites, I will estimate individual survival using capture-mark-recapture modelling, and I will use the Lande and Arnold (1983) approach to quantify selection on exploratory behavioural and performance traits. By applying the Lande and Arnold framework to these traits in the mouse population, I hope to acquire a clear picture of the adaptive landscape onto which behavioural, locomotor, and potentially cognitive traits evolve.

Research objectives

This project plans to combine measurements of diverse traits (morphological, performance, cognition) and survival with a long-term population monitoring of wild white-footed mice, to investigate the causes and consequences of behavioural variability.

More specifically, my aims are:

- To investigate a potential relationship between exploration and locomotor performance traits.
 - Test which open-field variables relate to sprint speed and/or grip strength
 - Test if these potential links differ in males vs females.
 - Potentially estimate the narrow-sense heritability (h^2) and genetic correlations (pending molecular work).
- To investigate if exploration co-vary with spatial learning abilities
 - Develop a cognitive test and estimate if the new measurements are repeatable
 - Test if more explorative individuals take longer to fulfil a learning task than slower explorers.
- To investigate if and how exploration, locomotor performance, and cognition traits affect survival.
 - Estimate viability selection differentials and gradients on these traits
 - Test for potential non-linear and correlational selection on the traits
 - Test if and how the link between exploration and survival changes depending on the year and the capture site.
- Test the preliminary assumptions of the co-adaptation views between performance and exploration traits:
 - Do individual showing higher degrees in behaviours such as aggressiveness, activity or boldness have lower survival than the individuals showing the opposite behavioural traits?
 - Do individuals showing high locomotor performance have higher survival than those showing low locomotor performance?

Proposed methodologies

The monitoring is taking place at Queen's University Biological Station from the beginning of May to the end of August. Mice are caught in fixed Longworth traps overnight and measurements including sex, age, reproductive status, and body mass, are taken upon capture. Mice also undergo several tests:

- Behavioural tests:
 - Bag test: directly at the capture site, the mouse is transferred from its trap into a mesh handling bag and the time spent immobile during 60s is recorded as a measure of docility (Martin and Réale 2008).
 - Handling test: directly at the capture site, the handler notes if the mouse bites the handler during the standard 5-15 minutes routine manipulations necessary to record body mass, age, sex, and parasite count.
 - Open-field test: in the laboratory, the mouse is introduced into an open arena consisting of a circular ($d = 140$ cm) plastic tank. Its behaviour is then filmed under moderate lighting for 10 minutes: enabling us to measure the distance moved, the average distance from center, the relative area, and number of defecations during the test.
- Performance tests:
 - Sprint speed: in the laboratory, the mouse is released in a box connected to a 3 m long by 10 cm wide racetrack with tactile sensors placed every 12.5 cm along the track, and chased along the racetrack. The highest speed recorded over twelve sensors (corresponding to a distance of 137.5 cm) is retained as the sprint speed of that individual on that day (Berberi and Careau 2019).
 - Grip strength: in the laboratory, the mouse held by the tail and allowed to grasp a metal grid connected to a force gauge positioned horizontally, then pulled backwards in the horizontal plane. The peak force (N) applied to the grid before the mouse lost grip is recorded as its grip strength for that trial.
- Cognitive test:
 - Morris Water Maze: in the laboratory, the mouse is introduced to a 1.5 diameter circular pool filled with 15 cm of water at ~ 22 °C. The water is made opaque with non-toxic paint and visual cues are placed outside in a way to remain visible from the pool. Each individual is allowed to find an escape from the pool (i.e., a small platform hidden 0.5 cm below the water level) for several 1-minute trials. This test enables us to measure the time it takes to a mouse to find a platform and its trajectory during multiple trials, to estimate its learning rate (Morris 2015). This test is conducted on a different day than the other laboratory tests and a least a week must be elapsed between successive testing.

To partition trait (co)variation at the among- and within-individual level, I will use multivariate linear mixed models (Dingemanse and Dochtermann 2013). All response variables (behavioural, performance, and cognition metrics) will be z-transformed to a mean = 0 and variance = 1. Explanatory variables fitted as fixed effects will include sex, reproductive status (active or not active), their interaction, age (juvenile or adult), body mass, and time of day for behavioural tests. Mouse ID will be fitted as a random effect with an unstructured correlation matrix which will provide all estimates of among-individual variance and covariance used to quantify among-individual correlations. When ongoing molecular and bioinformatics work will produce a relatedness matrix for the individuals in my datasets, it will be possible to include

this relatedness matrix as an additional random effect to further partition among-individual variance into permanent environment and additive genetic effects.

To estimate trait relationships to fitness (w), I will apply the approach developed by Lande and Arnold (1983). This classic framework allows the quantification of all linear and nonlinear (including correlational) selection needed to understand the correlated evolution of multiple correlated traits. It is usually done by fitting a multiple linear regression with relative fitness as the response variable and the traits of interest as predictors (in addition to their squared terms and second-order interactions for nonlinear selection). While linear (directional) selection gradients (β) indicate selection that changes the population mean, nonlinear selection gradients (γ) indicate selection that changes either the phenotypic variance of a single trait (i.e., quadratic selection; disruptive or stabilizing) or the phenotypic covariance between two traits (i.e., correlational selection).

Accurately estimating survival in an open population is challenging, especially when recapture probability is low (Gimenez et al. 2008). The problem of imperfect detection is even more severe when recapture probability is heterogeneous and varies according to a trait. Such trait-dependent recapture probability is very likely in personality studies, where personality-related sampling bias has been considered since the beginning (Wilson et al. 2011). In small rodents, the “trap happy” phenomenon is widely observed, in which some individuals seem to always get caught whenever a trap is set within their home range (Careau et al. 2008). Overall, the likelihood is very high that trappability covaries with personality, and this would introduce a bias in the selection gradients estimated on that personality trait. One solution for this is to jointly estimate selection and capture probability within a single model, using the capture-mark-recapture method. Since all individuals are marked with a unique ID, I will use a capture-mark-recapture model to estimate individual survival rates by considering which individuals were recaptured (or not) over time.

Expected products

1. Publication #1:

- Tentative title: The fast and the curious IV: relation between exploratory behaviour and locomotor performance in wild white-footed mice.
- Authors: Nicolas Bonin & Vincent Careau.
- Synopsis: There is empirical support for a co-adaptation between exploratory behaviour and locomotor performance traits in rodents, but most studies reporting this trend focussed on a single aspect of exploratory behaviour (i.e., distance moved in a novel environment). In this article, I considered multiple exploration variables obtained from an open-field test and used co-variance partitioning to investigate the relationship between exploratory and locomotor performance traits in wild white-footed mice. I also tested if this link differed between males and females.
- Methods/data: We captured a total of 1,174 individuals in this study and brought over 714 individuals (259 females and 451 males) to the laboratory for phenotyping.
- Preliminary results:
 - All metrics considered were significantly repeatable (Fig. 1) with estimate ranging from $R = 0.364 \pm 0.031$ (for the distance in the OF test) to 0.184 ± 0.027 (for relative area covered in the OF).
 - Two of the four OF variables considered were significantly correlated with sprint speed at the among-individual level (Fig. 1): There was a positive correlation between sprint speed and distance from the center ($r_{ind} = 0.332 \pm 0.085$, Fig. 1) and a negative correlation between sprint speed and relative area ($r_{ind} = -0.189 \pm 0.094$, Fig. 1). These results are in favor of the co-specialisation hypothesis (negative correlation between exploration and locomotor performance).

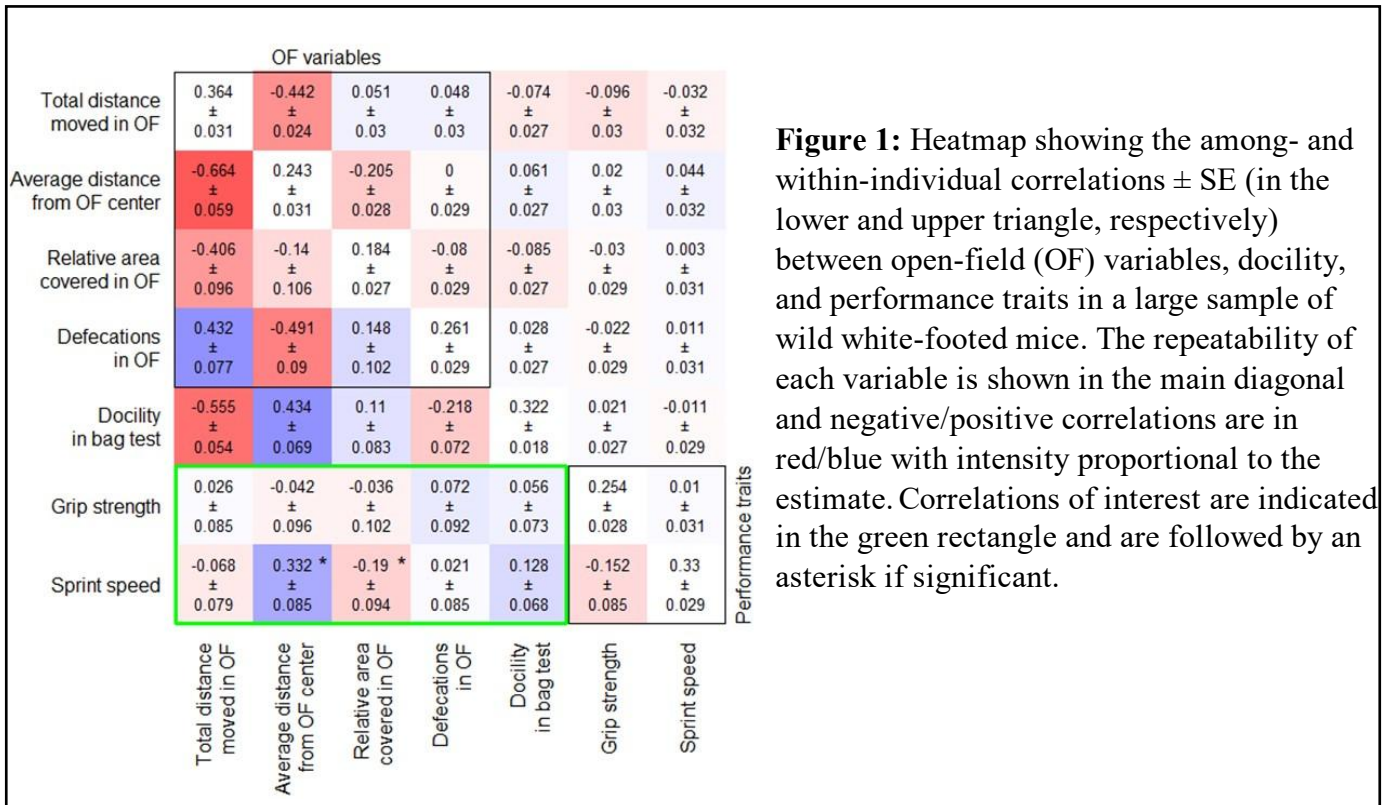


Figure 1: Heatmap showing the among- and within-individual correlations \pm SE (in the lower and upper triangle, respectively) between open-field (OF) variables, docility, and performance traits in a large sample of wild white-footed mice. The repeatability of each variable is shown in the main diagonal and negative/positive correlations are in red/blue with intensity proportional to the estimate. Correlations of interest are indicated in the green rectangle and are followed by an asterisk if significant.

2. Publication #2:

- a. Tentative title: Are exploratory behaviours linked to spatial learning in wild white-footed mice?
- b. Authors: Nicolas Bonin & Vincent Careau.
- c. Synopsis: Theory predicts that exploratory behaviour and learning traits should covary positively. However, there is not a strong empirical support in favor of this prediction. Applying a cognitive test to investigate spatial learning in free-living white footed-mice, I will test if and how learning is repeatable and related to exploratory behaviour in this wild rodent population.
- d. Methods/data: Preliminary Morris Water Maze tests were conducted over the last summer. The advice provided by Dr. McKay and his crew (who conducted similar tests on white-footed mice) helped trouble-shoot and fine tune the test in our population.

3. Publication #3:

- a. Tentative title: Personality, performance and cognition, relation to survival in a wild population of white-footed mice.
- b. Authors: Nicolas Bonin, Vincent Careau, and Rémi Choquet.
- c. Synopsis: One of the most important challenges in behavioural ecology is to identify sources of adaptive (co)variation in behaviour. Understanding how behaviour evolves requires estimating its relationship to fitness, which can be attained by using the approach developed by Lande and Arnold (1983). Using this approach, I aim to understand the potential correlated evolution of multiple traits, by quantifying how selection can affect exploratory behavioural, performance, and cognitive traits. The goal of this study is ultimately to gain insight on the adaptive landscape onto which behavioural, locomotor, and cognitive traits evolve.
- d. Methods/data: To learn more about capture-marking recapture models, I will participate to a workshop given by Drs. Rémi Choquet and Giacomo Tavecchia at the CEFÉ (Centre d'Ecologie Fonctionnelle et Evolutive) of Montpellier. This opportunity will hopefully lead to a collaboration.

Potential side projects

Here is a list of potential project ideas that could be suitable as developments or alternatives to current proposed chapters, or honours projects under my supervision:

- Use DNA sequencing to estimate the heritability of behavioural, performance and cognitive traits.
- Test if locomotor performance are linked with morphology: i.e., if there are significant morphological differences in feet, tail, and body length between fast/slow runners/climbers.
- Are there differences in behavioural plasticity between individuals? If yes do fast sprinter show different levels of behavioural plasticity (habituation) than slower sprinters?
- Results in chapter #1 (see above) indicates that heavier individuals are less active, less explorative, and spend more time at the periphery of the area than lighter mice. One idea would be to investigate why body mass (potentially body condition) influence exploratory behaviour (limit energetic costs?)
- Estimate the predictability of exploration behaviours (Keremany et al. 2023), and test if this metric is repeatable and linked with survival.
- Are individuals in better condition more aggressive than the others? Game theory predicts that if the costs of fights are high then only animals in good condition (with high resource holding potential) should be aggressive, while those in poor condition should be unaggressive since they have a low chance of winning (Sih et al. 2015).

Proposed research timeline

Winter semester 2025:

Finalisation/publication of the first chapter (covariation performance/exploration)

Workshop at the CEFE of Montpellier on capture-marking recapture models

Spring/summer semester 2025:

Field work at QUBS: data collection for chapter 2 (spatial learning)

Fall semester 2025:

Data analysis of chapter 2 (test the covariation between spatial learning and exploratory exploration traits)

Data analysis of chapter 3 (estimation of survival and its relationship with behaviour, performance and cognition)

Winter semester 2026:

Writing of chapters 2 and 3

Publication of chapter 2 (covariation learning/exploration)

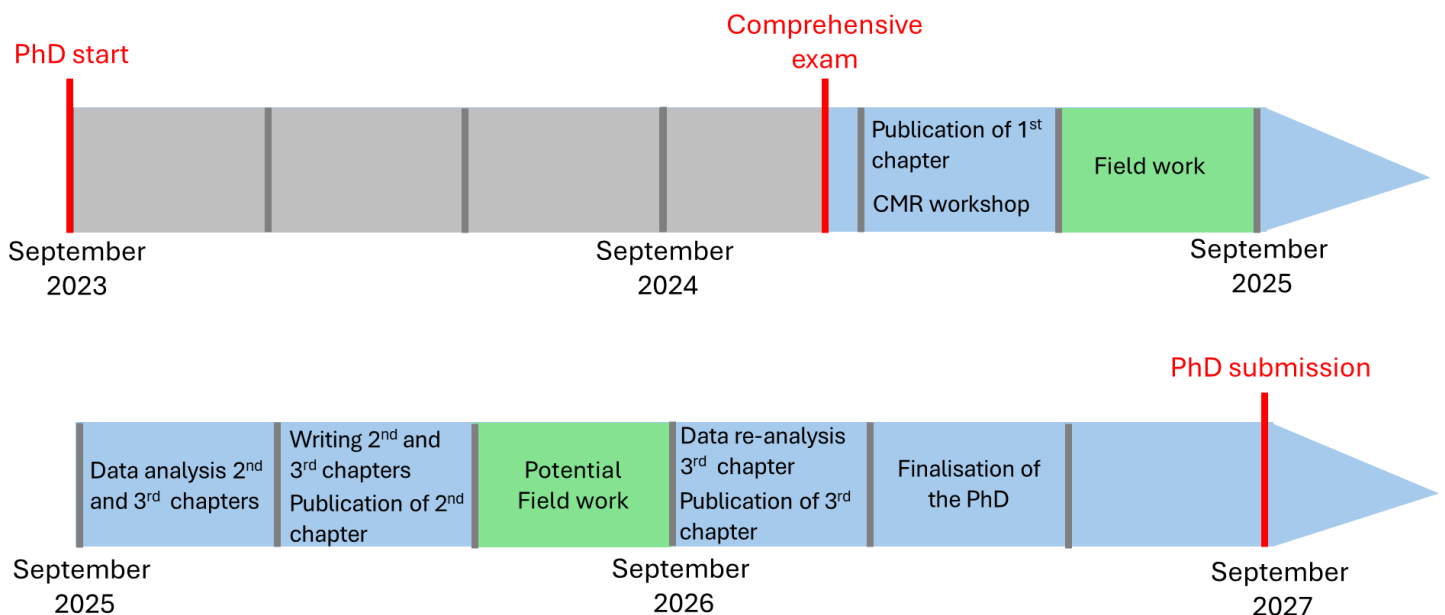
Spring/summer semester 2026:

Potentially more field-work

Fall semester 2026:

Potentially implementation of 2025 and 2026 data for estimating survival (chapter 3)

Publication of chapter 3 (covariation survival/exploration)



References

- Agnani P, Careau V (2023) The fast and the curious III: speed, endurance, activity, and exploration in mice. *Behav Ecol Sociobiol* 77:26. <https://doi.org/10.1007/s00265-023-03302-0>
- Agnani P, Thomson J, Schradin C, Careau V (2020) The fast and the curious II: performance, personality, and metabolism in Karoo bush rats. *Behav Ecol Sociobiol* 74:123. <https://doi.org/10.1007/s00265-020-02908-y>
- Bennett AF (1989) Integrated Studies of Locomotor Performance. In: Wake DB, Roth G (eds) *Complex organismal functions: integration and evolution in vertebrates* Wiley, Chichester 12
- Berberi I, Careau V (2019) Performance trade-offs in wild mice. *Oecologia* 191:11–23. <https://doi.org/10.1007/s00442-019-04450-9>
- Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* 23:361–368. <https://doi.org/10.1016/j.tree.2008.04.003>
- Blumstein DT, Lea AJ, Olson LE, Martin JGA (2010) Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. *J Evol Biol* 23:879–887. <https://doi.org/10.1111/j.1420-9101.2010.01967.x>
- Boon AK, Réale D, Boutin S (2007) The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett* 10:1094–1104. <https://doi.org/10.1111/j.1461-0248.2007.01106.x>
- Brommer JE (2013) On between-individual and residual (co)variances in the study of animal personality: are you willing to take the “individual gambit”? *Behav Ecol Sociobiol* 67:1027–1032. <https://doi.org/10.1007/s00265-013-1527-4>
- Bulmer MG (1976) The effect of selection on genetic variability: a simulation study. *Genet Res* 28:101–117. <https://doi.org/10.1017/S0016672300016797>
- Careau V, Garland T (2012) Performance, Personality, and Energetics: Correlation, Causation, and Mechanism. *Physiological and Biochemical Zoology* 85:543–571. <https://doi.org/10.1086/666970>
- Careau V, Thomas D, Humphries MM, Réale D (2008) Energy Metabolism and Animal Personality. *Oikos* 117:641–653
- Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. *Current Zoology* 57:491–498. <https://doi.org/10.1093/czoolo/57.4.491>
- Dewitt TJ, Sih A, Hucko JA (1999) Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. *Animal Behaviour* 58:397–407. <https://doi.org/10.1006/anbe.1999.1158>

- Diamond K, Trovillion D, Allen KE, et al (2014) Individual (co)variation of field behavior and locomotor performance in curly tailed lizards. *Journal of Zoology* 294:248–254. <https://doi.org/10.1111/jzo.12175>
- Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol* 82:39–54. <https://doi.org/10.1111/1365-2656.12013>
- Dingemanse NJ, Dochtermann NA, Nakagawa S (2012) Defining behavioural syndromes and the role of ‘syndrome deviation’ in understanding their evolution. *Behav Ecol Sociobiol* 66:1543–1548. <https://doi.org/10.1007/s00265-012-1416-2>
- Dingemanse NJ, Réale D (2005) Natural selection and animal personality. *Behaviour* 142:1159–1184. <https://doi.org/10.1163/156853905774539445>
- Dochtermann NA, Jenkins SH (2007) Behavioural syndromes in Merriam’s kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses. *Proc Biol Sci* 274:2343–2349. <https://doi.org/10.1098/rspb.2007.0622>
- Dougherty LR, Guillette LM (2018) Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20170282. <https://doi.org/10.1098/rstb.2017.0282>
- Dukas R (2013) Effects of learning on evolution: robustness, innovation and speciation. *Animal Behaviour* 85:1023–1030. <https://doi.org/10.1016/j.anbehav.2012.12.030>
- Garland T, Losos J (1994) Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, IL, USA. pp 240–302
- Gimenez O, Viallefont A, Charmantier A, et al (2008) The risk of flawed inference in evolutionary studies when detectability is less than one. *Am Nat* 172:441–448. <https://doi.org/10.1086/589520>
- Gould TD, Dao DT, Kovacsics CE (2009) The Open Field Test. In: Gould TD (ed) *Mood and Anxiety Related Phenotypes in Mice: Characterization Using Behavioral Tests*. Humana Press, Totowa, NJ, pp 1–20
- Griffin AS, Guillette LM, Healy SD (2015) Cognition and personality: an analysis of an emerging field. *Trends in Ecology & Evolution* 30:207–214. <https://doi.org/10.1016/j.tree.2015.01.012>
- Guillette LM, Reddon AR, Hurd PL, Sturdy CB (2009) Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes* 82:265–270. <https://doi.org/10.1016/j.beproc.2009.07.005>
- Javier Zamora-Camacho F (2022) The relationships between toad behaviour, antipredator defences, and spatial and sexual variation in predation pressure. *PeerJ* 10:e12985. <https://doi.org/10.7717/peerj.12985>

- Kermany N, Martin JGA, Careau V (2023) Individual (co)variation in locomotor activity, temporal plasticity, and predictability within a novel environment. *Behav Ecol Sociobiol* 77:93. <https://doi.org/10.1007/s00265-023-03365-z>
- Kern EMA, Robinson D, Gass E, et al (2016) Correlated evolution of personality, morphology and performance. *Animal Behaviour* 117:79–86. <https://doi.org/10.1016/j.anbehav.2016.04.007>
- Koteja P, Weiner J (1993) Mice, Voles and Hamsters: Metabolic Rates and Adaptive Strategies in Muroid Rodents. *Oikos* 66:505–514. <https://doi.org/10.2307/3544946>
- Lande R, Arnold SJ (1983) The Measurement of Selection on Correlated Characters. *Evolution* 37:1210–1226. <https://doi.org/10.2307/2408842>
- Laskowski K, Chang C, Sheehy K, Aguiñaga J (2022) Consistent Individual Behavioral Variation: What Do We Know and Where Are We Going? *Annual Review of Ecology, Evolution, and Systematics* 53:. <https://doi.org/10.1146/annurev-ecolsys-102220-011451>
- Martin JGA, Réale D (2008) Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 75:309–318. <https://doi.org/10.1016/j.anbehav.2007.05.026>
- Mazza V, Dammhahn M, Lösche E, Eccard JA (2020) Small mammals in the big city: Behavioural adjustments of non-commensal rodents to urban environments. *Global Change Biology* 26:6326–6337. <https://doi.org/10.1111/gcb.15304>
- McKay L, Hunnink L, Sheriff M (2022) A Field-Based Adaptation of the Classic Morris Water Maze to Assess Learning and Memory in a Free-Living Animal. *Animal Behavior and Cognition* 9:396–407. <https://doi.org/10.26451/abc.09.04.03.2022>
- Moiron M, Laskowski KL, Niemelä PT (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecol Lett* 23:399–408. <https://doi.org/10.1111/ele.13438>
- Montiglio P-O, Garant D, Pelletier F, Réale D (2012) Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 84:1071–1079. <https://doi.org/10.1016/j.anbehav.2012.08.010>
- Morand-Ferron J, Cole EF, Quinn JL (2016) Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews* 91:367–389. <https://doi.org/10.1111/brv.12174>
- Morris RGM (2015) The Watermaze. In: Bimonte-Nelson HA (ed) *The Maze Book: Theories, Practice, and Protocols for Testing Rodent Cognition*. Springer, New York, NY, pp 73–92
- Newar SL, Careau V (2018) The fast and the curious: locomotor performance and exploratory behaviour in eastern chipmunks. *Behav Ecol Sociobiol* 72:27. <https://doi.org/10.1007/s00265-018-2445-2>

- Perals D, Griffin AS, Bartomeus I, Sol D (2017) Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour* 123:69–79.
<https://doi.org/10.1016/j.anbehav.2016.10.006>
- Piquet JC, López-Darias M, van der Marel A, et al (2018) Unraveling behavioral and pace-of-life syndromes in a reduced parasite and predation pressure context: personality and survival of the Barbary ground squirrel. *Behav Ecol Sociobiol* 72:147.
<https://doi.org/10.1007/s00265-018-2549-8>
- Qi Y, Noble DWA, Wu Y, Whiting MJ (2014) Sex- and performance-based escape behaviour in an Asian agamid lizard, *Phrynocephalus vlangalii*. *Behav Ecol Sociobiol* 68:2035–2042. <https://doi.org/10.1007/s00265-014-1809-5>
- Réale D, Garant D, Humphries MM, et al (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:4051–4063.
<https://doi.org/10.1098/rstb.2010.0208>
- Reim E, Eichhorn D, Roy JD, et al (2019) Nutritional stress reduces flight performance and exploratory behavior in a butterfly. *Insect Sci* 26:897–910.
<https://doi.org/10.1111/1744-7917.12596>
- Shettleworth SJ (2010) *Cognition, evolution, and behavior*, 2nd ed. Oxford University Press, New York, NY, US
- Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:2762–2772. <https://doi.org/10.1098/rstb.2012.0216>
- Sih A, Mathot KJ, Moirón M, et al (2015) Animal personality and state-behaviour feedbacks: a review and guide for empiricists. *Trends Ecol Evol* 30:50–60.
<https://doi.org/10.1016/j.tree.2014.11.004>
- Sinervo B, Svensson E (2002) Correlational selection and the evolution of genomic architecture. *Heredity (Edinb)* 89:329–338. <https://doi.org/10.1038/sj.hdy.6800148>
- Smith PC, Carlson Scholz JA, Wilson SR (2012) Chapter 46 - Deer Mice, White-Footed Mice, and their Relatives. In: Suckow MA, Stevens KA, Wilson RP (eds) *The Laboratory Rabbit, Guinea Pig, Hamster, and Other Rodents*. Academic Press, Boston, pp 1075–1088
- Vessey SH, Vessey KB (2007) Linking behavior, life history and food supply with the population dynamics of white-footed mice (*Peromyscus leucopus*). *Integrative Zoology* 2:123–130. <https://doi.org/10.1111/j.1749-4877.2007.00053.x>
- Videliér M, Bonneaud C, Cornette R, Herrel A (2014) Exploration syndromes in the frog *enopus (ilurana) tropicalis*: correlations with morphology and performance? *Journal of Zoology* 294:206–213. <https://doi.org/10.1111/jzo.12170>
- White SL, Wagner T, Gowan C, Braithwaite VA (2017) Can personality predict individual differences in brook trout spatial learning ability? *Behav Processes* 141:220–228.
<https://doi.org/10.1016/j.beproc.2016.08.009>

- Wilson A, Binder T, Mcgrath K, et al (2011) Capture technique and fish personality: Angling targets timid bluegill sunfish, *Lepomis macrochirus*. *Canadian Journal of Fisheries and Aquatic Sciences* 68:749–757. <https://doi.org/10.1139/f2011-019>
- Wilson AJ, Réale D, Clements MN, et al (2010) An ecologist's guide to the animal model. *J Anim Ecol* 79:13–26. <https://doi.org/10.1111/j.1365-2656.2009.01639.x>
- Xia X, Millar J (1991) Genetic evidence of promiscuity in *Peromyscus leucopus*. *Behavioral Ecology and Sociobiology* 28:171–178. <https://doi.org/10.1007/BF00172168>