

Clever Creatures: Exploring Key Traits and Problem-Solving in the Common Brushtail Possum



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Philosophy*

1 **Statement of Originality**

2 I certify that, to the best of my knowledge, the intellectual content of this thesis is the product
3 of my own work and that all the assistance received in preparing this thesis and sources have
4 been acknowledged. This thesis has not been submitted for any degree or other purposes.

5 Name: Angelica Geisler-Edge

6 Date: 29th June 2025

7

8 **Artificial Intelligence Statement**

9 No content produced by generative AI tools has been used in the preparation of this thesis.

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13 **Preface**

14 This thesis is presented as two stand-alone data chapters, both written with the intention of
15 publication in international peer-reviewed journals. As the chapters build upon one theme,
16 some repetition was unavoidable.

17 Most of the ideas contained in this thesis are my own. All significant contributors have been
18 acknowledged at the start of each chapter.

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98 **Thesis Abstract**

99 The ability to solve problems is useful to the survival of animals, particularly when foraging. Animals
100 in urban environments must constantly adapt to novel problems, finding new sources of food and
101 ways of accessing them. Studying problem-solving performance of an urban species can help us to
102 understand how these animals approach problems in the real world. The main aim of my research was
103 to further our understanding of the drivers of problem-solving performance in a free-ranging urban
104 marsupial, the Common Brushtail Possum (*Trichosurus vulpecula*).

105 Intrinsic traits such as sex, body weight, body condition, personality and parasite carriage, are
106 expected to influence the problem-solving performance of possums. Before testing their effects on
107 problem-solving, I first tested for associations among these traits and defined them for my study
108 population. This revealed several significant relationships, for example males were slightly heavier
109 than females. Individuals were all healthy yet still varied in their personality traits. Few individuals
110 carried the pathogen, *Cryptosporidium parvum*, but individuals with a more exploratory personality
111 trait had a higher probability of parasite carriage.

112 Both intrinsic traits and mechanistic behaviours were important for problem-solving performance,
113 measured through likelihood to solve the puzzle and time to first solve the puzzle. The personality
114 trait, boldness, indirectly influenced the likelihood to solve the puzzle. The personality trait, vigilance,
115 and body condition had direct and indirect effects on the time taken to solve the puzzle. The
116 mechanistic behaviour, selectivity, had a significant direct effect on both likelihood of solving and time
117 taken to solve the puzzle. Possums improved their time to solve across subsequent trials within days
118 or weeks, demonstrating short-term learning. Long-term memory was evident in those possums that
119 had experience with the puzzle and recalled the solution to the puzzle over a year later. Overall,
120 individuals varied in their approach and problem-solving ability in a free-ranging urban population of
121 possums.

122 Demonstrating that possums vary in their personality despite all being healthy confirms that
123 personality is not driven by health. Similarly, as more exploratory possums were only *more likely* —
124 not certain — to carry the parasite, *C. parvum*, suggests again that personality is not driven by carriage
125 of this parasite. Demonstrating that possums can solve a novel problem, learn, and remember how to
126 do it long term, provides insight into the cognitive ability of this marsupial species. It also adds to the
127 limited evidence available on problem-solving by free-ranging animals, particularly in species other
128 than eutherian mammals and birds. The variation in ability to solve problems among individual
129 possums as a function of their personality provides evidence of the ecological significance of
130 personality, in affecting access to some (novel) resources. Whether such an influence ultimately
131 affects fitness, or whether animals with different personalities exploit the same urban environment in
132 different ways, remain to be seen.

Chapter 1

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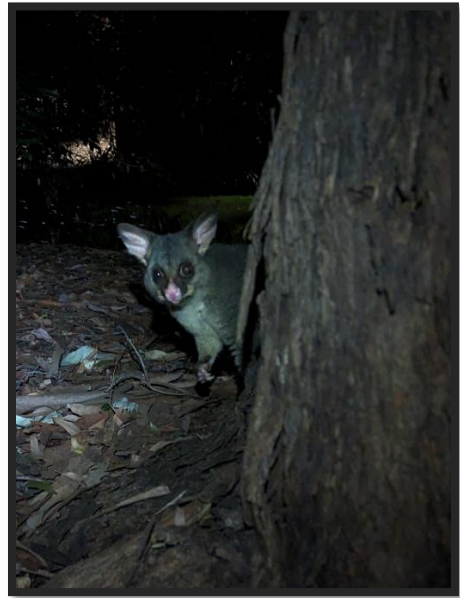
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General Introduction



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142 Chapter 1: General Introduction

143 Problem-solving by animals

144 Animals make a plethora of decisions every day, about the most effective way of foraging, the safest
145 place to rest or nest, or how to avoid threats such as predators. Primates, for example, make foraging
146 decisions, identifying which tree is most abundant in fruit (Trapanese et al., 2019). Predator avoidance
147 and the protection of offspring motivate wild Kalahari meerkats (*Suricata suricatta*) to decide the
148 safest location for a burrow (Strandburg-Peshkin et al., 2020). Rodent species vary in their foraging
149 decisions, with each species making different choices about whether to focus on feeding or avoiding
150 predators (Randler & Kalb, 2020). All of these decisions are, in a sense, general forms of problem-
151 solving. An animal's ability to solve such problems should help their survival and reproductive success
152 because it helps them to make beneficial choices given their environment.

153 More specifically, some animals have learnt to solve problems such as how to access difficult resources
154 in a novel way. For example, the bearded capuchin monkey (*Cebus libidinosus*) has learnt to use tools
155 when foraging, using stones to crack open encased fruits (Spagnoletti et al., 2012). Similarly, New
156 Caledonian crows (*Corvus moneduloides*) have been observed crafting tools from sticks to assist with
157 probing for food (Troschianko & Rutz, 2015). Novel solutions to old problems require an innovative
158 approach to problem-solving. So does trying to solve novel problems.

159 Solving novel problems

160 When animals are presented with novel problems, they need to be innovative, employing new
161 behaviours or using existing behaviours in a new way. For example, sulphur-crested cockatoos
162 (*Cacatua galerita*) already use their zygodactyl feet to manipulate food into their beaks when foraging,
163 but they have also learnt to use this gripping behaviour to open bin lids in urban spaces to access the
164 food inside (Klump et al., 2021).

165 Research into how animals solve novel problems helps us to understand something about their
166 cognitive ability, including how complicated a problem they can solve, whether they can learn over
167 the short term, and whether they remember and retain the ability over the long term. Captive lions
168 (*Panthera leo*), for example, were presented with a novel problem-solving task in the form of an
169 artificial puzzle box. Most individuals were able to solve the puzzle, reduce their latency to solve with
170 repeat trials, and recall the solution 7 months later; highlighting their cognitive abilities. (Borrego &
171 Dowling, 2016). A study on wild Asian elephants (*Elephas maximus*) revealed individual variation in
172 cognitive performance, with elephants differing in their approach to a problem-solving task, as well as
173 differing in personality and related behaviours (Jacobson et al., 2023).

174 Variation in approach to problem-solving among species is useful as it may explain why some species
175 are better at adapting to novel problems or novel environments than others. In Australia, the
176 introduced Indian myna (*Acridotheres tristis*) outperformed the native noisy miner (*Manorina
177 melanocephala*) in three problem-solving tasks, showing greater flexibility in its behaviours (Griffin &
178 Diquelou, 2015). The authors suggest that the difference in behavioural flexibility may help to explain
179 why introduced myna birds are outcompeting the native noisy miners.

180 Presenting artificial puzzles in a wild animal's natural environment provides a more ecologically
181 relevant context than testing the animal in captivity. Artificial problem-solving tasks are commonly
182 used in cognitive research, with both free-ranging and captive animals, to explore the innovative
183 abilities of a species and the individual variation in approaches to solving problems.

184 How do we study problem-solving?

185 Problem-solving in animals can be studied using different methods, including observing animals
186 solving naturally occurring problems, or setting up artificial tasks for captive or free-ranging animals.
187 For example, the bearded capuchin monkey (*Cebus libidinosus*) and New Caledonian crows (*Corvus
188 moneduloides*) were both observed using tools as a novel approach to the familiar, naturally occurring
189 problem of foraging in their environments (Spagnoletti et al., 2012; Troscianko & Rutz, 2015). Artificial

190 tasks were used to test problem-solving in captive Olrog's Gull (*Larus atlanticus*) to measure
191 innovation and approach to the task in a controlled environment (Castano et al., 2022); while artificial
192 puzzles were placed in the environment to demonstrate how, in the real world, wild raccoons (*Procyon*
193 *lotor*), an urban dweller, approaches novel problems (Lazure & Weladji, 2024). The type of approach
194 (e.g. natural vs artificial problem, captive or free-ranging animals) has a bearing on the extent to which
195 conditions of the experiment can be controlled, and how realistic or relevant it may be to natural
196 scenarios.

197 Food extraction tasks are a common way to examine problem-solving. These tasks aim to replicate
198 foraging behaviours of the animal and how the animal may approach problems during foraging. For
199 example, a food extraction task was set for African striped mice (*Rhabdomys pumilio*), solved by
200 pulling string to open the lid of a box revealing the food reward inside (Rochais et al., 2022). Another
201 way of testing problem-solving is to use an escape box task. Common Brushtail Possums (*Trichosurus*
202 *vulpecula*) were tested on their ability to escape a box through a door that could be configured to
203 open either by pushing or pulling (Wat et al., 2020). Both the food extraction task and escape box task
204 measure problem-solving ability, but differ in how the animal is motivated.

205 Quantifying whether or not an animal solves a problem can be revealing, but so too can quantifying
206 how animals go about solving the problem, i.e. their approach. Behaviours such as behavioural
207 flexibility, i.e. rate of switching between behaviours, and behavioural diversity, i.e. variation in
208 behaviours, have been used to quantify the approach an individual takes to problem-solving (Chow et
209 al., 2018; Lazure & Weladji, 2024).

210 Just as puzzle tasks are used to measure problem-solving performance, they can also reveal how well
211 animals retain information about solving the puzzle—offering insight into their ability to learn.

212

213

214 Learning and memory in animals

215 Some animals improve their problem-solving performance with repeat attempts at the task, measured
216 by increased likelihood of solving the problem or decreased time taken to solve the problem with
217 experience. If improvement is within a short period, generally with subsequent attempts, this is short-
218 term learning. Lions (*Panthera leo*), for example, reduced their latency to solve a puzzle in subsequent
219 trials, with 3-32 days between trials (Borrego & Dowling, 2016). There are many studies on short-term
220 learning, as it is usually feasible to take repeat measures of problem-solving performance in a short
221 time, particularly with captive animals.

222 Long-term memory is the retention of information over a long period of time (Ganci et al., 2025). It is
223 often more difficult to measure than short-term learning, because individuals are not always available
224 to be retested months or years after the initial puzzle attempt. Repeat trials are particularly
225 challenging with free-ranging populations as there may be turnover in the population or
226 migration/relocation.

227 The ability to learn has been used as an indicator of an animal's cognition, and animals that
228 demonstrate a strong ability to learn are generally considered to be "intelligent". The New Caledonian
229 crow has been studied extensively as a species considered to have a strong cognitive ability, with
230 evidence of improvement between trials of puzzle tasks (Jelbert et al., 2014; Troscianko & Rutz, 2015).
231 However, many species are often not considered intelligent and therefore understudied in cognitive
232 research. Reptiles, in particular, tortoises are generally not considered to have a strong cognitive
233 ability, yet there is now evidence of long-term memory demonstrated by Aldabra tortoises and
234 Galapagos tortoises (*Chelonoidis cf. nigra*) (Gutnick et al., 2020).

235 While understanding an animal's capacity to learn provides insight into cognition, the ability to learn
236 is also expected to have ecological benefits in non-static environments where new problems present
237 themselves — such as urban landscapes — or when animals move into new landscapes. Some bird
238 species, such as the bullfinch (*Loxigilla barbadensis*), have shown superior problem-solving abilities in

239 urban populations compared to their rural counterparts, suggesting that problem-solving may offer
240 adaptive advantages in urban environments (Audet et al., 2016).

241 Intraspecific variation in problem-solving

242 Individuals within a species are likely to vary in their approach and ability to solve problems, given
243 they may have different cognitive ability, experience and traits, such as sex, body weight, personality,
244 body condition, and parasite carriage. For example, common waxbills (*Estrilda astrild*) varied in their
245 body condition and personality, some individuals being more explorative than others (Carvalho et al.,
246 2021). Parasite carriage has also been shown to influence problem-solving performance. In one study,
247 sheep that tested positive to carrying *Toxoplasma gondii* were slower at solving a puzzle task
248 compared with those that tested negative (Shamsi et al., 2023).

249 Individual traits are expected to influence how animals approach problem-solving, in part due to
250 differences in motivation. For example, a female facing the energetic demands of breeding may be
251 more persistent when engaging with a food extraction task, motivated by the need to feed herself and
252 her offspring. In contrast, a male may be less motivated in the same context if his priorities are more
253 closely tied to competition or mating opportunities. However, although motivations could be affecting
254 approach between sexes, it is not necessarily altering success rates. For example, equal numbers of
255 male and female great tits (*Parus major*) were successful at a problem-solving task, and success was
256 linked to increased nestling survival (Cauchard et al., 2013). However, the study did not investigate
257 whether males and females differed in their approach to the task, such as in persistence or motivation.
258 The relationship between motivations and problem-solving success can also be species specific, as
259 evident in bowerbirds. Male Satin bowerbirds (*Ptilonorhynchus violaceus*) who were better problem
260 solvers, having greater success rates, also had higher mating success, whereas there was no evidence
261 of a relationship between problem solving success and mating success for the male spotted
262 bowerbird (*Ptilonorhynchus maculatus*) (Isden et al., 2013; Keagy et al., 2009).

263 Intrinsic traits, however, can also co-vary within an individual. For example, there are sex-based
264 differences in personality in both chimpanzees (*Pan troglodytes*) and white-faced capuchins (*Cebus*
265 *capucinus*) (Manson & Perry, 2013; Rawlings et al., 2020). If such intrinsic traits influence problem-
266 solving performance, covariation between these traits is important to consider. If traits co-vary, it
267 could complicate trying to identify specific traits that are linked to problem-solving success.

268 Problem-solving in an urban environment

269 Many animals have adapted to and thrive in urban spaces, living in close proximity to humans and
270 taking advantage of the abundance of resources. Urban spaces offer lots of opportunity for novel
271 problem-solving, as these spaces are constantly changing. For some animal species, thriving in such a
272 landscape may be partly due to their ability to innovate and problem-solve. For example, raccoons
273 (*Procyon lotor*), known to be successful urban dwellers, demonstrated innovative behaviour, with a
274 greater diversity of behaviours linked to a high success rate of problem-solving (Lazure & Weladji,
275 2024). While an urban environment is not novel to the individuals living there, such animals are still
276 presented with novel problems within this environment. Red foxes (*Vulpes vulpes*), for example, are
277 known to exploit urban landscapes and frequently access food from bins. However, when presented
278 with a novel food extraction task, urban foxes were found to be bolder but not more successful at
279 problem-solving than their rural counterparts (Morton et al., 2023).

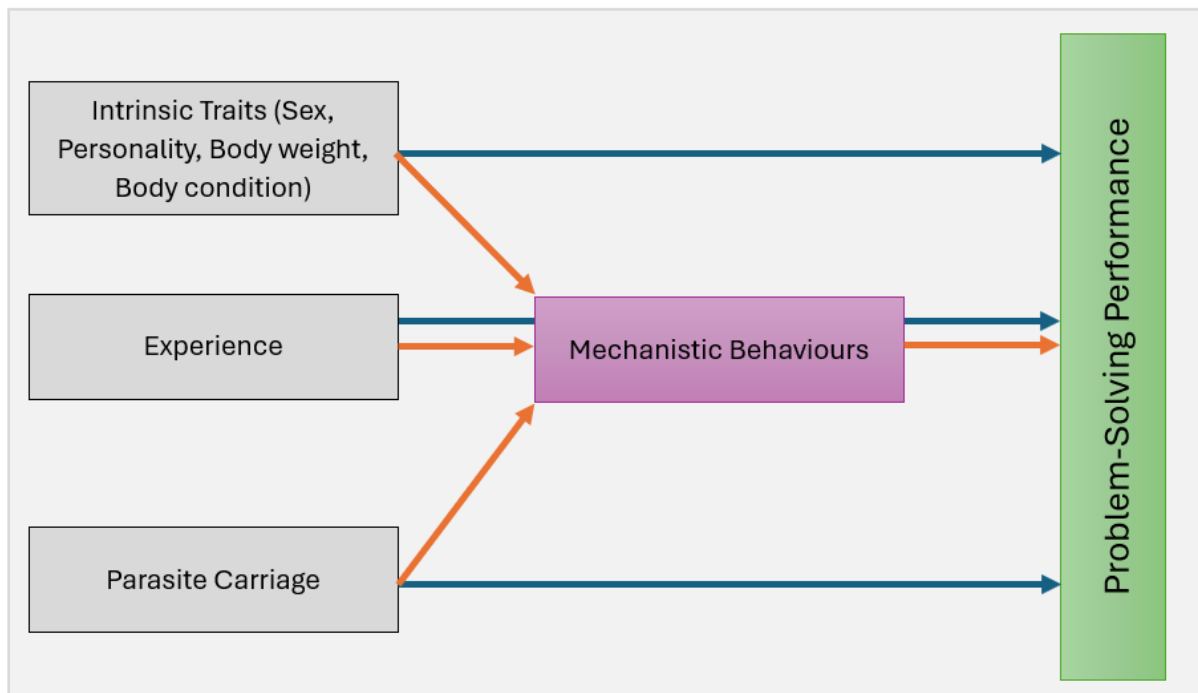
280 Food extraction puzzles – designed by researchers and often used in cognitive studies - may be
281 completely novel to animals in rural environments. But for urban animals, these sorts of puzzles apply
282 to their world, as they often come across artificial problems created by humans. This makes puzzle
283 tasks useful for studying how urban animals approach problem-solving in ecologically relevant
284 contexts.

285

286

287 Research Aims and Study System

288 My overall goal was to extend our understanding of several key drivers of problem-solving
289 performance in wild, free-ranging animals, including intrinsic traits, experience (testing short-term
290 learning and long-term memory) and parasite carriage (figure 1).



291

292 **Figure 1.** Conceptual model showing potential direct and indirect drivers of problem-solving
293 performance.

294

295 Using free-ranging animals of an urban dwelling species, the specific aims of my study were to:

- 296 (1) Explore a set of key intrinsic traits, and their associations, predicted to be relevant to problem-
297 solving performance (chapter 2)
- 298 (2) Test for direct or indirect effects of intrinsic traits and mechanistic behaviours on problem-
299 solving performance (chapter 3)
- 300 (3) Determine whether they demonstrate short-term learning and long-term memory (chapter 3).

Chapter 1: General Introduction

301 In this thesis, I explore these themes using wild Common Brushtail Possums (*Trichosurus vulpecula*).
302 This semi arboreal marsupial is a solitary species with a wide distribution across Australia (McDonald
303 et al., 2023; McLean, 2014). Possums are common to many urban areas, and individuals are readily
304 trapped in metropolitan Sydney (Eymann et al., 2013; Harris et al., 2023). Their abundance in urban
305 areas has been attributed to their high adaptability in cohabitating with humans, for example possums
306 are often found living in roofs of buildings and foraging through bins for food (Eymann et al., 2007).
307 Further evidence of their adaptability is shown in their population growth in New Zealand where they
308 were first introduced in the 1840s to establish a fur trade. This has led them to becoming a major
309 environmental and agricultural pest as they prey on invertebrates, eggs, and nestlings of native birds
310 as well as denning in the burrows of other animals (McDonald et al., 2023). The close proximity of
311 possums to humans in urban spaces is of concern as possums have been identified as carriers of
312 *Cryptosporidium*, an enteric disease causing pathogen which poses a public health risk (Hill et al.,
313 2008).

314 Thesis Structure

315 Chapter 2

316 The aim of this chapter was to examine key traits that I predicted to be informative of foraging and
317 problem-solving behaviour. I measured sex, body weight, personality, health, and gut parasite carriage
318 in my study species, the common brushtail possum. Using the collected data, I was able to test for
319 associations between these intrinsic traits to inform which of these may be relevant to problem-
320 solving. The findings from this chapter guided which traits I chose to consider in chapter 3.

321 Chapter 3

322 This chapter uses the findings of chapter 2 to suggest which intrinsic traits may be informative for
323 problem-solving performance. I investigated what influences problem-solving performance as
324 measured by first trial outcome, time to first solve, short-term learning and long-term memory.

Chapter 1: General Introduction

325 Various intrinsic traits and mechanistic behaviours were tested for their influence on problem-solving
326 in my study species. I use repeat trials of the puzzle to determine the learning abilities of brushtail
327 possums. The effect of parasite carriage on problem-solving performance is tested separately due to
328 a small sample size.

329 *Chapter 4*

330 This chapter summarises the findings of my research and suggests potential directions for future
331 studies.

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Chapter 2

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Individual variation in, and associations among, intrinsic
traits, health, and gut parasites of urban Common
Brushtail Possums

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438 Chapter 2: Individual variation in, and associations among, intrinsic traits, health, and
439 gut parasites of urban Common Brushtail Possums

440 Preface

441 Chapter 2 is a data chapter written, with some modification required, with the intention to submit to
442 a peer-reviewed journal. Contributors to this data chapter include A.R. Geisler-Edge, A.P.H.M. Herath,
443 M.L. Power, C. Marschner and C. McArthur.

444 Authors' contributions: A.R. Geisler-Edge and C. McArthur conceived the ideas and designed the
445 methodology; A.R. Geisler-Edge performed all field work and collected the data; A.P.H.M. Herath and
446 M.L. Power conducted the parasite screening; C. Marschner collected the biochemistry and
447 haematology data; A.R. Geisler-Edge and C. McArthur analysed the data and performed the statistical
448 analysis; A.R. Geisler-Edge and C. McArthur wrote the data chapter.

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459 Abstract

460 Foraging behaviour and solving problems to access food are predicted to vary intra-specifically based
461 on differences in traits of individuals. But which traits vary among individuals, how much they vary,
462 and whether they co-vary, must first be quantified for a given species before addressing their impact
463 on foraging. Here, I aimed to quantify a set of key traits that I predicted would be relevant to foraging
464 behaviours in the Common Brushtail Possum, and to explore relationships between these traits.
465 Possums (n = 130) were trapped in urban environments between 2013 and 2024. I quantified traits
466 including sex, personality, body weight; and for subsets of these possums, body condition, several
467 blood biochemical health parameters and whether possums carried the gut parasites *Cryptosporidium*
468 and *Giardia*. There was a significant difference in body weight between sexes with males 9.5% heavier
469 than females. Possums varied in the six personality traits previously found to affect diet and problem-
470 solving. Possums were in generally good body condition (average body condition score = 2.9 / 4); and
471 while the average body condition was 11.7% higher in males than females, the difference was not
472 significant. *Cryptosporidium parvum*, a zoonotic pathogen and cause of cryptosporidiosis in humans,
473 was carried in 12.7 % of the population. All possums fell within the healthy range for all biochemical
474 measures. As there was little variation in these health parameters in this population of brushtail
475 possums, variation in personality could not be attributed to variation in health. Given this, health
476 parameters will not be considered in chapter 3.

477 Introduction

478 For my study species, the Common Brushtail Possum (*Trichosurus vulpecula*), my aims in this chapter
479 were to (1) quantify a set of key traits – sex, body weight, personality, health, and gut parasites -
480 predicted to be relevant to foraging and problem-solving, and (2) test for any associations between
481 some of these traits. In Ch 3, I then explore links between traits that varied among individuals, and
482 foraging-related problem-solving, specifically a food extraction task. My focus was on adult possums
483 only.

484 Sexual size dimorphism has been studied extensively in mammalian species (Fokidis et al., 2007; Lu et
485 al., 2014; Mateju & Kratochvíl, 2013; Rossiter et al., 2006). The nature of such dimorphism varies
486 between mammalian species, such as whether the male or female typically has the larger body size
487 and the extent of such dimorphism. Brushtail possums do exhibit some sexual size dimorphism. For
488 example, Clinchy et al. (2004) measured size dimorphism based on body weight of brushtail possums
489 in New South Wales. There was only a significant difference between sexes of possums estimated to
490 be over 8 years of age; all other age groups were of similar size. For a population of brushtail possums
491 in Queensland, males were generally heavier than females, although this difference was again only
492 significant in possums aged around 4-5 years (males 18.8% heavier) (Isaac (2006)). Body size can be
493 measured in different ways such as body weight, length, or skull size (Schulte-Hostedde & Millar,
494 2000). I used body weight to investigate whether size was associated with sex of brushtail possums in
495 my study population.

496 Animal personality has been demonstrated across taxa (MacKinlay & Shaw, 2023) although few of
497 these studies examine whether personality differs by sex. The relationship has been tested in meadow
498 voles (*Microtus pennsylvanicus*), mole-rats (*Fukomys ansellii*), rock mice (*Micaelamys namaquensis*)
499 and Asian elephants (*Elephas maximus*), and none of these species show a significant difference in
500 personality between the sexes (Begall et al., 2022; Halliday et al., 2014; Oosthuizen & Lutermann,
501 2023; Selmann et al., 2018). The relationship between sex and personality traits has not been studied
502 before in the common brushtail possum.

503 Body condition has been studied in very few terrestrial mammals but has been shown to vary slightly
504 by sex and season in some species. For example, body condition differed significantly between sexes
505 in two species of bat (*Myotis daubentonii* and *Hypsugo savii*) (Rughetti & Toffoli, 2014). Females of
506 the species were larger than males, although the difference in body condition decreased in late Spring
507 as females may have lost weight from the energetic cost of lactating. In *Praomys tullbergi*, a small
508 African rodent, body condition tended to differ between sexes and seasons, but neither effect was

509 significant (Adjapong et al., 2023). Body condition has been measured previously in brushtail possums
510 (Harris, 2022) but has yet to be tested as a function of sex.

511 Personality may influence foraging strategies of individuals, and different foraging strategies may
512 involve different energetic and nutritional costs and benefits (McArthur et al., 2014). Personality may
513 therefore indirectly influence body condition of individuals, although few studies have investigated
514 this relationship. There was no significant link between personality and body condition in several
515 species of birds (*Estrilda astrild*, *Cyanistes caeruleus*) and lizards (*Podarcis hispanica*) (Carvalho et al.,
516 2021; Gaona-Gordillo et al., 2023; Rodríguez-Prieto et al., 2010). But diet — an outcome of foraging
517 decisions — is influenced by personality in brushtail possums (Herath et al. (2021)). It is therefore
518 worth exploring whether a relationship exists between body condition and personality.

519 In addition to body condition, haematology and biochemistry parameters can also offer a snapshot of
520 the health of animals. These haematological and biochemical parameters have been measured in
521 brushtail possums previously (Viggers & Lindenmayer, 1996; Webster et al., 2014). I chose to measure
522 these parameters in my study population.

523 *Cryptosporidium* spp. is a protozoan parasite that affects native wildlife and can cause enteric disease
524 in humans and domestic animals (Wait et al., 2017). Various *Cryptosporidium* species have been
525 identified in both wild and captive populations of Tasmanian devils, in 37.9% and 10.7% of individuals
526 within the respective study populations (Wait et al., 2017). *Cryptosporidium* spp. was also reported in
527 10.8% of a pooled group of free-ranging bandicoots (southern brown bandicoots (*Isodon obesulus*)
528 and long-nose bandicoots (*Peramelid nasuta*)) from two urban locations in Sydney (Dowle et al.
529 (2013)). In an urban population of common brushtail possums, 11.3% carried *Cryptosporidium* species,
530 defined as BTP1 genotype and genotypes related to those found in other marsupials (Hill et al., 2008).
531 In a large sample (n = 120 individual possums) across three locations in Sydney (including the possums
532 in my study), proactive possums were significantly more likely to carry *Cryptosporidium parvum* than
533 reactive possums, but there was no effect of sex (Herath et al unpubl.). Here, I examined whether

534 there was any relationship between *Cryptosporidium parvum* and sex or personality for just my study
535 possums used in CH 3.

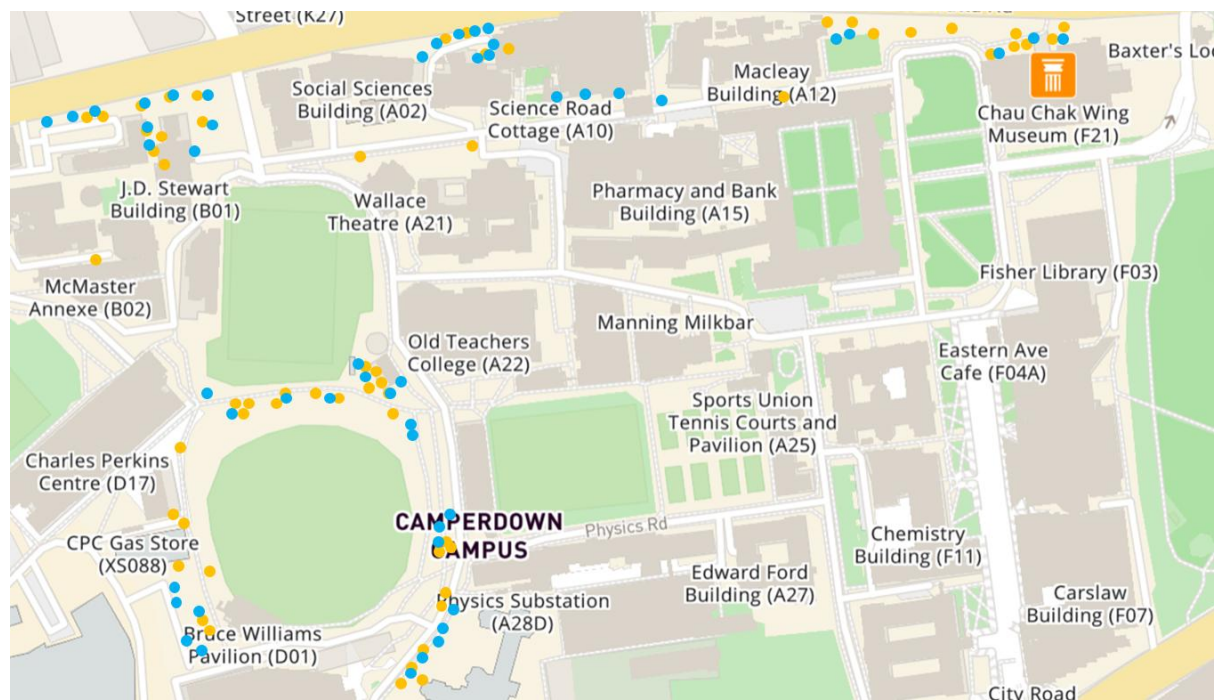
536 By quantifying individual variation in traits, and exploring any relationships between them, this
537 chapter provides insights into these characteristics in an urban population. It also allows me to decide
538 whether a particular trait is worth investigating further in chapter 3, where I quantify the impact of
539 intrinsic traits on the problem-solving ability of possums.

540 Materials and methods

541 *Site Description*

542 A large database has been developed with data on individual possums (physical and personality traits)
543 between 2013 and 2024. From this database, I used data for adults from urban environments in
544 Sydney, New South Wales, Australia: The University of Sydney Camperdown Campus (n = 115,
545 including n = 36 individuals of those that I trapped [see below]) or Macquarie University (n = 15).

546 I trapped 44 possum individuals (2023-2024) on the Camperdown campus of the University of Sydney
547 (33°53'18"S, 151°11'12"E). This is primarily an urban environment with large green spaces. Possums
548 were successfully trapped in areas with plenty of trees and shrubs with access to bins and roofs. Trap
549 sites were set at least 20 metres apart with multiple traps at each site.



551 **Figure 1.** Trap locations around University of Sydney Camperdown campus. Successful locations
552 remained consistent between 2021/22 (yellow dots) and 2023/24 (blue dots).

553 *Trapping Procedures*

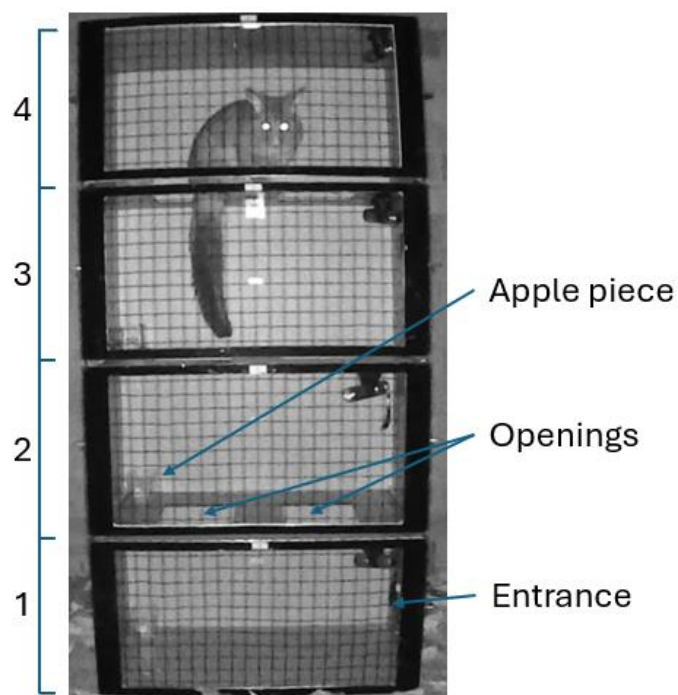
554 Tomahawk cages (63 x 25 x 25 cm) wrapped in builder's plastic were set between 1630 and 2130 in
555 green spaces away from foot traffic. Each trap was baited with half a peanut butter sandwich and a
556 quarter of apple. The traps were then checked regularly between 2100 and 0530, ensuring that all
557 traps were empty and packed up at the end of the night. Each possum was transferred to a handling
558 bag and weighed using a 5kg spring balance. The individual was checked for a Passive Integrated
559 Transponder (PIT) tag using a Biomark HPR Lite Handheld PIT Tag Reader. If there was no PIT tag
560 present, a PIT tag was inserted under the skin of the possum and their sex was recorded.

561 *Personality Testing*

562 I measured six personality traits in each possum after removing the possum from the trap into a
563 handling bag. **Docility** was measured using a handling bag test (Martin & Réale, 2008; Mella et al.,
564 2016). This was the time the possum spent immobile while the handling bag was suspended in the air

565 for one minute. The possum was then transferred from the handling bag to a bookcase-like arena
566 (61.5 x 45.0 x 129.0 cm) (Mella et al., 2016). The arena had 4 compartments, each connected by 2
567 holes through which a possum could climb (see figure 2). A quarter piece of apple was set on each of
568 the levels. Once the possum was in the arena, it was filmed for five minutes with people away from
569 the arena to avoid interference in behaviour.

570 Following (Mella et al., 2016), **explorative** behaviour was measured as the amount of time the
571 possum spent in its unpreferred levels. The preferred level was defined as the level in which the
572 possum spent the most amount of time, whereas unpreferred levels were the other three. **activity**
573 was all time spent moving or engaging with the arena in any way, whereas **Mobility** was measured as
574 just time spent moving front or hindlimbs. Time spent eating in the arena was considered indicative
575 of **boldness**. Finally, **vigilance** was time spent where the possum is immobile and staring out of the
576 arena.



577

578 **Figure 2.** Personality arena (from Mella et al. 2016). Arena consisted of levels 1-4 (bottom to top), with
579 two openings between each level. The possum entered the arena through an external opening on
580 level 1. Apple pieces were placed in small plastic containers fixed to each level.

581 *Health Data Collection*

582 During handling, all possums were given a score between 1 and 4, at 0.5 increments, rating their body
583 condition (Table 1). This provided a crude measure of health.

584 **Table 1.** Definition of body condition scoring system

Body Condition Score	Definition
4	Excellent – plump shape, high amounts body fat and muscle around spinal column and hip bones
3	Good – sufficient fat and muscle so that rib and hip bones are not prominent
2	Fair – slightly underweight, more obvious shape of rib and hip bones when felt
1	Poor – underweight, prominent rib and hip bones, minimal body fat along spinal column

585
586 We were able to investigate biochemical health parameters of a subset of possums (n = 21 individual
587 possums) from blood samples taken between July 2023 and January 2024. The same trapping
588 procedure was used as previously described but the bait was reduced to a quarter piece of sandwich
589 as an excess of food prior to sedation may cause vomiting. Once a possum was transferred to a
590 handling bag and weighed, its suitability for anaesthesia and blood sampling was then based on brief
591 observation by the veterinarian (Dr C Marschner) of the animal’s condition. All captured animals were
592 considered suitable.

593 Individuals were sedated using inhalation anaesthesia based on the protocols established by Holz
594 (2002). Once sedated, the possum was laid with its upper half raised and exposed for blood collection.
595 Blood was drawn from the cephalic vein in the forearm using a butterfly needle. 2-3 mL of blood was
596 collected and transferred to a 1.3 mL lithium heparin that was then stored at 4 degrees ready for
597 analysis. Reference ranges were provided by Marschner et al. (2025), which had been established
598 using Reference Value Advisor V2.1 (Geffré et al., 2011). The reference interval for “healthy”
599 biochemical values was defined by comparing these values against the veterinarian’s independent
600 definition of “healthy” based on the behaviour and physical examination of each possum at the time
601 of blood sampling.

602 *Parasite Data Collection*

603 Presence of *Cryptosporidium* and *Giardia* was measured from the scats of known brushtail possums.
604 From October 2021 to April 2024, scats were collected from possums that had been trapped using the
605 above methods. Multiple scats were collected from the traps and transferred to two sterile vials
606 without additives. One vial was stored in a freezer and the other a fridge until they were later scanned
607 for parasites.

608 *Presence of Cryptosporidium*

609 Methods for parasite screening were provided and performed by Dr A Herath (Herath et al unpubl.).
610 Genomic DNA was extracted from 150mg of each scat sample using an ISOLATE Faecal DNA kit (Bioline,
611 London, UK) and stored at -20°C.

612 Prior to PCR amplifications, samples were combined with an equal volume of Gene Releaser (Bio
613 Ventures, Inc, TN, USA) and microwaved for seven minutes in a 500W microwave directly.
614 *Cryptosporidium* was considered present if amplified at 18S rDNA locus (~825 bp) (81) and again
615 amplified at actin locus (~800 bp).

616 For samples testing positive to *Cryptosporidium*, amplicons were purified using the QIAquick PCR
617 Purification Kit (Qiagen, Hilden, Germany) and sequenced in the forward and reverse directions
618 (Ramaciotti Centre for Genomics, Randwick, Australia). Forward and reverse sequences were aligned
619 and assessed manually for quality. Consensus sequences were extracted using Geneious version 8.0.5
620 (Biomatters, New Zealand). BLAST searches were conducted on consensus sequences to identify
621 *Cryptosporidium* species. After initial sequence analysis, some samples were only partial sequences of
622 the expected product due to a quality drop at ~440 base pairs due to multiple peaks appearing in
623 chromatogram (n = 16) and cloning was performed to enable parasite species identification.

624 Based on BLAST identifications, a consensus sequence identified as *Cryptosporidium parvum* in
625 brushtail possums was generated.

626 Statistical Analysis

627 All statistical analysis were carried out using R version 4.4.0 (R Core Team, 2021).

628 The overall dataset consists of data on individual possums collected over 11 years (n = 130 individual
629 possums). Data were not always available for all variables, and so data sets were reduced further, with
630 different sets of individuals and sample sizes, when examining associations between particular traits.

631 I ran multiple one-way ANOVAs to test for associations between some of my variables ('car' package,
632 (Fox & Weisberg, 2019)). Data met assumptions for normality and homogeneity of variance. I tested:

633 (1) body weight (continuous response variable) as a function of sex (explanatory variable, fixed
634 factor, 2 levels, male and female). As multiple body weight measurements were available per
635 individual, its average body weight was used for analysis. Three possums lacked data for sex
636 and body weight, reducing the dataset to 127 individuals (51 females, 76 males).

637 (2) each personality trait - docility, exploration, vigilance, boldness, activity, and mobility — as a
638 function of sex. I was able to use the full dataset of 130 individual possums to test docility. For
639 the remaining five traits, three possums were missing data so n = 127.

640 (3) body condition as a function of sex using a subset of the dataset (n = 68 possums (27 females,
641 41 males)) that had body condition measures available.

642 I tested the association between body condition and personality traits using a linear model with a
643 gaussian distribution. I used three personality traits (exploration, boldness, and vigilance) that I
644 explore further in chapter 3 to explain likelihood of problem-solving.

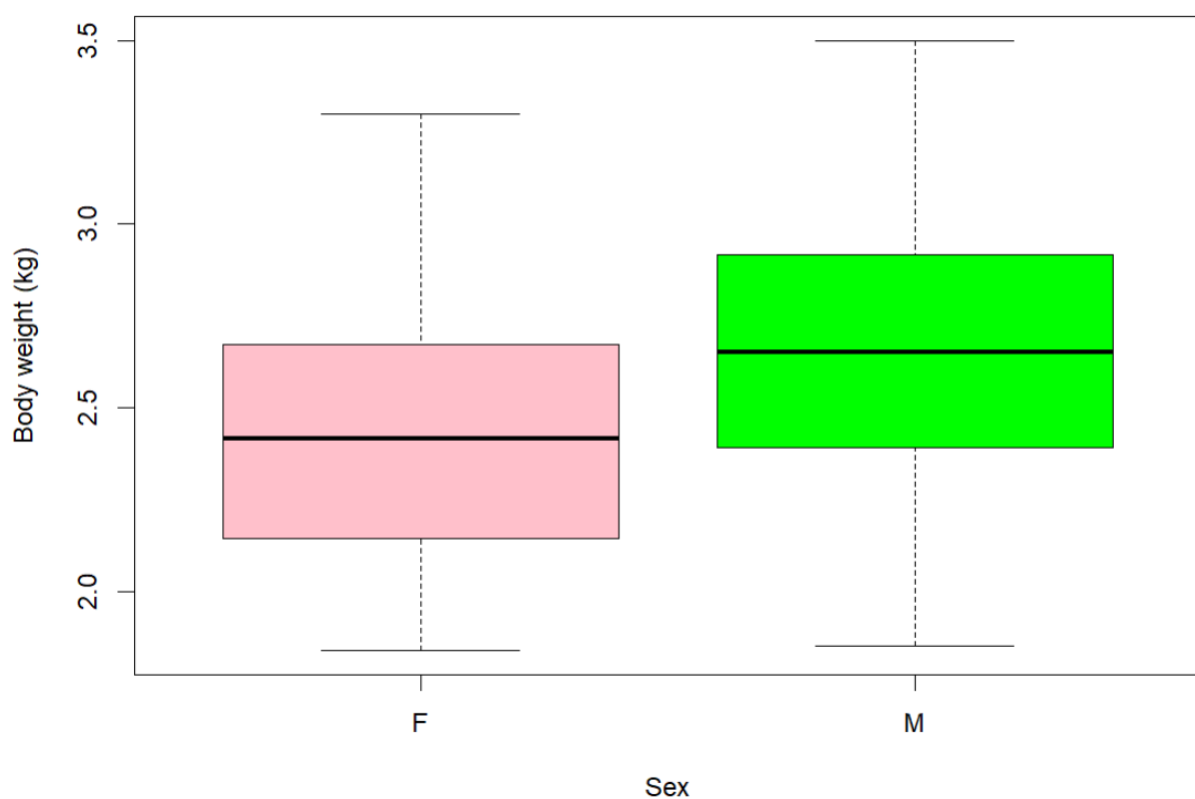
645 The final measure I was interested in investigating was the presence of *Cryptosporidium parvum*. The
646 dataset consisted of 55 individual possums (25 females, 30 males) that had scat samples collected and
647 tested, and that I used to test problem-solving ability in chapter 3. All relevant scats were collected
648 within three years. If any of the scats had a presence of *C. parvum*, it was considered positive. Those
649 who tested positive had all completed their first puzzle trial (see chapter 3) within two months of the

650 positive scat being collected. I tested the association between presence of *C. parvum* and sex using a
651 chi-square test of independence.

652 I tested the association between presence of *C. parvum* and the personality trait, exploration, using a
653 generalised linear model with a binomial family and logit link function. Exploration was chosen as it
654 has previously been found that more exploratory individuals are more likely to carry *C. parvum* (ref
655 Anushika's manuscript).

656 Results

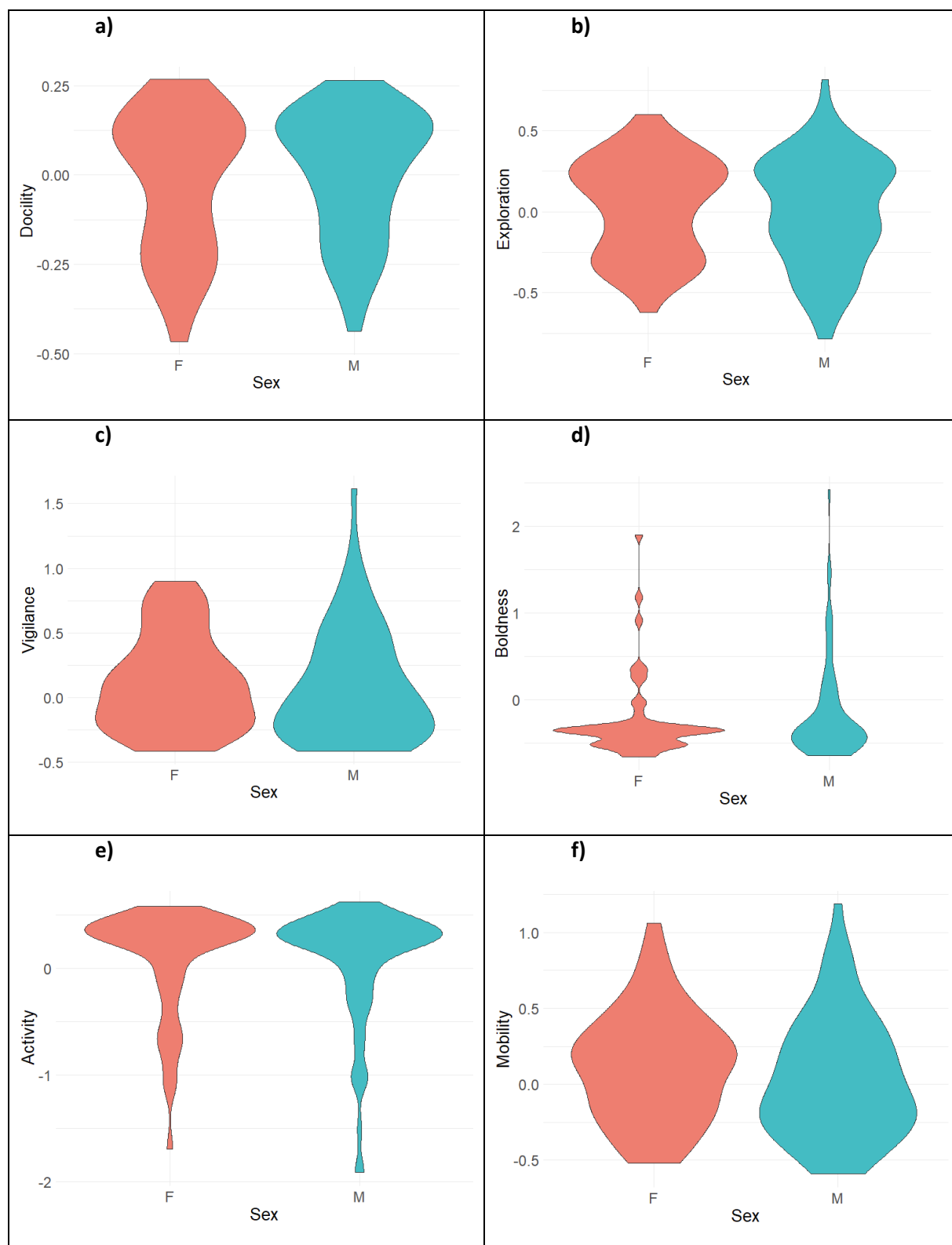
657 There was a significant effect of sex on body weight ($F_{1,123} = 11.415$, $p < 0.005$) with males slightly
658 (9.5%) larger than females (figure 2).



659
660 **Figure 3.** Boxplot of body weight of adult common brushtail possums by sex (n = 127; 51 females, 76
661 males).

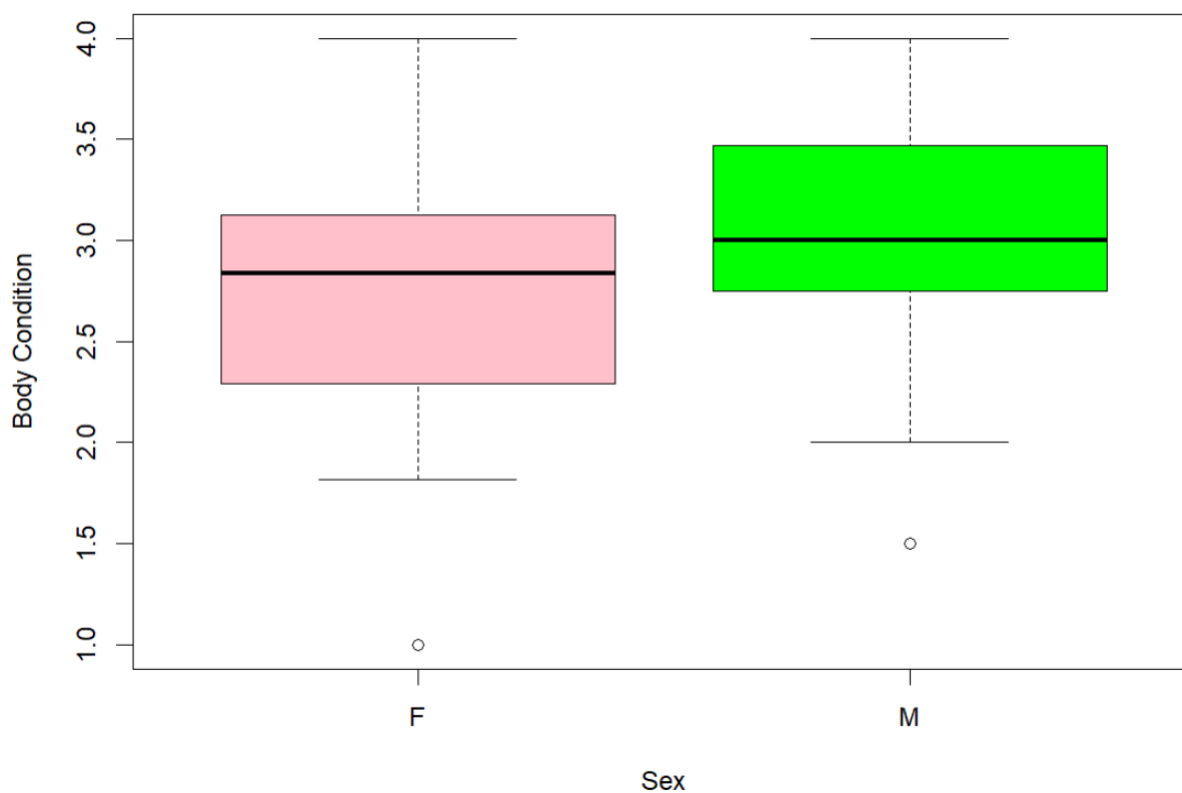
662 There was no significant difference between sexes for any of the personality traits: docility [$F_{1,128} =$
663 0.6788, $p = 0.41$] (figure 3a), exploration [$F_{1,125} = 0.1912$, $p = 0.66$] (figure 3b), activity [$F_{1,125} = 0.0413$,

664 $p = 0.84$] (figure 3e), vigilance [$F_{1,125} = 0.1934$, $p = 0.66$] (figure 3c), boldness [$F_{1,125} = 0.9447$, $p = 0.33$]
 665 (figure 3d), and mobility [$F_{1,125} = 1.4313$, $p = 0.23$] (figure 3f).



666 **Figure 4.** Violin plots showing variation between sexes for six personality traits; a) $n = 130$ individual
 667 possums; 53 females, 77 males; b) – e) $n = 127$ individual possums; 51 females, 76 males.

668 There was no significant effect of sex on body condition ($F_{1,66} = 3.5536$, $p = 0.06$), although males were
669 in slightly higher body condition than females (figure 4).



670
671 **Figure 5.** Boxplot of body condition of adult common brushtail possums by sex (n = 68; 27 females, 41
672 males).

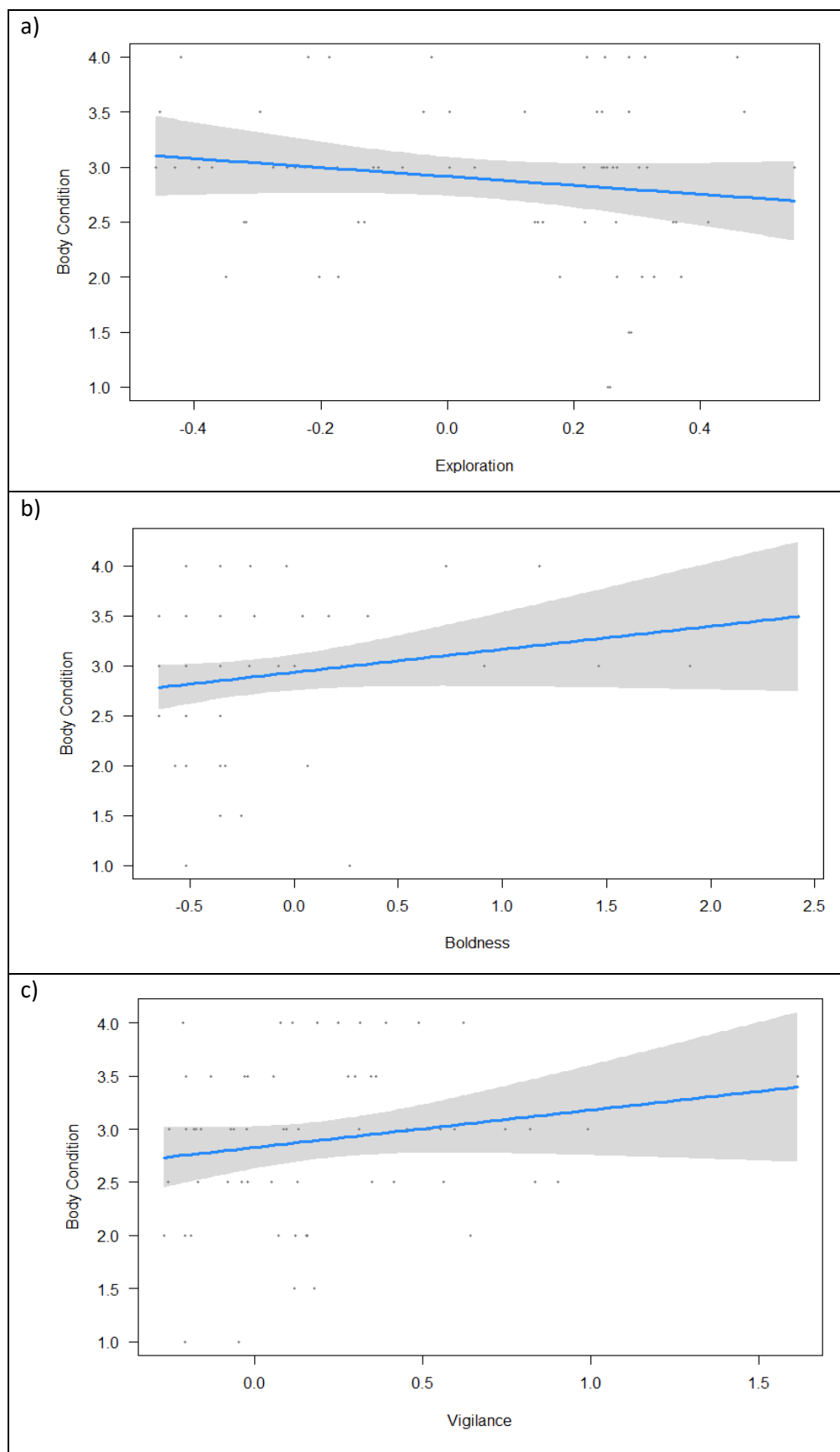
673 There was no significant relationship between body condition and any of the tested personality traits:
674 exploration [$F_{1,65} = 1.6588$, $p = 0.20$], boldness [$F_{1,65} = 2.6798$, $p = 0.11$], and vigilance [$F_{1,65} = 2.1423$,
675 $p = 0.15$].

676

677

678

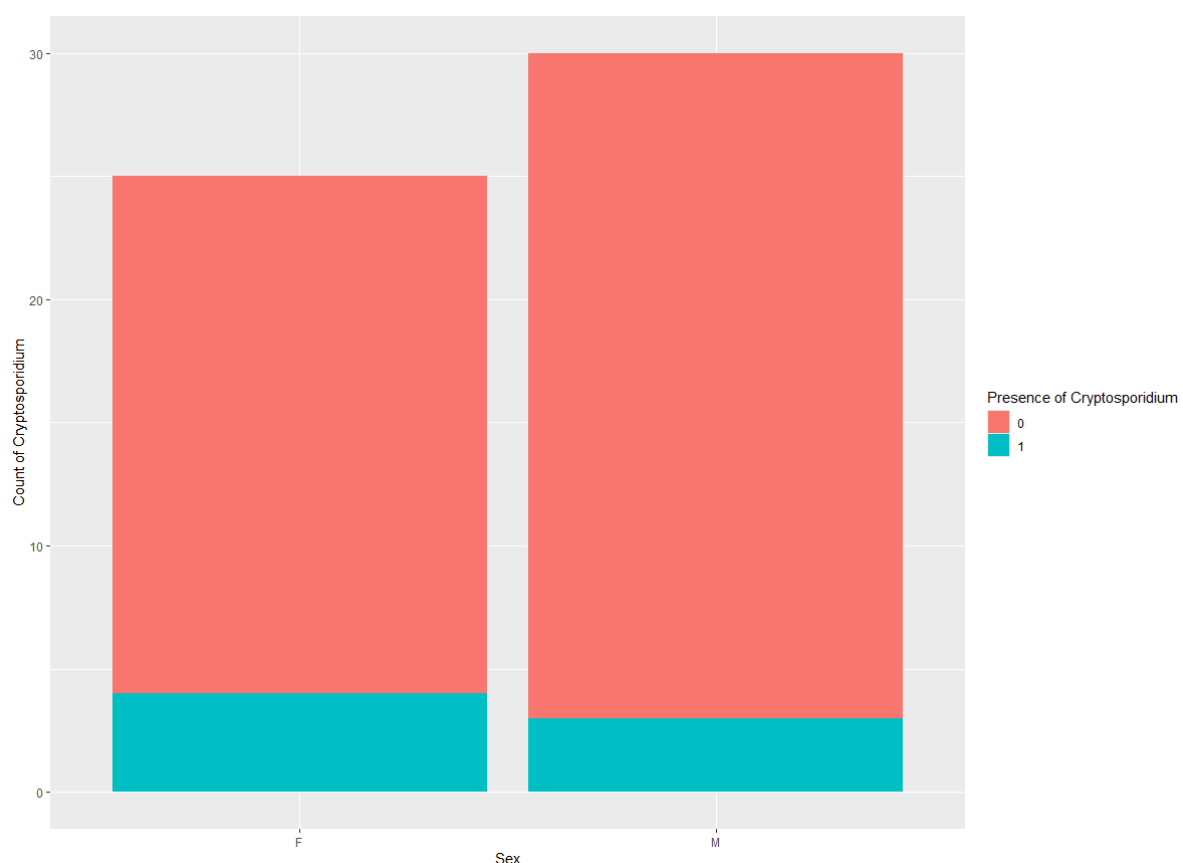
679



680 **Figure 6.** Plots between body condition and three personality traits (n = 67 individual possums) with
681 95% confidence intervals. None of the relationships were significant.

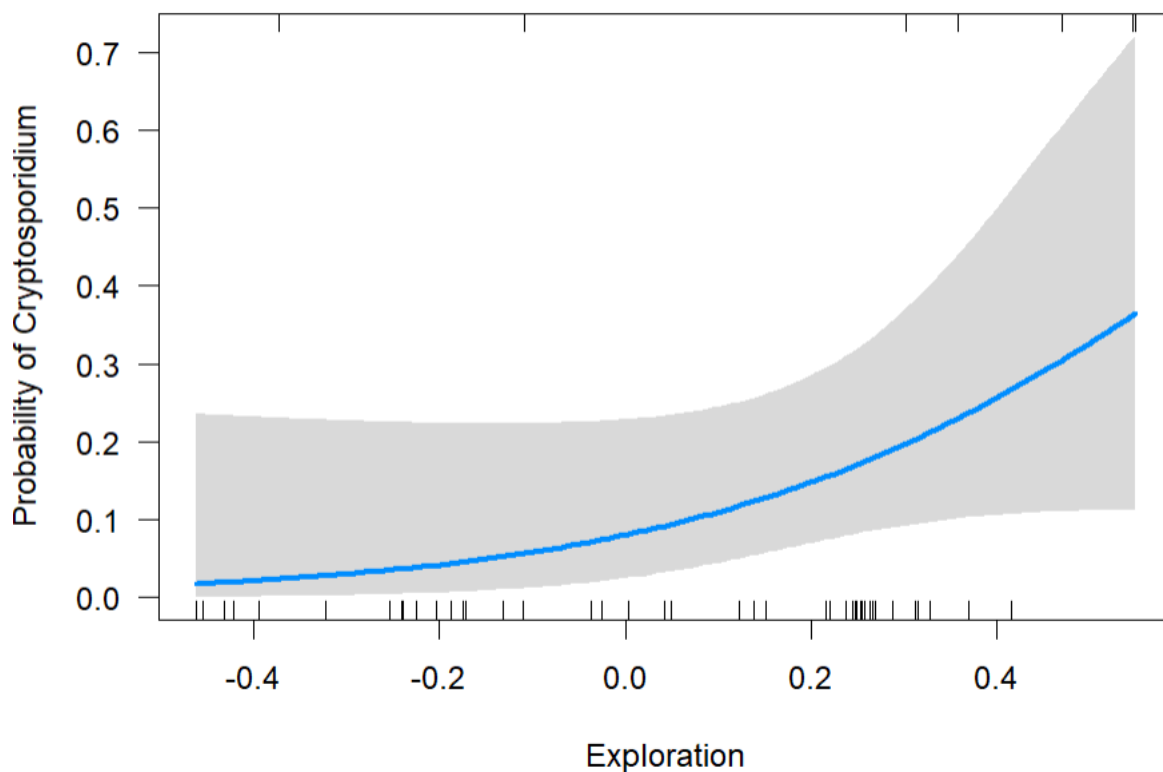
682 All possums were healthy based on a physical and behavioural examination conducted by the vet
683 during handling. Haematology and biochemistry parameters, indicative of good health, could
684 therefore be defined for this population (Tables 2 & 3) as now published in (Marschner, Geisler-Edge,
685 Chao & Courtman, 2025). In two individual possums, Alanine aminotransferase (crucial to liver
686 function) measures were out of the healthy range, as indicated by the vet. Cross-referencing with
687 handling notes indicated that one had a skin disease and the other a cleft pallet, possibly related to
688 the variation in this health parameter.

689 Of the total population of possums, 12.73% carried *Cryptosporidium parvum*: 4 of 25 females and 3 of
690 30 males (Fig 7). There is no significant association between presence of *C. parvum* and sex (X^2 (df =1,
691 n = 55) = 0.440, p = 0.51).



692
693 **Figure 7.** Presence of *Cryptosporidium parvum* by sex (n = 55 individual possums; 25 females, 30
694 males).

695 There is a significant association between likelihood of carrying *Cryptosporidium parvum* and the
696 explorative trait (X^2 (df =1, n = 54) = 3.9404, p = 0.047).



697

698 **Figure 8.** Plot showing the relationship (with 95% confidence intervals) between exploration and
699 likelihood of carrying the parasite *Cryptosporidium parvum* (n = 54 individual possums).

700 Discussion

701 For my study population, I quantified key traits that I predict will be relevant to foraging and problem-
702 solving. I then tested for associations amongst some of these traits.

703 Adult male possums in my population were significantly heavier (9.5%) than females, consistent with
704 previous studies (Clinchy et al., 2004; Isaac, 2006). Male-male competition may drive this sexual size
705 dimorphism, as the species is polygynous. In Mongolian gerbils (*Meriones unguiculatus*) – a
706 polygynous species - for example, males are larger in body mass and body length than females
707 (*Meriones unguiculatus*) (Wang, 2017).

708 Individual possums did vary in their personality traits but not as a function of sex. This result is
709 consistent with previous research on other mammals, such as the spotted hyena (*Crocuta crocuta*)
710 and California sea lion (*Zalophus californianus*) (Ciardelli et al., 2017; Greenberg & Holekamp, 2017).
711 Studies considering the relationship between personality and sex have varied by whether they used
712 juveniles, adults, wild-caught or captive individuals as their study species but none found a significant
713 difference in personality between sexes (Begall et al., 2022; Ciardelli et al., 2017; Greenberg &
714 Holekamp, 2017; Halliday et al., 2014; Oosthuizen & Lutermann, 2023; Seltmann et al., 2018).

715 Male possums were in slightly (but not significantly) better body condition than females, possibly
716 because female possums bear the costs of breeding, such as energy expenditure during lactation.
717 Decreased body condition for lactating females has been documented across several species of
718 mammals including the humpback whale (*Megaptera novaeangliae*), muskox (*Ovibos moschatus*),
719 reindeer (*Rangifer tarandus*), and European badger (*Meles meles*) (Bårdsen et al., 2010; Christiansen
720 et al., 2016; Desforges et al., 2019; Woodroffe & Macdonald, 1995). Male possums may also have
721 greater access to resources – foods that could increase their body condition – as males have larger
722 home range sizes and therefore the possibility of more rubbish bins, plants, and fruits available to
723 them (Wat et al., 2019). Despite all possums being healthy, individuals of the population still varied in
724 their personality traits. Possums also varied slightly by body condition and parasite presence.

725 In my population, body condition did not vary as a function of either of the three personality traits
726 (exploration, boldness, and vigilance). In a population in an urban-woodland boundary in Sydney,
727 exploratory possums had a broader diet and were more likely to eat vegetation found on the ground
728 less exploratory possums (Herath et al., 2021). The results of my study and Herath et al. (2021)
729 suggests that, even if the diet of possums in my study varied as function of personality, all individuals
730 had sufficient access to resources. It is possible that the university campus – a green space with many
731 rubbish bins- provided an abundant food environment.

732 Upon visual examination, all possums were considered healthy. Two possums showed some
733 abnormality – one with a possible skin condition and the other with a damaged upper mouth palate.
734 This was reflected in the blood results, although most parameters indicated that these individuals
735 were otherwise in good health.

736 *Cryptosporidium parvum* is detrimental to the fitness of livestock species (Olson et al., 2004). Whether
737 carrying *C. parvum* incurs fitness costs for brushtail possums is unknown. However, as all possums in
738 my study population were in good health, carriage of *C. parvum* did not appear to incur a noticeable,
739 or lasting, health cost. Given that likelihood of *C. parvum* parasite carriage did not differ by sex in this
740 population, female possums do not seem to be disadvantaged. In contrast, female alpacas have been
741 found to be more likely to carry gut parasites (e.g. *Camelostrongylus*, *Eimeria*, *Capillaria*) – suspected
742 to be due to the weakening of their immunity as a result of reproductive costs (Szopieray et al., 2024).

743 More exploratory possums in my study population had a greater likelihood of *C. parvum* carriage. In
744 an urban-woodland habitat, more exploratory possums had a greater % of their home range in urban
745 habitat (Wat et al., 2019) and ate a more diverse diet including plants found at ground level than less
746 exploratory possums (Herath et al., 2021). Even if these traits benefit the individual (e.g. providing
747 greater access to more high-quality resources), it may also increase their chance of exposure to
748 parasites, particularly one such as *C. parvum*, which is carried by humans, domestic animals and
749 wildlife in urban environments (Herath et al unpubl.).

750 Several of the key traits that I have explored are likely to influence the problem-solving ability of my
751 study species as these traits have been relevant in research on problem-solving in brushtail possums
752 by Wat et al. (2020) and Harris et al. (2023). Relevant traits will therefore be included in chapter 3.

753 The traits that I will explore further in chapter 3 are sex, personality, body weight, body condition, and
754 parasite load. Associations between some of these traits will have to be considered when examining
755 their influence on problem-solving, as there may be direct or indirect effects. Biochemistry and

756 haematology parameters will not be further considered in chapter 3 as this population was in good
757 health with only slight variation in parameters, so unlikely to affect problem-solving ability.

758

759 Appendix

760 **Table 2.** Haematology results of common brushtail possums in my study population (Marschner et al., 2025).

Haematology	n	RI	Min-Max	Median	Mean	SD	90% CI min	90% CI max	Method
Red blood cells (RBC) (10 ¹² /L)	23		4.25-7.07	5.76	5.85				
Nucleated red blood cells (NRBC) %	21		0-6.1 %	0.70%	1.27				
Reticulocytes (10 ⁹ /L)	23	25.64-132.62	30.90-119.5	83.9	78.33	24.46	10.78-46.55	119.92-144.5	robust untransformed
Haemoglobin (HGB) (g/L)	23	89.00-149.90	91.00-145.00	123.7	122.9	14.4	77.70-99.20*	141.60-155.90*	robust transformed
Haematocrit (HCT) (L/L)	23	0.27-0.43	0.29-0.42	0.37	0.37	0.04	0.22-0.31*	0.42-0.45	robust transformed
Mean corpuscular volume (MCV) (fL)	23		56.70-68.00	62.2	62.98				
Mean corpuscular haemoglobin (MCH) (pg)	23		19.00-22.10	21.1	21.04				
Mean corpuscular haemoglobin concentration (MCHC) (g/L)	23		315.00-359.00	332	334.4				
Mean platelet volume (MPV) (fL)	23	7.08-11.62	7.40-11.20	9.3	9.35	1.06	6.51-7.68*	10.92-12.25*	robust untransformed
Red cell distribution width -SD (fL)	23		26.60-37.30	30.8	31.41				
Red cell distribution width -CV (%)	23		12.20-16.70	14.5	14.58				
Platelet distribution width (PDW) (fL)	19	4.52-14.29	6.30-15.00	9.6	9.98	2.25	too few data	too few data	robust untransformed

White Blood Cells (WBC)(10⁹/L)	23		1.30-8.06	2.81	3.63				
Neutrophils (10⁹/L)	22		0.23-6.32	1.31	1.92				
Lymphocytes (10⁹/L)	22	0.29-2.56	0.41-2.33	1.51	1.48	0.52	0-0.72	2.26-2.83	robust transformed
Monocytes (10⁹/L)	23		0.02-0.25	0.08	0.1				
Eosinophils (10⁹/L)	23		0-0.14	0	0.03				
Basophils (10⁹/L)	23		0-0.04	0	0.002				

761

762 **Table 3.** Biochemistry results of common brushtail possums in my study population (Marschner et al., 2025).

Biochemistry	n	RI	Min-Max	Median	Mean	SD	90% CI min	90% CI max	Method
Alkaline Phosphatase (ALP)	18	15.51-1496.61	194.06-1548.29	734.32	756.06	341.64	too few data (<20)	too few data (<20)	standard untransformed
Gamma-Glutamyl Transferase (GGT)	20		2.46-12.04	5.71	6.12				
Alanine Aminotransferase (ALT)	18	0-53.90	4.37-46.73	27.42	28	11.82	too few data (<20)	too few data (<20)	standard transformed
Aspartate Aminotransferase (AST)	19	19.37-89.09	25.04-86.01	53.95	54.05	16.06	too few data (<20)	too few data (<20)	robust untransformed
Protein Total	22	51.42-68.20	50.50-65.31	59.67	59.65	3.93	48.83-54.04	65.59-70.29	robust untransformed
Globulins	22		17.84-30.58	25.24	25.35				

Albumin	22	29.28-39.26	30.68-38.42	34.22	34.3	2.33	28.08-30.58*	37.66-40.50*	robust untransformed
Bilirubin Total	21	0.79-19.85	0.92-16.25	3.7	5.08	4.02	0.49-1.21	10.73-33.12*	robust transformed
Creatine Kinase (CK)	19	28.51-932.94	43.08-916.42	300.93	353.05	217.04	too few data (<20)	too few data (<20)	robust transformed
Cholesterol	22	1.45-4.92	2.05-4.59	3.66	3.47	0.79	0.72-2.29*	4.61-5.23	robust transformed
Glucose	22	2.31-10.32	2.31-10.31	6.31	6.14	1.86	1.43-3.47*	9.19-11.32*	robust untransformed
Calcium	22		1.95-2.92	2.4	2.37				
ISE.Chloride	22	102.65-118.02	102.23-117.63	109.4	110.24	3.54	100.77-104.96*	114.62-120.68*	robust transformed
ISE.Potassium	20	2.82-5.98	2.93-5.61	3.69	3.86	0.7	2.70-3.00	4.86-8.02*	robust transformed
ISE.Sodium	21	140.64-155.74	143.85-158.55	148.44	148.94	3.52	138.44-143.78*	152.81-158.77*	robust transformed
Phosphate	22		0.60-1.98	1.22	1.21				
T4	17		0.02-12.26	2.81	4.02				
Creatinine	21	42.86-120.92	54.98-110.39	83.59	81.97	18.04	32.04-54.09*	108.89-130.83*	robust untransformed
Urea	19	3.10-10.83	3.80-8.78	6.35	6.16	1.69	too few data (<20)	too few data (<20)	robust transformed

764 **Table 4.** Results of the parasite analysis of scats of common brushtail possums. Average body weight
 765 in kilograms. Carriage of *Cryptosporidium parvum* and *Giardia* spp. (1 = presence; 0 = absence). All
 766 individuals with *Cryptosporidium parvum* indicated as present happened to only have the parasite
 767 recorded as present in one of multiple scat sampling events.

Possum ID	Sex	Body Weight (kg)	Body Condition	No. of Scats Sampled	Cryptosporidium	Giardia
447107	Female	2.18	3.0	2	0	0
447108	Female	2.88	3.0	3	1	0
447124	Female	2.70	3.5	3	0	0
447147	Female	2.77	3.0	3	0	0
447154	Female	2.65	3.5	3	0	0
447158	Female	2.40	2.5	1	0	0
447214	Male	2.55	3.5	1	0	0
447230	Male	2.70	3.5	1	0	0
447356	Male	2.68	2.0	3	0	0
447357	Male	2.88	2.5	3	0	0
447369	Male	3.55	NA	1	0	0
447387	Female	2.15	NA	1	0	0
447465	Male	3.08	2.5	3	0	0
447487	Male	2.85	NA	1	0	0
447489	Male	3.35	3.0	1	0	0
447512	Male	2.55	3.0	1	0	0
447525	Female	2.74	4.0	5	0	0
447532	Female	2.35	3.5	1	0	0
447544	Male	3.40	3.5	1	0	0
447567	Male	3.45	3.0	1	0	0
447572	Male	3.25	2.0	1	0	0
447624	Female	2.25	4.0	1	0	0
447643	Male	3.25	2.5	1	0	0
447808	Male	2.65	2.0	1	0	0
447841	Female	2.72	3.0	11	0	0
447843	Male	3.4	3.5	1	0	0
447902	Female	2.25	1.0	1	0	0
447947	Male	2.23	3.0	2	0	0
456866	Unknown	1.55	NA	1	0	0
458386	Female	1.95	2.0	1	0	0
458519	Male	2.45	3.0	6	1	0
458801	Male	2.20	3.0	1	0	0
458927	Male	2.05	3.0	4	0	0
458953	Male	2.15	2.0	1	0	0

458983	Male	1.75	3.0	1	0	0
458997	Male	2.00	3.0	1	0	0
459185	Female	1.46	3.0	5	0	0
461217	Female	2.00	4.0	1	0	0
462078	Male	2.70	3.0	2	0	0
463012	Male	2.95	4.0	1	0	0
1156317	Female	2.27	1.0	7	0	0
6128227	Female	2.47	3.0	9	1	0
6130891	Male	2.42	3.0	3	0	0
6131194	Female	2.28	3.0	7	0	0
6135876	Female	2.70	3.0	3	0	0
6137410	Male	2.80	3.5	2	0	0
6137720	Female	2.80	2.0	1	0	0
6137838	Male	2.20	4.0	1	0	0
6137856	Female	2.87	3.0	3	1	0
6137891	Female	2.30	4.0	1	0	0
6138024	Male	3.02	3.5	10	1	0
6138055	Male	2.75	3.0	2	0	0
6138073	Female	2.45	3.0	1	0	0
6138303	Female	2.80	4.0	2	0	0
6138321	Female	2.66	2.0	4	1	0
6138335	Male	1.90	3.0	1	1	0

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Chapter 3

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What intrinsic characteristics and mechanistic behaviours influence problem-solving by Common Brushtail Possums?



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908 Chapter 3: What intrinsic characteristics and mechanistic behaviours influence
909 problem-solving by Common Brushtail Possums?

910 Preface

911 Chapter 3 is a data chapter written, with some modification required, with the intention to submit to
912 a peer-reviewed journal. Contributors to this data chapter include A.R. Geisler-Edge, H.R. Harris, A.
913 Greenville, A.P.H.M. Herath, M.L. Power and C. McArthur.

914 Authors' contributions: A.R. Geisler-Edge and C. McArthur conceived the ideas and designed the
915 methodology; H.R. Harris collected data previously which has been built on in this chapter; A.R.
916 Geisler-Edge performed all field work and collected the data; A.P.H.M. Herath and M.L. Power
917 conducted the parasite screening; A.R. Geisler-Edge, A. Greenville and C. McArthur analysed the data
918 and performed the statistical analysis; A.R. Geisler-Edge and C. McArthur wrote the data chapter.

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929 Abstract

930 Animals frequently demonstrate problem-solving behaviour as they attempt to access food while
931 foraging. Individuals vary in their problem-solving ability, and we can attempt to explain these
932 differences by examining the intrinsic traits and mechanistic behaviours influencing their approach
933 and problem-solving performance. My aim was to test for indirect and direct effects of intrinsic traits
934 and mechanistic behaviours on problem-solving using the Common Brushtail Possum (*Trichosurus*
935 *vulpecula*) as my study species. I first measured intrinsic traits of possums that I had trapped: sex,
936 personality, body weight, body condition and parasite carriage. I then recorded the same individuals
937 attempting food extraction puzzles and quantified their behaviours. I used a structural equation
938 modelling approach to investigate multiple indirect and direct main effects of predictors of problem-
939 solving performance. I also used simple GLMs to test several specific hypotheses. Individuals within
940 my study population varied in the problem-solving success based on body condition and personality
941 traits. Selectivity and change in time spent engaged with the functional part of the puzzle directly
942 affected problem-solving. Possums demonstrated an ability to recall the solution to the presented
943 puzzle over both a short and long time period; one of the few studies showing evidence of long-term
944 memory in a wild animal. Although there was a small sample size of possums carrying the parasite,
945 *Cryptosporidium parvum*, there was a significant effect of parasite carriage on the time spent engaged
946 with functional parts of the puzzle problem-solving. My findings demonstrate both intrinsic traits and
947 mechanistic behaviours influenced the overall approach and performance in problem-solving of
948 individual possums. Whether such individual differences lead to differences in fitness, or simply
949 reflects different ways animals may access resources in their environment, remains to be revealed.

950 Introduction

951 Animals frequently demonstrate problem-solving behaviour as they search for food and shelter, or
952 escape predators and other threats. When foraging, for example, wild capuchin monkeys (*Cebus*
953 *libidinosus*) hammer nuts to access food, which requires finding the right tool and best way to use it

954 to break them (Spagnoletti et al., 2012). Sulphur-crested cockatoos work out how to use their beaks
955 and feet in particular ways to open bin lids to access food in urban environments (Klump et al., 2021).
956 In animal research, we attempt to replicate such problem-solving scenarios using food extraction
957 puzzles, creating foraging challenges in an artificial environment that compare to those animals may
958 face in the real world.

959 Problem-solving can be indicative of the level of cognitive function of a species or individual. Food
960 extraction tasks, for example, were used to assess problem-solving in New Caledonian crows (*Corvus*
961 *moneduloides*) (Jelbert et al., 2014). The success rate of these crows was over 50% for 4 of 6 tasks,
962 comparable to human children who also completed the tasks.

963 Food extraction tasks may be set up in the animal's natural environment or in a captive environment.
964 Chen et al. (2022) tested the personality traits and problem-solving abilities of budgerigars
965 (*Melopsittacus undulatus*) in captivity and demonstrated a relationship between personality and
966 likelihood to solve a food extraction task. However, whether such relationships hold in the species'
967 natural environment is unknown. Studying an animal in its natural environment incurs greater and
968 often uncontrolled background variation, but this may also be more informative as to what influences
969 animals in the real world. For example, Chow, Uchida, et al. (2021) studied problem-solving in free-
970 ranging Eurasian red squirrels (*Sciurus vulgaris*) in an urban environment. They found that human
971 disturbance was one of the variables influencing problem-solving performance: a factor that would be
972 missed in a captive study.

973 Problem-solving ability can be measured as likelihood to succeed and time taken to solve. Improving
974 problem-solving with more attempts and/or over time is indicative of learning and memory retention
975 in the short- or long-term (depending on the timeframe). Individuals are likely to differ in their
976 approach to solving problems because the characteristics that influence their approach may vary
977 among individuals. For example, individuals may vary in the proximate "mechanistic" behaviours they
978 use when solving the problem. Intrinsic traits, such as differences in sex, personality traits, body

979 condition and body weight, may also influence problem-solving directly, or indirectly by influencing
980 their use of mechanistic behaviours.

981 Mechanistic behaviours can influence the likelihood of an individual successfully solving a food
982 extraction task. For example, Eurasian red squirrels (*Sciurus vulgaris*) with greater behavioural
983 flexibility, i.e. rate of switching between behaviours, were more likely to solve a puzzle on their first
984 attempt (Chow et al., 2018). Similarly, behavioural diversity, i.e. variation in behaviours, led to a higher
985 success rate in the food extraction task performed by raccoons (*Procyon lotor*) (Lazure & Weladji,
986 2024b). Selectivity is a measure of the functional behaviours performed as a proportion of the total
987 engaged behaviours. As functional behaviours are those that lead to solving the presented puzzle,
988 high selectivity should improve problem-solving performance. This relationship has been shown in
989 eastern grey squirrels (*Sciurus carolinensis*) as increasing selectivity led to an improved (i.e., reduced)
990 time to solve the puzzle (Chow et al., 2016). Persistence, i.e. work time (the proportion of time spent
991 engaged with the puzzle), has also been shown to be a predictor of success in a food extraction task,
992 demonstrated by African lions (*Panthera leo*) and snow leopards (*Panthera uncia*) (O'Connor et al.,
993 2022).

994 Experience is another driver of problem-solving performance. Captive studies usually allow for
995 repetition of a food extraction task with their study individuals. As a result, learning over the short-
996 term has been extensively researched in multiple taxa. With repeat trials, over four consecutive days,
997 by Olrog's gulls (*Larus atlanticus*), the likelihood of solving a food extraction task increased (Castano
998 et al., 2022); and with repeat trials over consecutive days (max 5 trials) by African lions (*Panthera leo*)
999 and snow leopards (*Panthera uncia*), time taken to solve decreased (O'Connor et al., 2022). Short-
1000 term learning has also been shown in free-ranging populations. Wild eastern grey squirrels (*Sciurus*
1001 *carolinensis*) improved their likelihood to solve, and time taken to solve, a food extraction task with
1002 repeat trials over 6-8 weeks (Chow, Clayton, et al., 2021).

1003 Learning and memory retention of that learning (recall) long-term in captive populations has also been
1004 studied across a few taxa. Aldabra giant tortoises (*Aldabrachelys gigantea*) and Galapagos giant
1005 tortoises (*Chelonoidis niger*) were able to recall the solution to a task 3 months from the learning date
1006 (Gutnick et al., 2020). In contrast, Shetland ponies, also kept in captivity, were unable to recall the
1007 solution to a task after one year (Gabor & Gerken, 2018). Apart from a few recent studies, research
1008 into long-term memory retention in wild populations is scarce, likely because it is difficult to re-test
1009 the original study individuals years later when they are free-ranging. Nevertheless, wild raccoons
1010 (*Procyon lotor*) have shown long-term memory retention, with the likelihood of solving a food
1011 extraction task increasing over subsequent years (Lazure & Weladji, 2024a). Wild North Island robins
1012 (*Petroica longipes*) were also able to recall the solution to a food extraction task close to two years
1013 since their initial encounter with the task (Shaw & Harvey, 2020).

1014 In addition to the behaviours animals perform, their intrinsic traits may influence their problem-
1015 solving ability. For example, male and female gibbons (*Hylobatidae*; all four genera included) differed
1016 in their approach to problem-solving (Cunningham et al., 2011). As females gained experience with
1017 the puzzle, they improved their time to solve, potentially because the high energetic costs of
1018 reproduction are a motivator for females to learn. Personality has also been shown as relevant to
1019 problem-solving in several species. More exploratory individuals of the fawn-footed mosaic-tailed rat
1020 (*Melomys cervinipes*) were more likely to solve and had a faster solve time than less exploratory
1021 individuals (Rowell & Rymer, 2021). These individuals may be better at interacting with foreign objects
1022 in their environment and less neophobic than less exploratory individuals. In wild grey mouse lemurs
1023 (*Microcebus murinus*), good body condition was associated with efficiency in problem-solving
1024 (Huebner et al., 2018). The relationship between body condition and problem-solving may be
1025 applicable in the species' natural environment; the ability to solve problems may contribute to good
1026 body condition, or being in a good state of body condition may boost the individual's ability to solve
1027 problems. Parasite carriage has also been shown to affect problem-solving. Sheep carrying
1028 *Toxoplasma gondii*, for example, were slower to solve the presented problem (Shamsi et al., 2023).

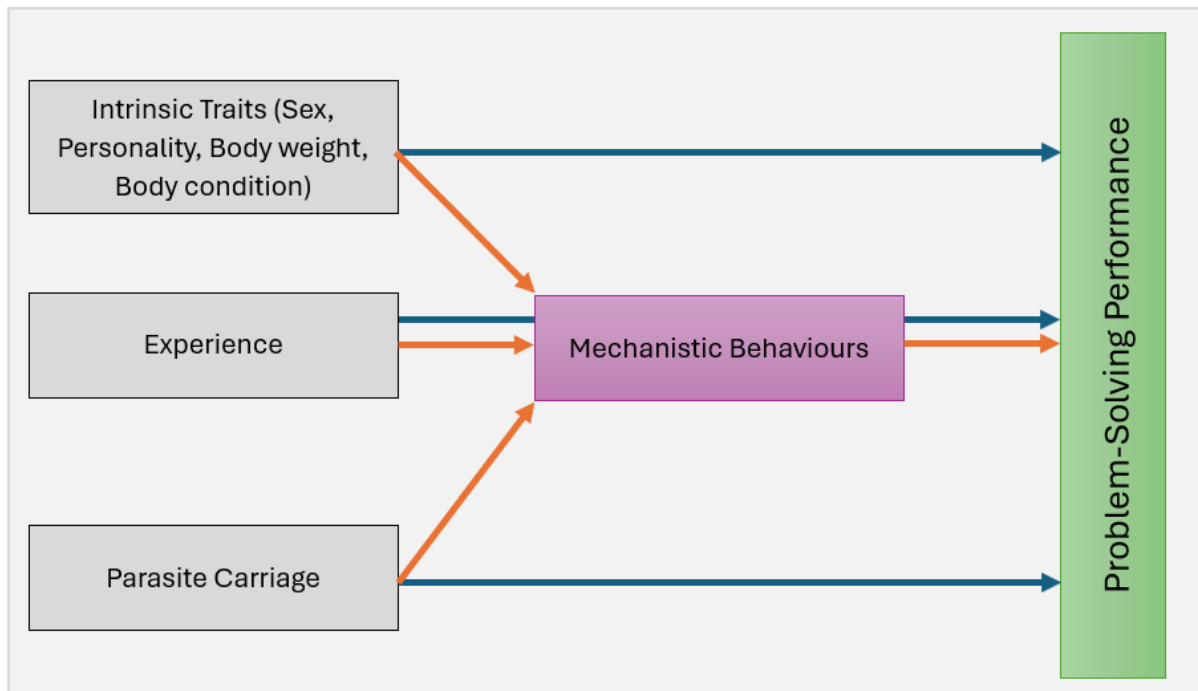
1029 Such a relationship could have implications for the wellbeing and fitness of animals in their natural
1030 environment.

1031 The overall goal in this chapter was to explore the direct and indirect influence of intrinsic traits and
1032 mechanistic behaviours on problem-solving, using the Common Brushtail Possum (*Trichosurus*
1033 *vulpecula*). In testing problem-solving with an escape box task, Wat et al. (2020) found that individual
1034 characteristics affecting problem-solving varied by the difficulty of the task. Possums that were highly
1035 persistent were less likely to solve the easier escape box task, as they focused on nonfunctional parts
1036 of the puzzle, but were more successful at the difficult escape box task. Personality also influenced
1037 performance, with more exploratory, more vigilant and more active individuals more likely to solve
1038 the puzzle. Harris et al. (2023) assessed problem-solving of possums using a food extraction task.
1039 Again, persistence was an indicator of likelihood to solve. Behavioural diversity also increased
1040 likelihood of solving, but, for those who did solve the puzzle, also increased the time taken to solve it
1041 (Harris, 2022). Possums have been recorded as carriers of the protozoan parasite, *Cryptosporidium*
1042 *spp.* (Hill et al., 2008). *Cryptosporidium spp.* affects native wildlife and can cause enteric disease in
1043 humans and domestic animals (Wait et al., 2017). *Cryptosporidium parvum* carriage in possums has
1044 been shown to differ based on personality of the individual but not sex (Herath et al. unpubl.). The
1045 relationship between problem-solving performance and *C. parvum* carriage has been tested for
1046 possums previously, with no significant effect (Harris, 2022); but this was with a very low sample size.
1047 My specific aims were to explore the relationships shown in the conceptual model in Figure 1; using a
1048 food extraction task to test for

1049 (1) direct or indirect effects of intrinsic traits and mechanistic behaviours on problem-solving
1050 performance quantified by (a) first trial outcome [AIM 1] and (b) time to first solve [AIM 2],

1051 (2) influence of experience as measured by learning over the short-term [AIM 3] and long-term
1052 memory/recall [AIM 4],

1053 (3) any influence of parasite (*C. parvum*) carriage on problem-solving [AIM 5].



1054

1055 **Figure 1.** Conceptual model showing potential direct and indirect drivers of problem-solving
1056 performance.

1057 Materials and methods

1058 *Site Description and possum trapping*

1059 The study was based on the University of Sydney Camperdown Campus, an urban environment just
1060 3.7 km from the CBD. The campus has a high density of buildings plus several green spaces, including
1061 two sports ovals surrounded by trees where most possums were trapped.

1062 The study comprised possums from two sessions for data collection: (1) those trapped by Hannah
1063 Harris (between October 2021 and March 2022) and (2) those trapped by myself (between January
1064 2023 and April 2024), using essentially the same methods.

1065 For my session, I trapped at 8 sites on campus over a total of 34 nights. Sites were selected based on
1066 previous sightings, successful trapping locations in Session 1, and nearby possum scats. Sites were at

1067 least 20 metres apart and I placed 5 to 13 traps per site. I trapped 44 individuals - 24 males, 18 females,
1068 and 2 of unknown sex (these escaped before being sexed).

1069 Possums were trapped using Tomahawk cages (63 x 25 x 25 cm) that were partially wrapped in
1070 builder's plastic to protect animals from inclement weather and provide a "safe haven". Each trap was
1071 baited with a quarter piece of apple to provide hydration, and a one slice of peanut butter covered
1072 bread. Traps were set close to vegetation and away from pedestrian view. We began setting traps
1073 between 1630 and 1730 (dependent on approx. time of sunset). We then checked traps regularly
1074 between 2100 and 0530.

1075 *Measuring traits of trapped possums*

1076 Once a possum was trapped, it was transferred from the trap into a handling bag. Individual metrics
1077 were taken close to the trap site. The possum was weighed inside the handling bag using a 5kg scale.
1078 If required, personality tests were performed (see below) before other measures were taken. This
1079 order ensured handling did not interfere with or affect behaviour in personality tests. The animal was
1080 sexed, and body condition measured on a range between 1 and 4, with 0.5 increments (table 1). Age
1081 was recorded for each possum based on their weight. Individuals ≥ 1.8 kg were considered adults and
1082 those <1.8 kg were considered juveniles. Before releasing the possum, it was also scanned for a Passive
1083 Integrated Transponder (PIT) tag using a Biomark HPR Lite Handheld PIT Tag Reader. If the possum
1084 was not previously tagged, I implanted a tag during handling. This allowed for continued identification
1085 of the individual throughout this and future studies. Possums would also need to be identified from
1086 camera footage for later problem-solving trials. A unique pattern was shaved into a small patch of the
1087 individual's fur and this pattern recorded to later identify this possum based on sight.

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1091 **Table 1.** Definition of body condition scoring system

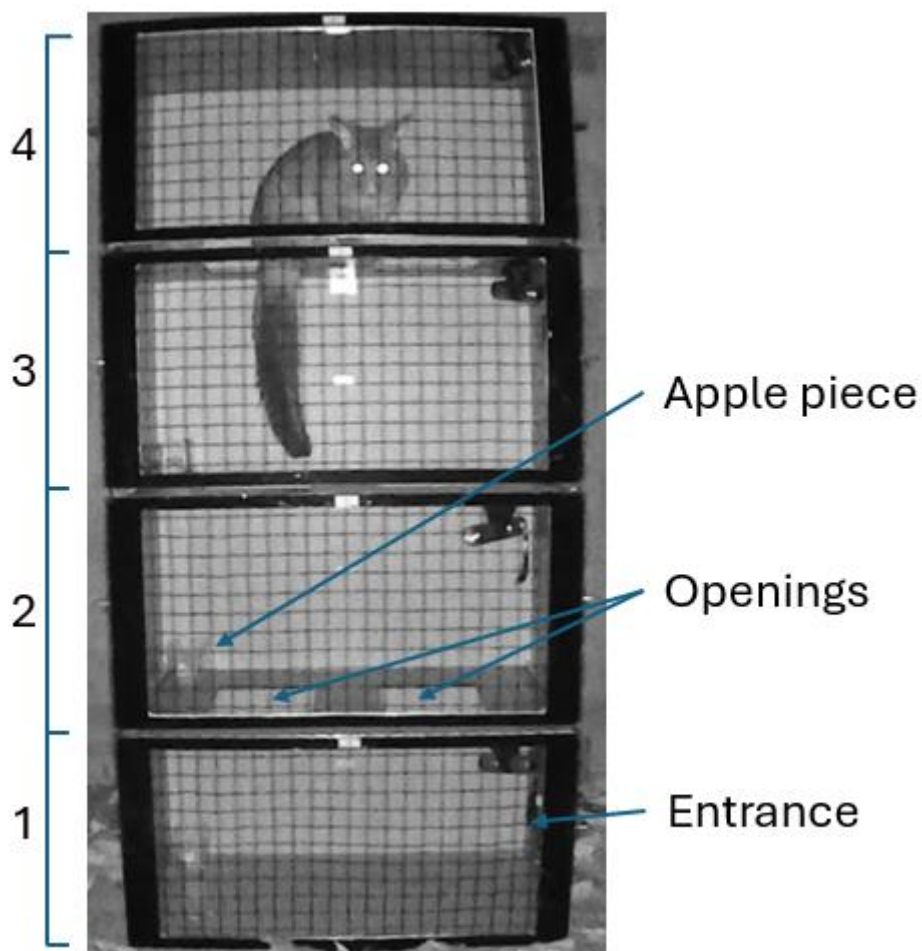
Body Condition Score	Definition
4	Excellent – plump shape, high amounts body fat and muscle around spinal column and hip bones
3	Good – sufficient fat and muscle so that rib and hip bones are not prominent
2	Fair – slightly underweight, more obvious shape of rib and hip bones when felt
1	Poor – underweight, prominent rib and hip bones, minimal body fat along spinal column

1092

1093 *Quantifying Personality*

1094 Once a possum was transferred from trap to handling bag, I performed a handling bag test as a
1095 measure of **docility** (Martin & Réale, 2008; Mella et al., 2016). This test measured the time the possum
1096 spent immobile in the handling bag for one minute. The possum was then moved into a personality
1097 testing arena (61.5 x 45.0 x 129.0 cm) (fig. 2) (Design C: module with levels, Mella et al., 2016). The
1098 arena has four levels with two entry points from one level to the next. A quarter slice of apple was
1099 placed on each level in a small container before the trial began. The possum was encouraged to enter
1100 the arena from the handling bag through a hole (diameter 15 cm) at the bottom level. Recording the
1101 possum's behaviour started when the possum had fully entered the arena. The individual was filmed
1102 for 5 minutes using a Boblov KJ21 Body Camera attached to a tripod. Behaviours performed in this
1103 arena were later scored using Boris v.7.13.8 (Friard & Gamba, 2016). Five personality measures were
1104 taken from the arena test as described in table 2. The arena was thoroughly disinfected with 70%
1105 ethanol between uses to avoid disease transmission or any effect of odour of other possums. If
1106 possible, personality tests were run at least twice. The personality tests could be conducted twice for

1107 an individual in one week, but no more repeats could be conducted until the following week. Of the
1108 possums that I trapped, 2 individuals had completed 3 personality tests, 21 individuals completed 2
1109 personality tests, 15 individuals completed only 1 personality test, and the remaining 6 individuals did
1110 not complete a personality test hence no longer considered. Those who did not complete the
1111 personality test had either escaped prior to testing or were judged as being too young (back riding
1112 juveniles).



1113

1114 **Figure 2.** Personality arena (from Mella et al. 2016). Arena consisted of levels 1-4 (bottom to top), with
1115 two openings between each level. The possum entered the arena through an external opening on
1116 level 1. Apple pieces were placed in small plastic containers fixed to each level.

1117

1118 **Table 2.** Six personality trait behaviours and description of how each was quantified using videos from
 1119 the arena test.

Personality Trait	Description
Activity	All time spent moving and engaging with the arena (5 minutes minus time spent not moving or vigilant).
Mobility	Time spent semi plus fully moving. Semi moving being defined as any movement of the front limbs while in one spot. Fully moving being any movement of the front and hindlimbs, e.g. walking or climbing.
Exploration	Total time spent in all unpreferred levels. The preferred level was that which the possum spent most of its time, therefore the unpreferred levels were all else.
Vigilance	Time spent looking out of the arena directly at the camera.
Boldness	Time spent eating apple pieces.

1120

1121 The personality data that I collected on 44 individual possums was added to a larger dataset.

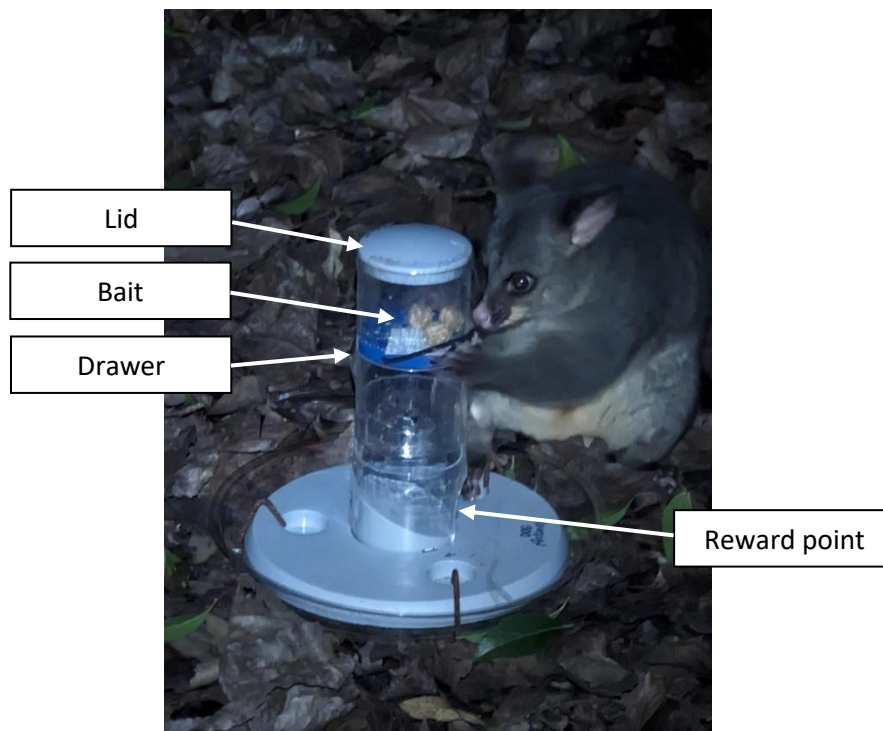
1122 Personality data was collected for a total of 224 individuals over 11 years. This dataset was used to
 1123 create measures of personality traits (BLUPs).

1124

1125 *Problem-Solving Tests*

1126 Problem-solving ability was tested using a food-extraction puzzle (figure 3) following the same
 1127 methods as Harris (2022). Each puzzle (TRIXIE Gambling Tower Activity Dog Feeder) was set with three
 1128 universal bait balls that sat on top of a square of paper towel on the top drawer that fitted into the
 1129 tower puzzle. Bait balls were made from a mix of oats, golden syrup, and peanut butter (ratio 10:2:5)
 1130 with a small amount of water if necessary. The lid of the puzzle was sealed with Sellotape to prevent

1131 the possum from accessing the reward from the top. The puzzle could be solved by pulling the drawer
1132 out of the tower, allowing the bait to drop to the bottom.



1133

1134 **Figure 3.** Photo of the puzzle set in the field with a possum demonstrating how to access the reward.

1135 The puzzles were set in locations where possums had been previously trapped. Two motion-triggered
1136 ScoutGuard SG2060-K cameras were set one metre away from each puzzle to film for three minutes
1137 after being triggered. Possums were identified on camera by the unique shave pattern that had been
1138 shaved into their fur during trapping procedures.

1139 During the time of this data collection, one possum individual was dominating the puzzles and solving
1140 them before any other could attempt them. To overcome this challenge, I trapped this individual prior
1141 to setting the puzzles.

1142 A “trial” was classed (following Harris 2022) as continued interaction with the puzzle for at least 10
1143 seconds. The puzzle needed to be closed and baited from the start of the trial. The trial ended when
1144 the individual solved the puzzle or following five or more minutes of no engagement with the puzzle.

1145 Behaviours during these trials were later scored using Boris v.7.13.8, based on an ethogram designed
1146 by Harris (2022).

1147 Behaviours were categorised based on whether they were engaged/not engaged or functional/not
1148 functional (table 3). Engaged behaviours were any behaviour where the individual interacts with the
1149 puzzle. Functional behaviours were only those engaged behaviours that led to the release of the bait.

1150 **Table 3.** Description of each of the three categories of behaviours used by the individuals during the
1151 problem-solving task.

Category	Behaviour/s
Not Engaged	Any behaviours that are not involved with the puzzle, e.g. vigilance, grooming, exploring.
Engaged and Not Functional	Eyeline fixed on the puzzle. The possum may be touching the puzzle but not in a manner that would release the bait, e.g. scratching/biting the tower.
Engaged and Functional	Pulls the drawer out of the tower, releasing that bait completely

1152

1153 The scored behaviours were used to determine mechanistic behaviours as outlined in table 4. These
1154 behaviours were predicted to have direct effects on whether the individual solved the puzzle and how
1155 quickly it solved the puzzle.

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1161 **Table 4.** Definitions of mechanistic behaviours used by the individuals during the problem-solving task.

Mechanistic Behaviours	Description
Behavioural Diversity	The number of engaged behaviours (including both functional and non-functional) used during a trial (Griffin & Guez, 2014).
Behavioural Flexibility	The rate of switching between engaged behaviours per total engaged time during the trial (Chow et al., 2018).
Work Time	The proportion of time spent engaged with any part of the puzzle apparatus relative to the total time of trial (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013).
Functional Part Engaged	The proportion of time spent engaged with the functional part (drawer) relative to the total time of the trial (Wat et al., 2020).
Selectivity	The proportion of time spent performing functional behaviours relative to the total time engaged with the puzzle (Chow et al., 2018).

1162

1163 *Addressing the problem-solving aims*

1164 To investigate whether intrinsic traits and mechanistic behaviours had any effect on problem-solving
 1165 in possums, I only included possum individuals (n = 42) who (1) had engaged in at least one problem-
 1166 solving trial, (2) had data for all individual metrics and (3) were adults. Datasets were reduced further
 1167 when additional conditions were necessary (see below). Of these 42 individuals: 22 were trapped and
 1168 tested only by Hannah Harris in 2021/2022 (Session 1; Harris, 2022); 10 were trapped during both
 1169 mine and Hannah’s studies (Session 1 & 2); 10 were trapped in only my study (Session 2: 2023/2024).
 1170 The 10 individuals who were trapped during both studies attempted to solve the puzzle during both
 1171 sessions. These are referred to as the “OLD” cohort for the remainder of this thesis. For these 10
 1172 individuals, the time between their last recorded trial for session 1 and first recorded trial for session
 1173 2 was: 14 months for 5 possums, 15 months for 1 possum, 20 months for 1 possum, 21 months for 1

1174 possum, and 22 months for 2 possums. The 10 individuals trapped only in session 2 will be referred to
1175 as the “NEW” cohort.

1176 Aim 1: First Trial Outcome

1177 The 42 possum individuals could all be used to test this aim as I was interested in whether they solved
1178 the puzzle or not. The puzzle was solved once the drawer had been pulled out and bait was released.

1179 For 32 individuals, their first trial was in session 1; and the remaining 10 “new” individuals were only
1180 tested in session 2 so their first trial was in session 2.

1181 Aim 2: Time to First Solve

1182 Time to solve was measured as the time taken between the first interaction with the puzzle and the
1183 time of bait released, for an individual’s first ever successful attempt regardless of trial number or
1184 session. There was at least one successful attempt by 31 individuals.

1185 Aim 3: Learning over the short-term

1186 To test learning over the short-term, I compared the time to solve the puzzle between each
1187 individual’s first ever successful attempt and their second successful attempt. To keep this to learning
1188 in a short-term period, both attempts needed to be within one session. These conditions were met by
1189 19 possum individuals.

1190 Aim 4: Long-term memory and recall

1191 To test for long-term memory, I compared the time to solve the puzzle for an individual’s first
1192 successful attempt in session 2 (n = 14), using (1) possums with puzzle experience in Session 1 (“old”
1193 cohort; n = 7) , i.e. last tested 1-2 years previously and (2) possums without experience in Session 1
1194 (“new” cohort; n = 7).

1195 Aim 5: Effect of Parasite Carriage on Problem-Solving

1196 As for chapter 2, methods for parasite screening were provided and performed by Dr A Herath (Herath
1197 et al. unpubl.). Genomic DNA was extracted from 150mg of each scat sample using an ISOLATE Faecal

1198 DNA kit (Bioline, London, UK) and stored at -20°C. Prior to PCR amplifications, samples were combined
1199 with an equal volume of Gene Releaser (Bio Ventures, Inc, TN, USA) and microwaved for seven minutes
1200 in a 500W microwave directly. *Cryptosporidium* was considered present if amplified at 18S rDNA locus
1201 (~825 bp) (81) and again amplified at actin locus (~800 bp).

1202 For samples testing positive to *Cryptosporidium*, amplicons were purified using the QIAquick PCR
1203 Purification Kit (Qiagen, Hilden, Germany) and sequenced in the forward and reverse directions
1204 (Ramaciotti Centre for Genomics, Randwick, Australia). Forward and reverse sequences were aligned
1205 and assessed manually for quality. Consensus sequences were extracted using Geneious version 8.0.5
1206 (Biomatters, New Zealand). BLAST searches were conducted on consensus sequences to identify
1207 *Cryptosporidium* species. After initial sequence analysis, some samples were only partial sequences of
1208 the expected product due to a quality drop at ~440 base pairs due to multiple peaks appearing in
1209 chromatogram (n = 16) and cloning was performed to enable parasite species identification. Based on
1210 BLAST identifications, a consensus sequence identified as *Cryptosporidium parvum* in brushtail
1211 possums was generated.

1212

1213

1214 Statistical Analysis

1215 All statistical analysis were carried out using R version 4.4.0 (R Core Team, 2021).

1216 Personality

1217 To quantify the personality traits of the individuals in my study, I pooled my data with that collected
1218 on a total of 224 possum individuals over the last 11 years. Individuals varied in the number of
1219 handling-bag tests and arena tests that had been performed, so the number of tests included per
1220 individual was limited to 4. 71 individuals performed the handling-bag test only one time, 54
1221 individuals were tested two times, 34 were tested three times, 19 were tested four times, 8 were

1222 tested five times, 12 were tested six times, 6 were tested seven times, 3 were tested eight times, 4
1223 were tested nine times, and 1 was tested ten times. Personality traits were statistically significant with
1224 and without the inclusion of 71 individuals lacking repeat measures, therefore all individuals were
1225 included within the following analysis. Using the data from the 224 individuals within the long-term
1226 database, I was able to robustly quantify a personality index for each of the following traits: docility,
1227 activity, mobility, exploration, vigilance, and boldness. I used the method of Dingemans and
1228 Dochtermann (2013), comparing models with and without PossumID as a random effect following Wat
1229 et al. (2020). Test number was always included in the final models. Analysis was run using the R
1230 package lme4 (Bates et al., 2015).

1231 *Problem-Solving*

1232 A structural equation modelling (SEM) approach was taken to investigate (1) which intrinsic traits and
1233 mechanistic behaviours were most influential to problem-solving performance and (2) the direction
1234 and significance of these drivers. SEMs were run using R package PiecewiseSEM (Lefcheck, 2016) and
1235 were designed following the hypothesised model outlined in Figure 1, testing main effects only
1236 (interactions between variables could not be incorporated). SEMs require a complete set of data (no
1237 missing data for any variable) to run. As I only had a small data set for parasite carriage, I excluded this
1238 variable from the SEMs and tested the effect of parasite carriage on problem-solving separately.

1239 Each SEM tested the effect of a single personality trait, body weight/condition, and sex. Each SEM also
1240 tested the effect of two mechanistic behaviours (described in table 4), provided they were not highly
1241 correlated ($R \geq 0.7$), selected from the following: behavioural diversity, behavioural flexibility, work
1242 time, functional part engaged, and behavioural selectivity. Although some mechanistic behaviours
1243 were highly correlated, those that were correlated were not included in the most parsimonious models
1244 together so were not important.

1245 Average body weight and body condition were significantly correlated ($R = 0.59$, $p < 0.001$), so were
1246 not both included in one SEM. Rather, I tested each in the most parsimonious model to see which was

1247 best fitting. Several personality traits were also significantly correlated, resulting in behavioural
1248 syndromes (see results below). However, each trait was tested separately in the SEMs (following
1249 (Harris, 2022)). This was because each trait quantified a distinct behaviour, and specific traits influence
1250 an individual's ecology, such as their diet (Herath et al., 2021) and home range size (Wat et al., 2019).
1251 A global goodness-of-fit test was performed on each SEM output. SEM outputs with a Fisher's C p-
1252 value <0.05 were rejected. The most parsimonious model was determined based on AIC values.
1253 Models that have an AIC difference from the best fitting model between 0 and 2 are considered to
1254 have a substantial level of empirical support (Burnham and Anderson (2002)). While some models fell
1255 within 2 AIC units of the best fitting model, there were no significant relationships in any of the models.
1256 For this reason, I ultimately decided to only continue with the best fitting models.

1257

1258 Aim 1: First Trial Outcome

1259 There were 42 adult possums with all individual metrics available who also had a first trial attempt.
1260 Trial outcome was determined as either a success or failure. The SEM consisted of three models.
1261 Models 1 and 2 were linear models with gaussian distributions. Model 3, with *Trial Outcome* (binary,
1262 problem-solving success/failure) as the response variable was a generalised linear model, with
1263 binomial distribution and a logit link function. The most parsimonious SEM for this aim was:

1264 *Model 1: Selectivity ~ Body Condition + Sex + Boldness*

1265 *Model 2: Behavioural Flexibility ~ Body Condition + Sex + Boldness*

1266 *Model 3: Trial Outcome ~ Body Condition + Sex + Boldness + Selectivity + Behavioural Flexibility*

1267

1268 Aim 2: Time to First Solve

1269 There were 31 adult possums who had solved at least one trial. Time to first solve was based on their
1270 first successful attempt. The SEM consisted of three models. All models were linear models with
1271 gaussian distributions. The most parsimonious SEM for this aim was:

1272 *Model 1: Selectivity ~ Body Condition + Sex + Vigilance*

1273 *Model 2: Behavioural Flexibility ~ Body Condition + Sex + Vigilance*

1274 *Model 3: Time to Solve ~ Body Condition + Sex + Vigilance + Selectivity + Behavioural Flexibility*

1275

1276 Aim 3: Learning over the short-term

1277 There were 19 individuals who had solved the puzzle at least twice. Learning over the short-term was
1278 determined by the change in time to solve between their first and second successful attempts. The
1279 most parsimonious SEM for this aim was:

1280 *Model 1: Change in Selectivity ~ Body Condition + Sex + Activity*

1281 *Model 2: Change in Functional Part Engaged ~ Body Condition + Sex + Activity*

1282 *Model 3: Change in Time to Solve ~ Body Condition + Sex + Activity + Change in Selectivity + Change*
1283 *in Functional Part Engaged*

1284

1285 Aim 4: Long-term memory and recall

1286 To test for long-term memory, I compared the time to first solve the puzzle in session 2 between the
1287 “old” and “new” cohorts (n = 7 “old” individuals; n = 7 “new” individuals). I ran a linear model with
1288 time to solve as the response variable, with cohort, the personality trait vigilance, and their interaction
1289 as the explanatory variables. Vigilance was chosen as it had a significant direct effect on time to solve
1290 (figure 8). I then ran the same linear model with exploration, instead of vigilance, as this personality
1291 trait influenced problem-solving by common brushtail possums in an escape-box task (Wat et al.,
1292 2020). I also ran the linear model with body condition as it had a significant indirect effect and near
1293 significant direct effect on time to solve (figure 8).

1294 Aim 5: Effect of Parasite Carriage on Problem-Solving

1295 Of the 42 possum individuals who had attempted problem-solving trials, only 36 had parasite data
1296 available for carriage of *Cryptosporidium parvum*.

1297 To test the effect of *C. parvum* carriage on first trial outcome (binary, problem-solving success/failure)
1298 as the response variable (n = 36 individual possums) I ran a generalised linear model, with *C. parvum*
1299 carriage (presence or absence) as the sole explanatory variable, using a binary distribution and a logit
1300 link function.

1301 As parasite carriage may affect how individuals behave (as seen in other species: (Barber et al., 2017;
1302 Moore, 2013)), hence how they may approach problem-solving, I also tested for a relationship
1303 between each mechanistic behaviour and *C. parvum* carriage. The sample size for these models
1304 included individuals with parasite carriage data available (n = 36) regardless of whether they
1305 succeeded or failed their first trial. However, the sample was reduced to 35 possums as one individual
1306 did not have mechanistic behaviour data available.

1307 For each mechanistic behaviour, I ran a linear model with a gaussian distribution and the presence or
1308 absence of *Cryptosporidium parvum* as the sole explanatory variable. Models were tested for
1309 normality and homogeneity of variance. The linear model testing functional part engaged did not
1310 initially meet the assumptions. I performed an arcsine square root transformation on the response
1311 variable to satisfy the assumptions.

1312 Only 2 of the 5 possums carrying *C. parvum* solved their first trial. Given this very low sample size, I
1313 did not proceed to further test for an effect of *C. parvum* carriage on time to first solve, short-term
1314 learning, or long-term memory.

1315 Results

1316 *Personality*

1317 Six personality traits were statistically significant: docility, activity, mobility, exploration, vigilance, and
1318 boldness. The repeatability of these traits ranged from 0.21 (exploration) to 0.46 (boldness) (Table 5).
1319 Most traits were significantly correlated indicating behavioural syndromes (Table 6); for example,
1320 more exploratory individuals also had high mobility and activity.

1321 **Table 5.** Repeatability measures for each significant personality trait (n = 224 individual possums).

Test	Personality trait	Repeatability	SE	P
Handling-bag test	Docility	0.44	0.044	<0.0001
Arena	Activity	0.38	0.059	<0.0001
	Mobility	0.20	0.060	<0.0001
	Exploration	0.21	0.060	<0.0001
	Vigilance	0.40	0.058	<0.0001
	Boldness	0.46	0.054	<0.0001

1322

1323 **Table 6.** Behavioural syndromes (n = 224 individual possums). Green tiles are significant (p < 0.05).

1324 Orange tiles are not significant.

Personality Trait	Activity	Mobility	Exploration	Vigilance	Boldness
Docility	-0.57	-0.49	-0.75	-0.20	-0.47
Activity		0.57	0.85	0.55	0.41
Mobility			0.77	0.36	-0.16
Exploration				0.46	0.19
Vigilance					-0.20

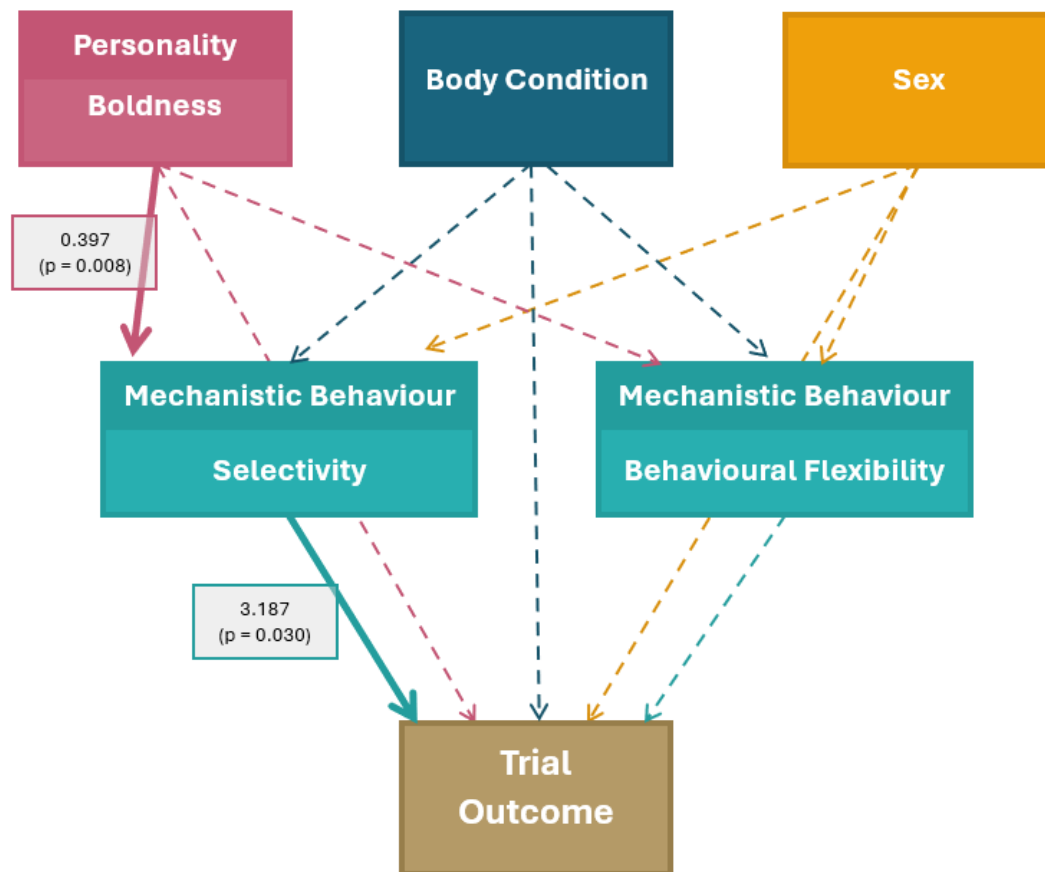
1325

1326 *Problem-Solving*

1327 Aim 1: First Trial Outcome

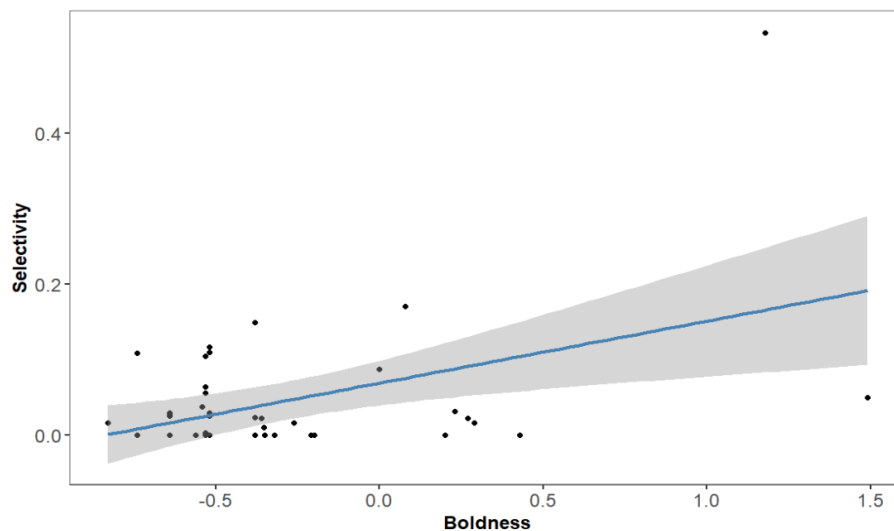
1328 Of the 42 adult individuals that attempted the problem-solving trial, 23 solved the puzzle in their first
 1329 trial while 19 did not. For first trial outcome, the best fitting SEM output included boldness, body
 1330 condition, sex, selectivity and behavioural flexibility as explanatory variables (figure 4). Selectivity had
 1331 a direct significant effect on trial outcome, meaning that possums that spent more time engaged with

1332 functional parts of the puzzle were more likely to succeed. Boldness had a significant indirect effect
 1333 on trial outcome via selectivity. Individuals with a higher boldness score were more likely to be
 1334 selective in their behaviour and therefore more likely to solve the puzzle.



1335
 1336 **Figure 4.** Most parsimonious SEM model (based on AIC values) showing the direct and indirect drivers
 1337 of first trial outcome (success/failure) (n = 42 individual possums). Solid lines indicate significant
 1338 relationships ($p < 0.05$). Thin dashed lines indicate other relationships tested with no statistical
 1339 significance. For significant relationships, standardised coefficients and p values are shown.

1340
 1341 Individual possums with a higher boldness score were significantly more selective in their behaviours
 1342 ($p < 0.05$) (figure 5).

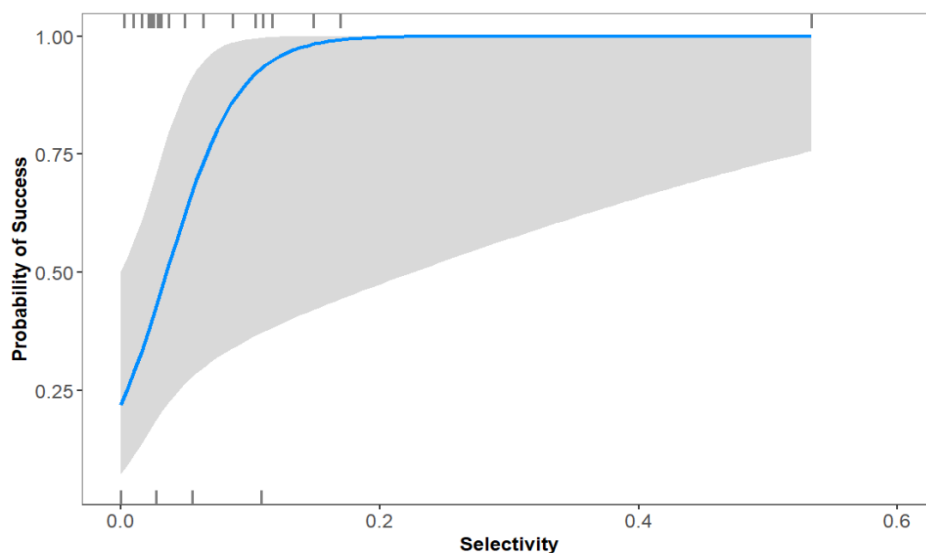


1343

1344 **Figure 5.** Relationship between the intrinsic personality trait, boldness, and the mechanistic
1345 behaviour, selectivity (n = 42 individual possums). Blue line is the predicted relationship, dots
1346 represent raw data, and shaded area represents the 95% confidence interval for the predictions.

1347

1348 Individual possums who were more selective in their behaviours had a significantly greater likelihood
1349 of solving their first trial ($p < 0.05$) (figure 6).

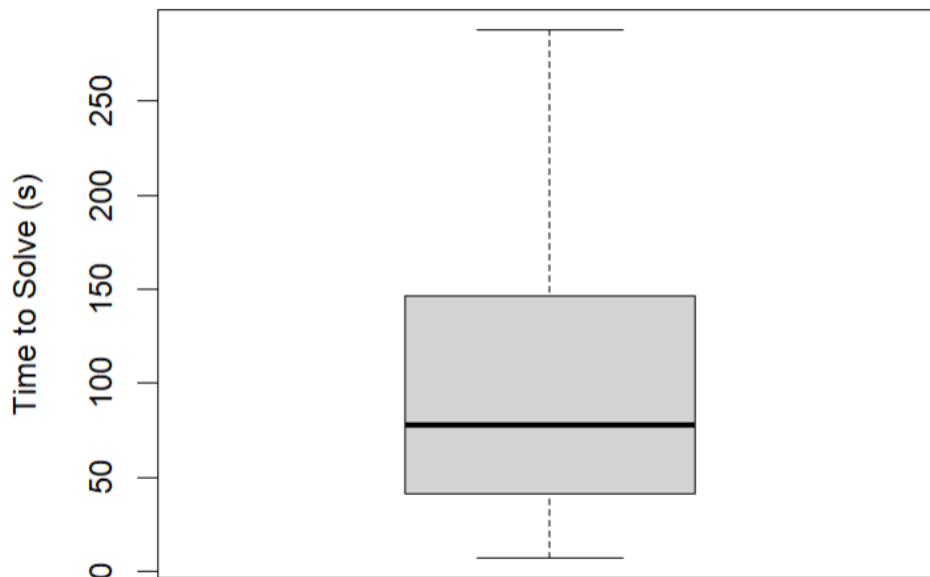


1350

1351 **Figure 6.** Effect of selectivity on probability of success in solving the puzzle in first trial (n = 42 individual
1352 possums). Blue line is the predicted relationship, rugs represent raw data, and shaded area represents
1353 the 95% confidence interval for the predictions. Some rugs represent more than one individual.

1354 Aim 2: Time to First Solve

1355 There were 32 individuals that solved at least one puzzle trial. For the first successful trial, the median
1356 time taken to solve the puzzle was 77.3 seconds (min = 7.5s, max = 287.5s; figure 7).

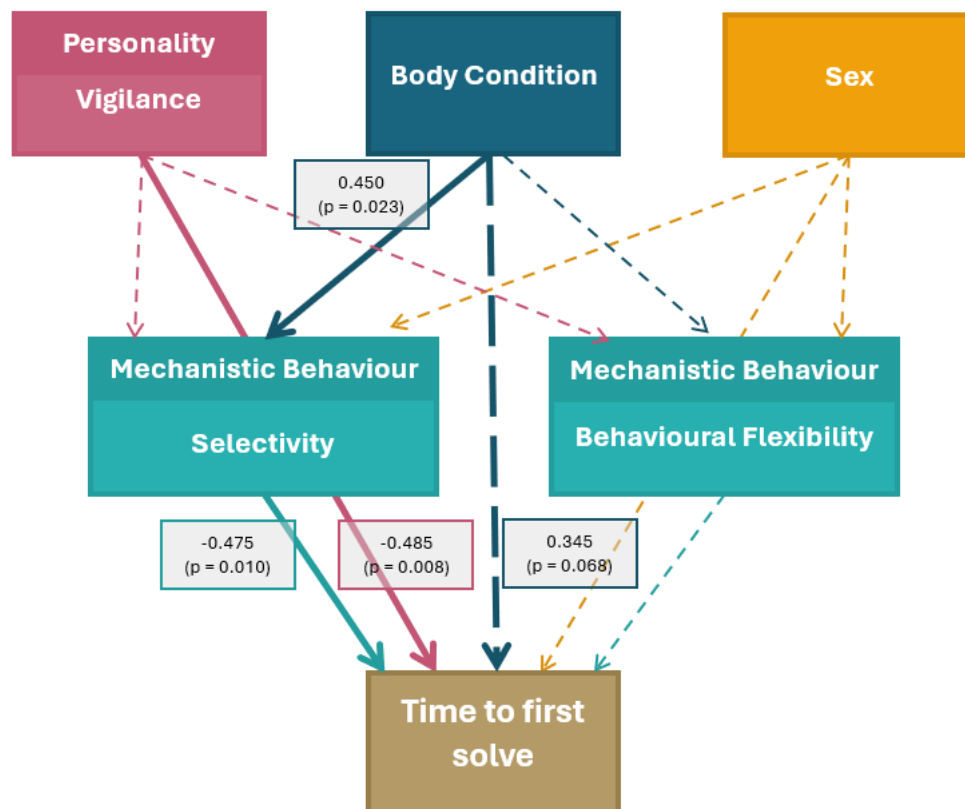


1357

1358 **Figure 7.** Boxplot of the time taken by possums to solve their first successful trial (n = 31 individual
1359 possums used in the SEM).

1360

1361 For time to first solve, the best fitting SEM output included vigilance, body condition, sex, selectivity
1362 and behavioural flexibility as explanatory variables (figure 8). Selectivity had a direct significant effect
1363 on time to first solve, meaning that possums that spent proportionally more time engaged with
1364 functional parts of the puzzle solved the puzzle faster. Body condition had a significant indirect effect
1365 on time to first solve via selectivity. Individuals in better body condition were more likely to be
1366 selective in their behaviour and therefore solved the puzzle faster. The personality trait, vigilance, had
1367 a direct significant effect on time to first solve. More vigilant individuals solved the puzzle faster.



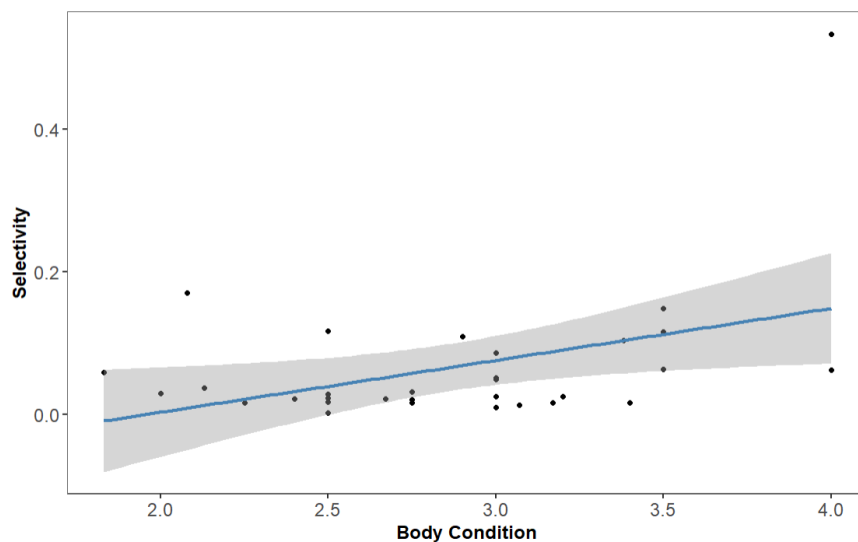
1368

1369 **Figure 8.** Most parsimonious SEM model (based on AIC values) showing the direct and indirect drivers
 1370 of time to first solve the puzzle ($n = 31$ individual possums). Solid lines indicate significant relationships
 1371 ($p < 0.05$). Thick dashed lines are near significant ($p > 0.05$, $p < 0.07$) and therefore potentially
 1372 important. Thin dashed lines indicate other relationships tested with no statistical significance. For
 1373 significant or near significant relationships, standardised coefficients and p values are shown.

1374

1375 Possums in better body condition were significantly more selective in their behaviours ($p < 0.05$)
 1376 (figure 9).

1377

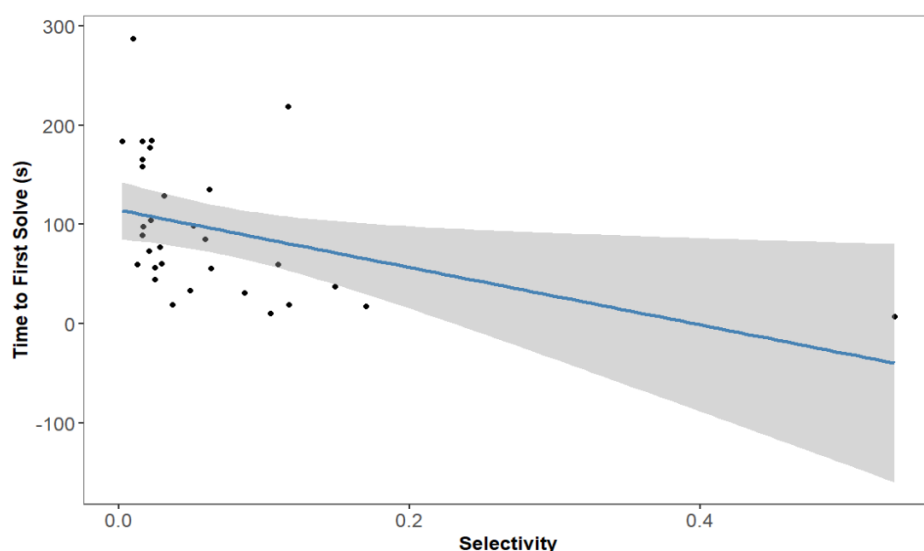


1378

1379 **Figure 9.** Relationship between the intrinsic trait, body condition, and the mechanistic behaviour,
1380 selectivity (n = 31 individual possums). Blue line is the predicted relationship, dots represent raw data,
1381 and shaded area represents the 95% confidence interval for the predictions.

1382

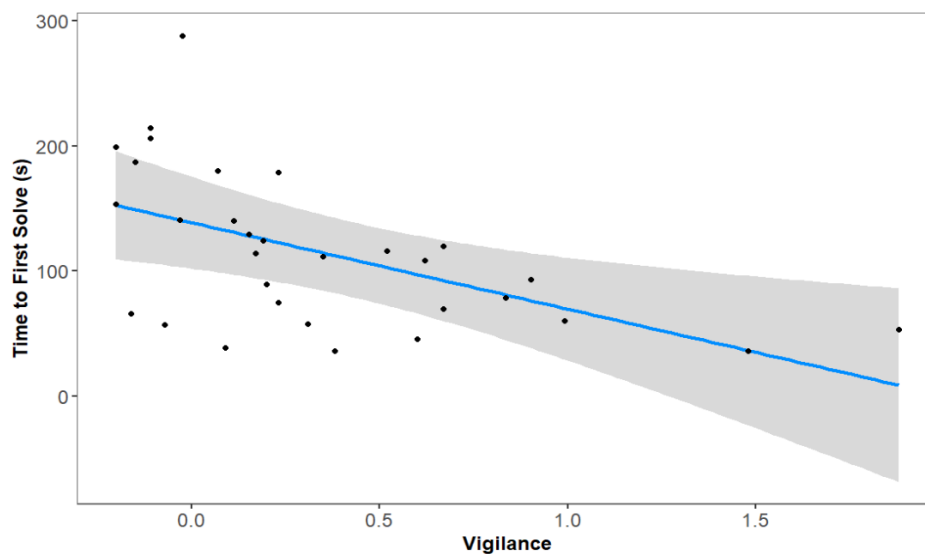
1383 Individual possums who were more selective in their behaviours had a faster time to first solve the
1384 puzzle ($p < 0.05$) (figure 10).



1385

1386 **Figure 10.** Effect of selectivity on time to first solve the puzzle (n = 31 individual possums). Blue line is
1387 the predicted relationship, dots represent raw data, and shaded area represents the 95% confidence
1388 interval for the predictions.

1389 More vigilant possums had a faster time to first solve the puzzle ($p < 0.05$) (figure 11).



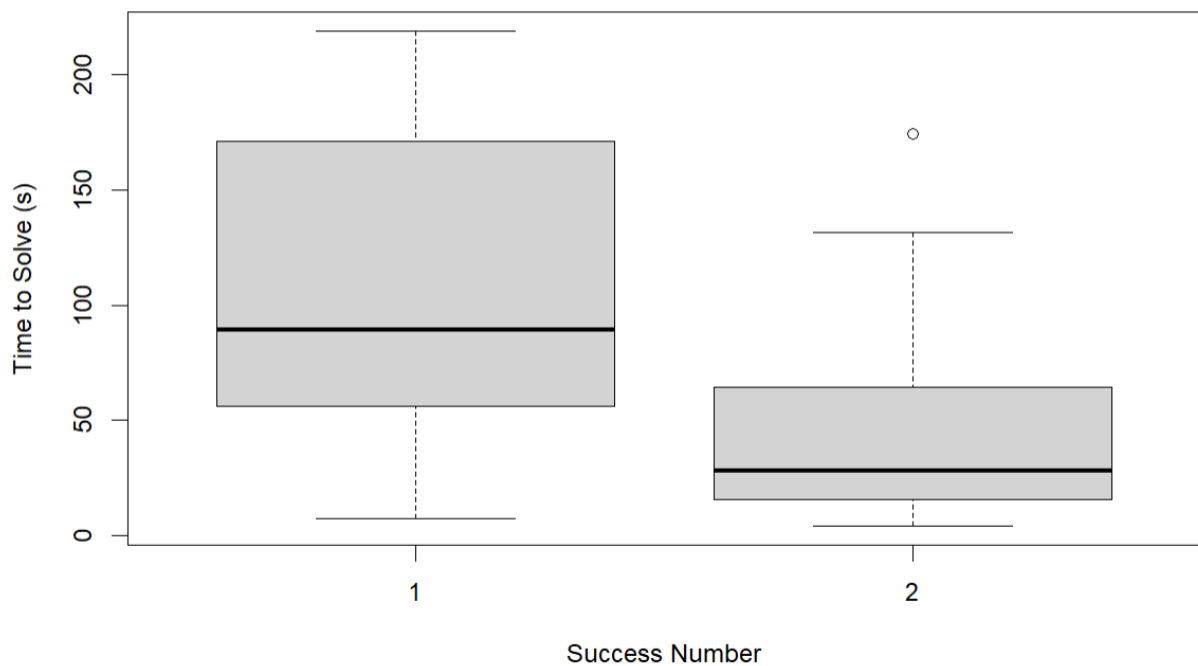
1390

1391 **Figure 11.** Effect of intrinsic personality trait, vigilance, on time to first solve the puzzle ($n = 31$
1392 individual possums). Blue line is the predicted relationship, dots represent raw data, and shaded area
1393 represents the 95% confidence interval for the predictions.

1394

1395 Aim 3: Learning over the short-term

1396 There were 19 individuals that solved at least two puzzle trials within a session. The median time taken
1397 to first solve the puzzle was 89.4 seconds (min = 7.5s, max = 218.6s; figure 12). The median time taken
1398 to solve the puzzle during the second successful attempt was 28.3 seconds (min = 4.3s, max = 174.2s;
1399 figure 12).

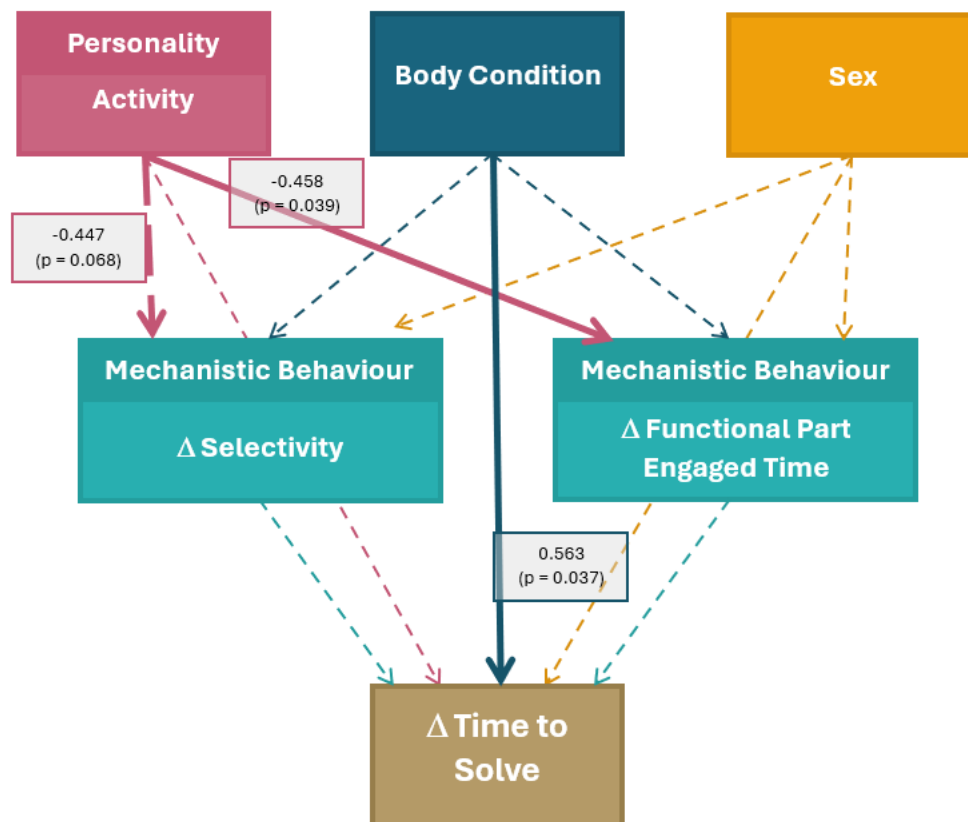


1400

1401 **Figure 12.** Comparison of time taken to solve the puzzle between first and second successful trials (n
1402 = 19 individual possums).

1403

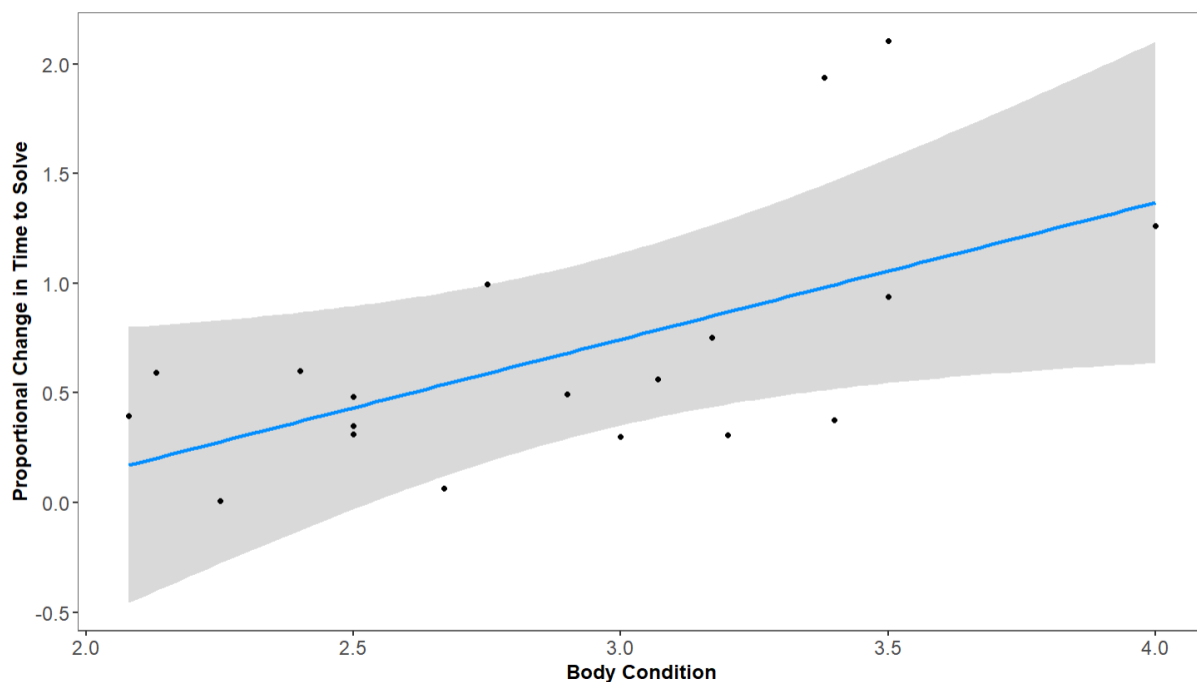
1404 For change in time to solve (between 1st and 2nd solve), the best fitting SEM output included activity,
1405 body condition, sex, change in selectivity and change in functional part engaged as explanatory
1406 variables (figure 13). Body condition had a direct significant effect on change in time to solve.
1407 Individuals in lower body condition were more likely to improve their time to solve (figure 14). Activity
1408 had a significant effect on change in functional part engaged time. Less active individuals spent a
1409 greater proportion of total time engaged with the functional part (figure 15). Activity also had a near
1410 significant effect on selectivity. Less active individuals improved in their selectivity between puzzle
1411 solves (figure 16).



1412

1413 **Figure 13.** Most parsimonious SEM model (based on AIC values) showing the direct and indirect drivers
 1414 of change in time to first solve the puzzle (n = 19 individual possums). Solid lines indicate significant
 1415 relationships (p < 0.05). Thick dashed lines are near significant (p > 0.05, p < 0.07) and therefore
 1416 potentially important. Thin dashed lines indicate other relationships tested with no statistical
 1417 significance. For significant or near significant relationships, standardised coefficients and p values are
 1418 shown.

1419 Individuals in lower body condition were significantly more likely to improve their time to solve (p <
 1420 0.05) (figure 14).

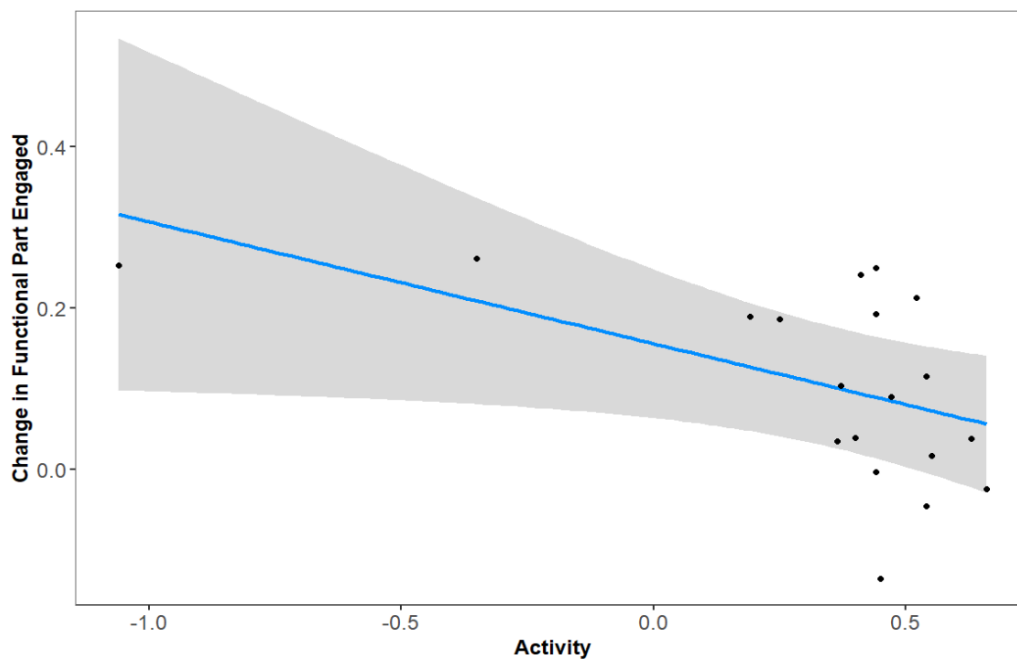


1421

1422 **Figure 14.** Effect of the intrinsic trait, body condition, on change in time to solve the puzzle (2nd
1423 successful attempt as a proportion of the 1st successful attempt; n = 19 individual possums). Values <1
1424 indicate faster time to solve at 2nd successful attempt compared with 1st. Blue line is the predicted
1425 relationship, dots represent raw data, and shaded area represents the 95% confidence interval for the
1426 predictions.

1427

1428 Less active individuals spent a significantly greater proportion of total time engaged with the
1429 functional part ($p < 0.05$) (figure 15).

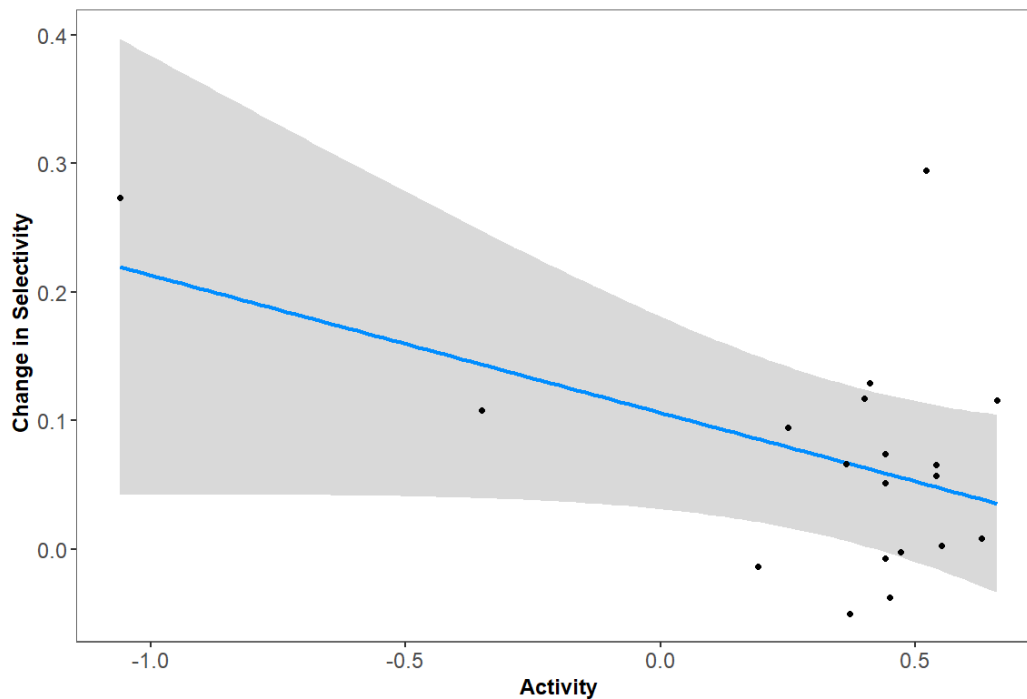


1430

1431 **Figure 15.** Effect of the intrinsic personality trait, activity, on change in functional part engaged (n =
1432 19 individual possums). Change in functional part engaged is the proportional difference in functional
1433 part engaged between 1st successful attempt and 2nd successful attempt. Positive values increased in
1434 their functional part engaged between successful attempts and negative values decreased in their
1435 functional part engaged between successful attempts. Blue line is the predicted relationship, dots
1436 represent raw data, and shaded area represents the 95% confidence interval for the predictions.

1437

1438 Less active individuals improved in their selectivity between puzzle solves ($p = 0.0682$) (figure 16).



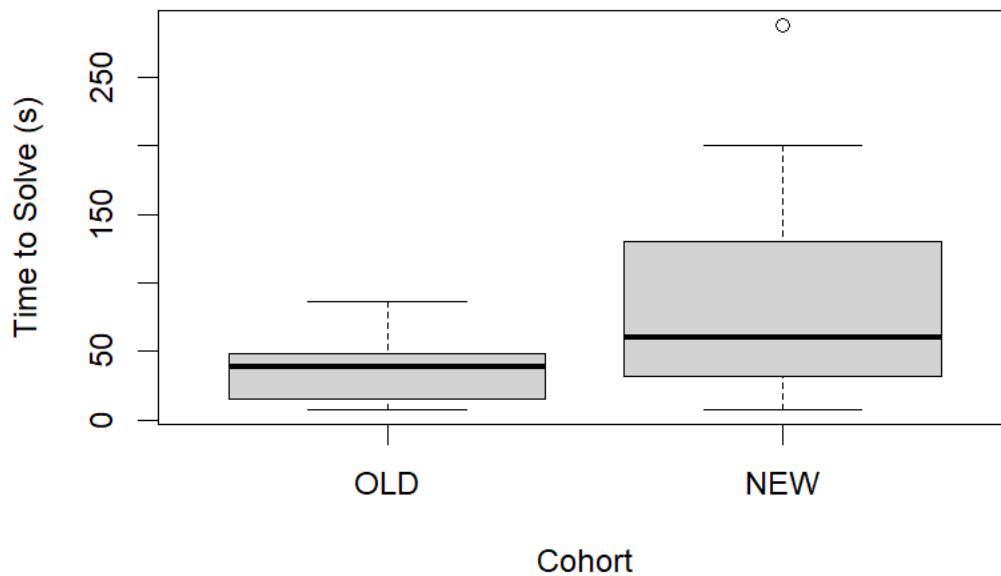
1439

1440 **Figure 16.** Effect of the intrinsic personality trait, activity, on change in selectivity (n = 19 individual
1441 possums). Change in selectivity is the proportional difference in selectivity between 1st successful
1442 attempt and 2nd successful attempt. Positive values increased in their selectivity between successful
1443 attempts and negative values decreased in their selectivity between successful attempts. Blue line is
1444 the predicted relationship, dots represent raw data, and shaded area represents the 95% confidence
1445 interval for the predictions.

1446

1447 Aim 4: Long-term memory and recall

1448 In Session 2, 20 individual possums attempted the puzzle, 10 from the old cohort and 10 from the new
1449 cohort. From each cohort, 7 of the 10 solved the puzzle in their first trial in Session 2. Of these 7 for
1450 the “old” cohort, the median time to solve was 38.2s (min = 7.7s, max = 86.4s; figure 17). Of the 7 for
1451 the “new” cohort, the median time to solve was 60s (min = 7.5s, max = 200.1s; figure 17).



1452

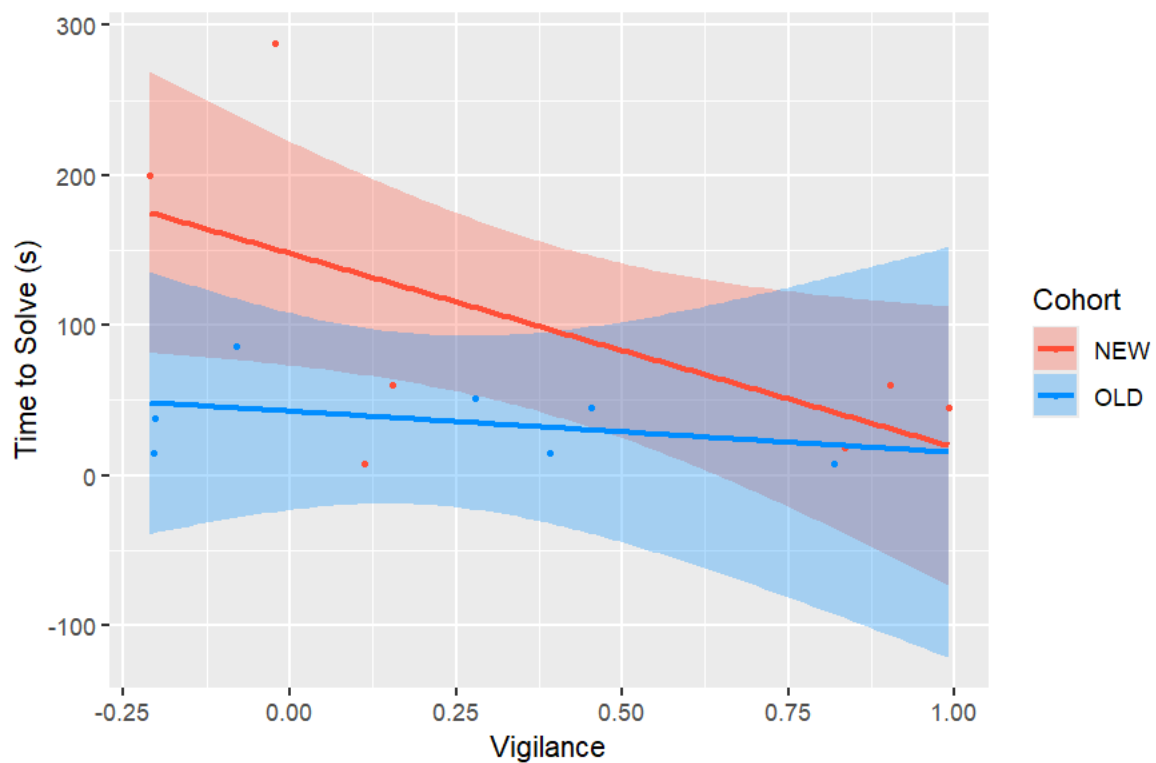
1453 **Figure 17.** Boxplot of time to solve the puzzle in their first successful trial in Session 2 for each cohort
1454 (n = 7 “old” individual possums; n = 7 “new” individual possums).

1455

1456 There was a marginal effect of the personality trait, vigilance, and of cohort as main effects on time to
1457 first solve the puzzle in session 2 ($F_{1,10} = 4.3498$, $p = 0.0636$; $F_{1,10} = 4.3495$, $p = 0.0636$ respectively).

1458 The interaction between vigilance and cohort was not significant ($F_{1,10} = 1.2751$, $p = 0.2852$).

1459 Individuals from the “old” cohort tended to solve faster than those from the “new” cohort. Individuals
1460 of the “new” cohort who were more vigilant tended to solve the puzzle faster than those who were
1461 less vigilant. This trend was less obvious among the “old” cohort as all individuals solved the puzzle
1462 quickly (figure 18).



1463

1464

Figure 18. Plot showing the interaction between vigilance and cohort on time to first solve the puzzle in session 2 (n = 14 individual possums). Solid line is the predicted relationship, dots represent raw data, and shaded area represents the 95% confidence interval for the predictions.

1465

1466

1467

1468

There was a significant effect of the personality trait, exploration, and of cohort as main effects on time to first solve the puzzle in session 2 ($F_{1,10} = 14.867$, $p = 0.003$; $F_{1,10} = 17.934$, $p = 0.002$ respectively).

1469

1470

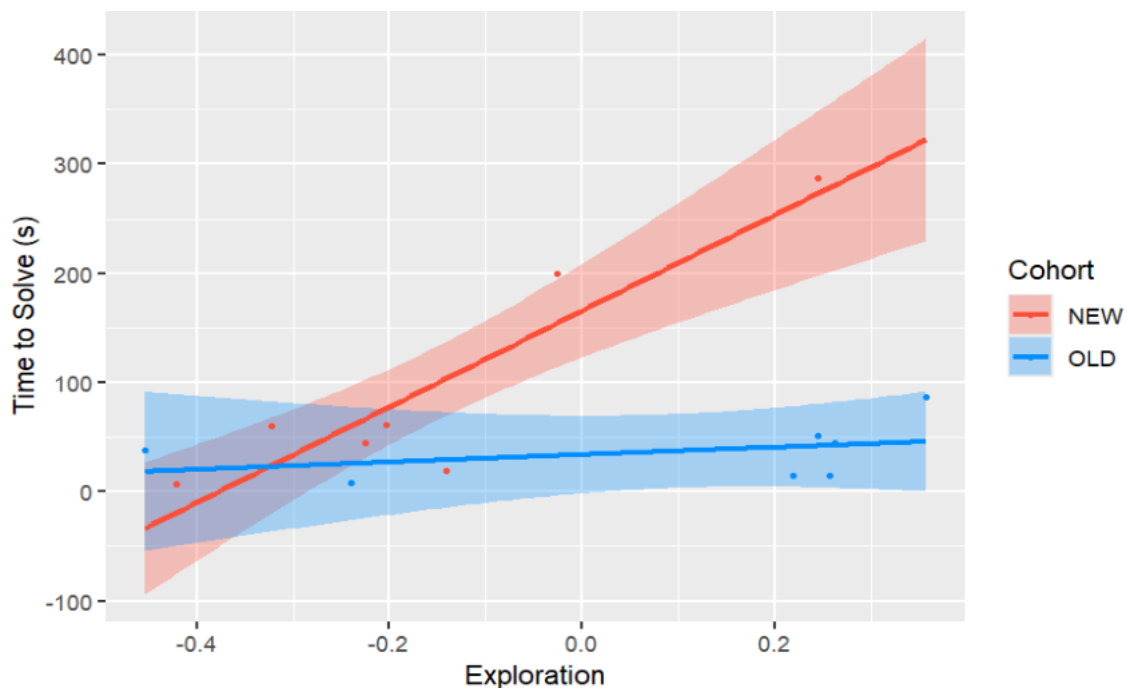
The interaction between exploration and cohort was significant ($F_{1,10} = 19.291$, $p = 0.001$). Of the “new” cohort, the more exploratory the individual the longer it took to solve the puzzle. In contrast,

1471

1472

among the “old” cohort, all individuals solved the puzzle quickly irrespective of the exploration trait (figure 19).

1473



1474

1475 **Figure 19.** Plot showing an interaction between exploration and cohort on time to solve (n = 14
1476 individual possums). Solid line is the predicted relationship, dots represent raw data, and shaded area
1477 represents the 95% confidence interval for the predictions.

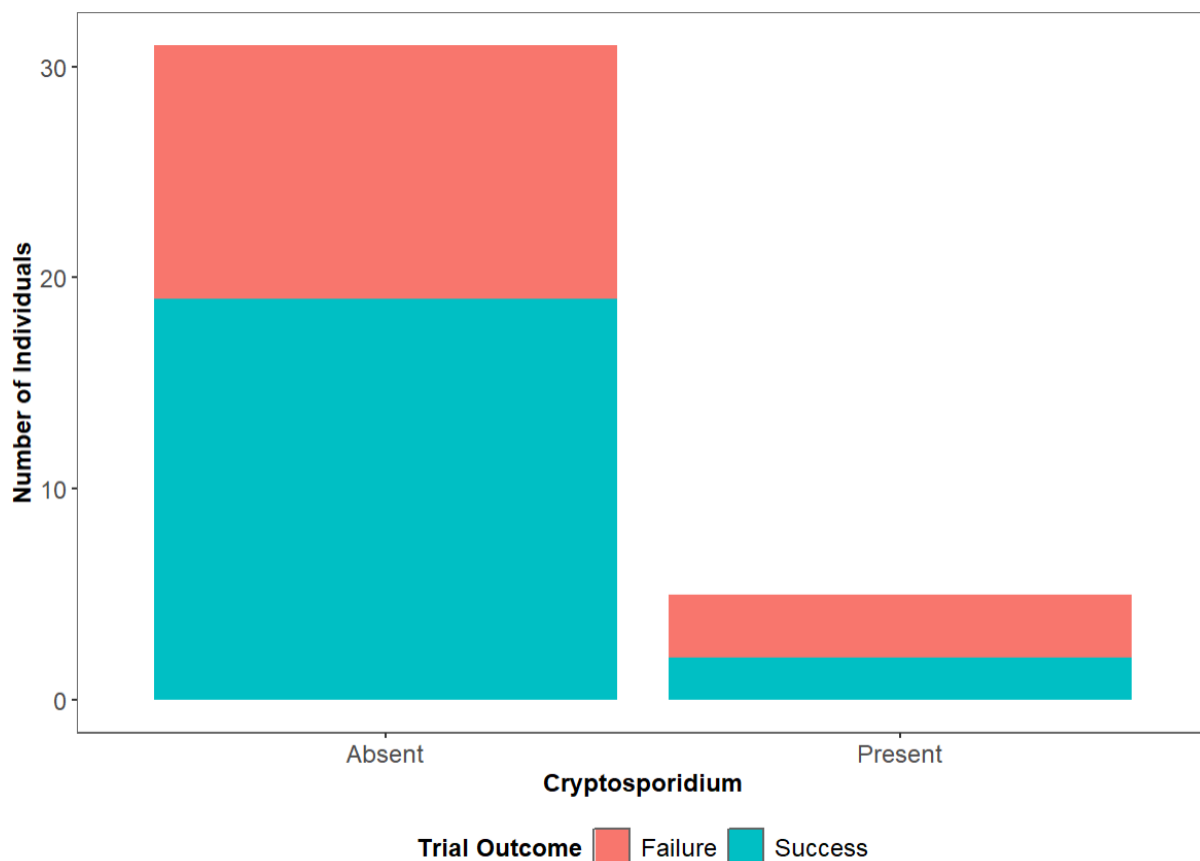
1478

1479 There was no significant effect of the intrinsic trait, body condition, and of cohort as main effects on
1480 time to first solve the puzzle in session 2 ($F_{1,10} = 0.218$, $p = 0.650$; $F_{1,10} = 1.983$, $p = 0.189$ respectively).
1481 The interaction between body condition and cohort was not significant ($F_{1,10} = 0.078$, $p = 0.786$).

1482

1483 Aim 5: Effect of Parasite Carriage on Problem-Solving

1484 There were 36 possums who had scats collected and tested as well as attempted a puzzle trial. Of this
1485 sample, only 5 individual possums tested positive for *C. parvum*. There was no significant effect of *C.*
1486 *parvum* on the likelihood of individuals solving their first trial (χ^2 (df =1, n = 36) = 0.791, $p = 0.37$)
1487 (figure 20).

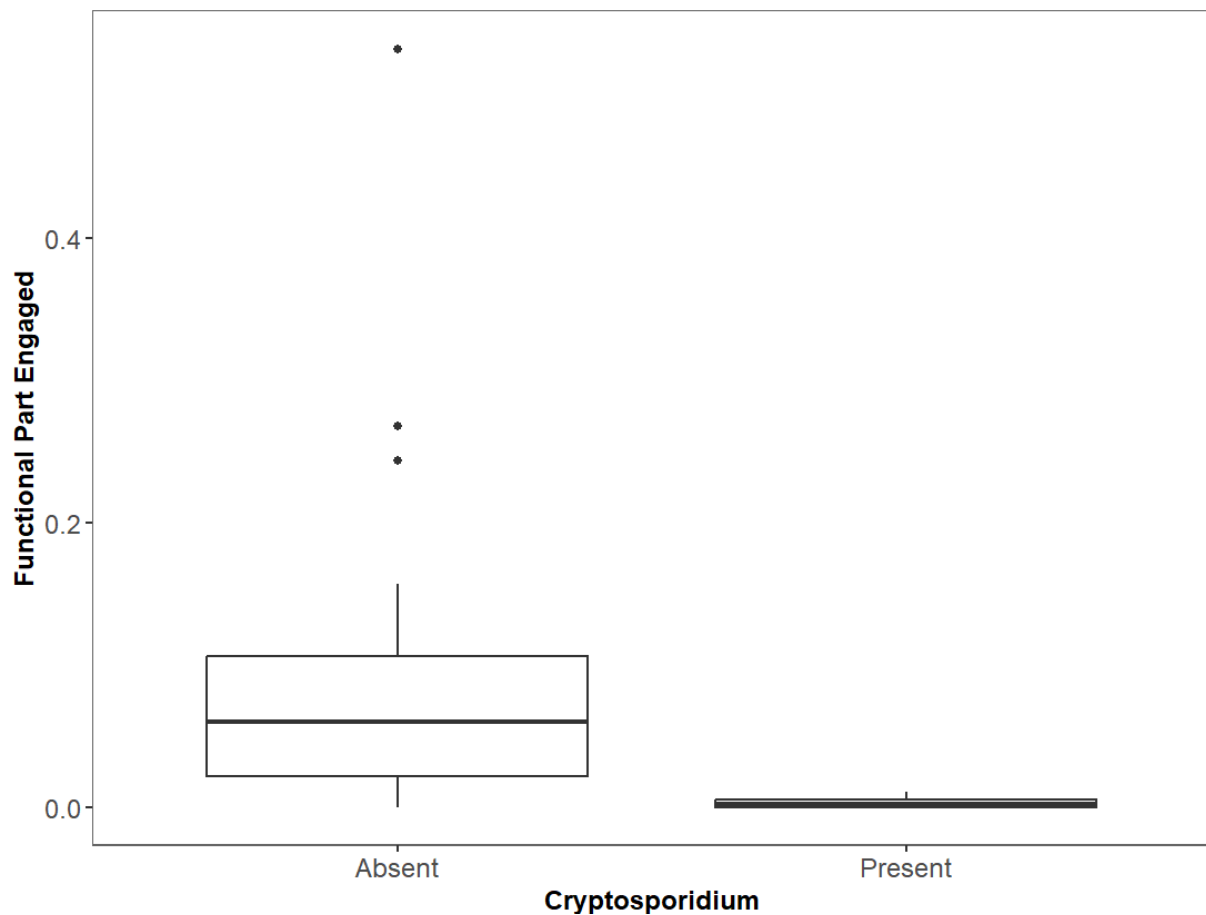


1488

1489 **Figure 20.** Barchart showing the likelihood of solving the first trial as a function of carrying
1490 *Cryptosporidium parvum* (Absent (n = 31), Present (n= 5); total n = 36 individual possums).

1491

1492 There was a significant effect of *C. parvum* presence on functional part engaged during first puzzle
1493 trial ($F_{1,33} = 4.8412$, $p = 0.03$). Possums carrying *C. parvum* spent less time engaged with the functional
1494 part of the puzzle during their first trial (figure 21).

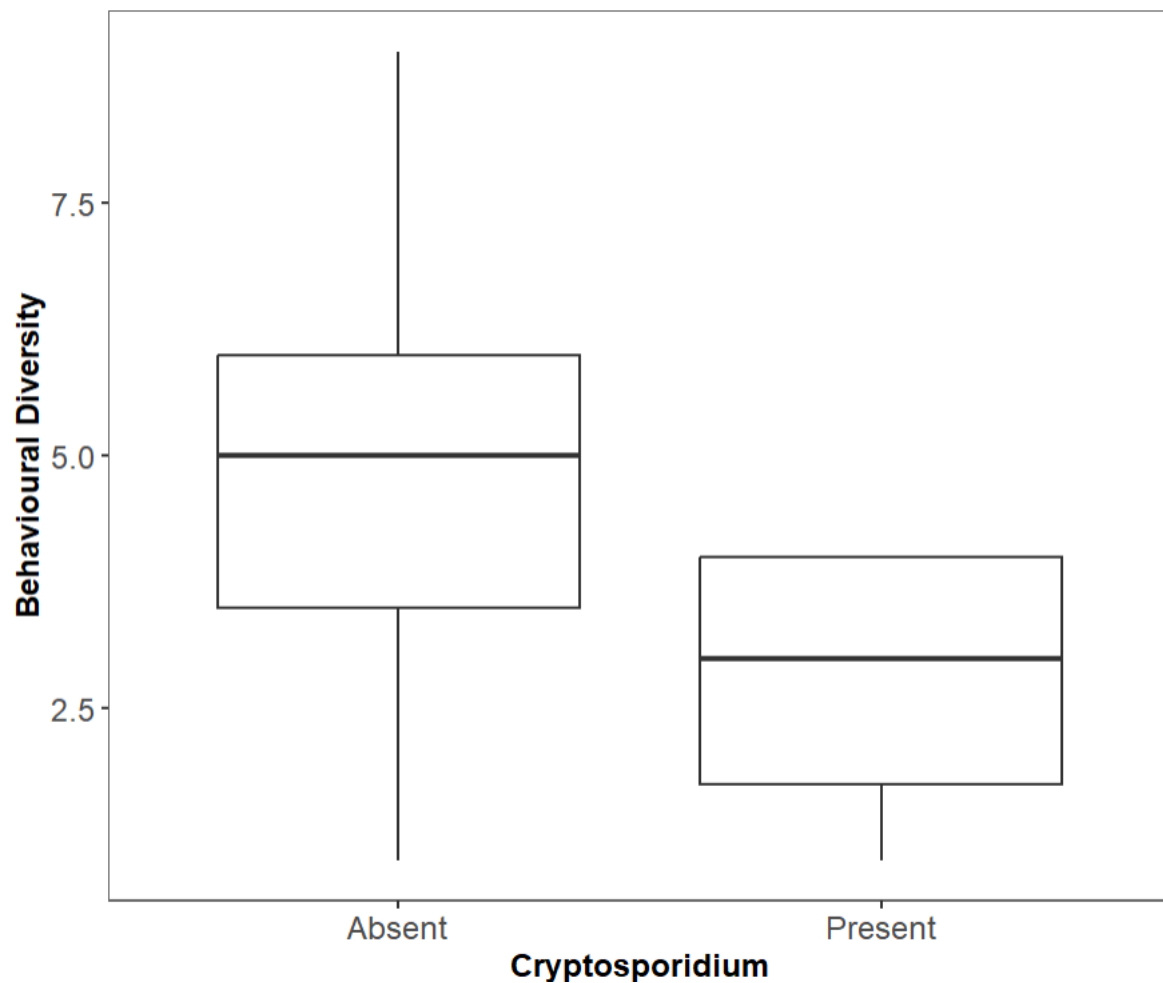


1495

1496 **Figure 21.** Boxplot of functional part engaged during first trial as a function of carrying *Cryptosporidium*
1497 *parvum* (Absent (n = 31), Present (n= 4); total n = 35 individual possums).

1498

1499 There was a marginal effect of *C. parvum* on behavioural diversity during the first trial ($F_{1,33} = 3.1673$,
1500 $p = 0.08$). Possums carrying *C. parvum* had lower behavioural diversity (figure 22).



1501

1502 **Figure 22.** Boxplot of behavioural diversity during first trial as a function of carrying *Cryptosporidium*
1503 *parvum* (Absent (n = 31), Present (n= 4); total n = 35 individual possums).

1504 There was no significant effect of *Cryptosporidium parvum* on any of the other mechanistic behaviours
1505 (appendix 1).

1506

1507 Discussion

1508 Problem-solving performance of individual possums in my study population was driven by both
1509 intrinsic traits and mechanistic behaviours. The most important intrinsic traits were personality and
1510 body condition. Each measure of problem-solving performance varied in which personality trait was
1511 most important. Selectivity was a key mechanistic behaviour.

1512 The personality trait, boldness, had an indirect effect on first trial outcome. Bolder individuals may be
1513 more confident in approaching a novel task. Boldness may be beneficial for an individual in an
1514 everchanging urban environment, although the range of boldness in tested individuals indicates that
1515 there is more than one way of surviving the urban landscape. Boldness has been a key trait in other
1516 species, for example, as a predictor of problem-solving success in striped field mice (*Apodemus*
1517 *agrarius*) (Mazza & Guenther, 2021). For my study, boldness increased likelihood of solving via an
1518 increase in selectivity. High selectivity directly drove an increased likelihood of solving the first trial.

1519 Selectivity was not only associated with likelihood of solving the puzzle but also less time taken to
1520 solve the puzzle. Functional behaviours are those that result in solving the puzzle. As selectivity
1521 measures the time spent on functional behaviours as a proportion of the total engaged time, it is
1522 reasonable to expect that high selectivity should lead to a faster solve time. This is consistent with
1523 previous studies on selectivity. Selectivity was directly associated with efficient problem-solving in
1524 eastern grey squirrels (*Sciurus carolinensis*) (Chow et al., 2016). Harris et al. (2023) also found that
1525 increased time spent performing functional behaviours led to a decrease in time to solve for brushtail
1526 possums.

1527 Time to first solve was indirectly affected by body condition via selectivity. Individuals in higher body
1528 condition were slightly more selective in their behaviours. The individuals who had both high body
1529 condition and selectivity may apply their strong problem-solving ability during foraging to access
1530 resources. This trend was also found by Huebner et al. (2018) where solving efficiency predicted body
1531 condition, although in this case the response and explanatory variables were switched compared with
1532 my study. A selective approach to foraging may be beneficial when accessing resources, gaining the
1533 individual a better body condition.

1534 Although good body condition indicated a faster time to solve, body condition also had a direct
1535 relationship with change in time to solve between first and second solves; i.e. short-term learning.
1536 Individuals with a lower body condition score were more likely to improve their time to solve, although

1537 all individuals did show short-term learning regardless of body condition. Individuals in lower body
1538 condition may be more motivated to solve the puzzle, hence whether or not they were initially fast
1539 problem solvers, they were motivated to improve their time in accessing the food reward.

1540 Individuals with a more vigilant personality were more effective problem solvers, with less time taken
1541 to solve their first trial. As these individuals showed a tendency to be more alert and wary, this may
1542 have driven them towards a quick approach to problem solving, preferring to solve the puzzle as fast
1543 as possible to avoid risk from predators or other threats. Vigilance has been previously shown as
1544 important to problem-solving in brushtail possums, with more vigilant individuals more likely to
1545 succeed at an escape box test (Wat et al., 2020).

1546 The personality trait, activity, has previously been informative of likelihood to solve an escape box test
1547 in brushtail possums (Wat et al., 2020). For my study population, more active individuals were less
1548 likely to improve in their selectivity or engagement with the functional part of the puzzle. As these
1549 mechanistic behaviours are important to solving the puzzle, active individuals were less likely to be
1550 successful problem solvers. These individuals may have been overly active and not necessarily focused
1551 on the puzzle task.

1552 This study provides the first evidence of learning and long-term recall in wild brushtail possums:
1553 individuals who had attempted the puzzle 1 to 2 years prior, solved it faster than those who were
1554 novel to the task. An effect of personality also became evident in investigating this relationship. More
1555 exploratory individuals in the (New) cohort, i.e., with no prior experience, took longer to solve and
1556 less exploratory individuals, who may have been more focused on solving the puzzle and therefore
1557 solved it faster. However, individuals in the (Old) cohort, i.e., those who did have prior experience
1558 from 1 to 2 years ago, were all fast problem solvers with little difference based on personality. This
1559 finding indicates that once possums had learnt this novel task, their recall to do so over the long term
1560 overrode any influence of personality on problem-solving performance.

1561 *Cryptosporidium parvum* carriage had no significant effect on likelihood of solving, however the
1562 sample size of those carrying the pathogen was very low. However, there was evidence of an effect of
1563 *C. parvum* carriage on how the individual approached the problem. Carriers spent less of their time
1564 engaged with the functional part. They were also less diverse in their behaviours, meaning that they
1565 showed less range of motor skills. Since both of these mechanistic behaviours can ultimately influence
1566 problem-solving performance, a larger sample size may reveal more effects of *C. parvum* carriage on
1567 an individual's ability to solve.

1568 My findings demonstrate that the influences on problem-solving performance are complex in wild
1569 animals, and both mechanistic behaviours and intrinsic traits play a role. This study has explored those
1570 relationships and provided evidence of learning over both short- and long-term time periods in a wild
1571 population. By studying possums in their natural environment with a food extraction task, we
1572 understand that individuals vary in their approach to problem-solving, and in turn are likely to vary in
1573 their approach to accessing resources in the wild while foraging.

1574

1575

1576 Appendix

1577 **Appendix 1.** Output of linear models run on each mechanistic behaviour with *C. parvum* carriage as
 1578 sole explanatory variable.

Mechanistic Behaviour	$F_{1,33}$ value	p - value
Behavioural Diversity	4.841	0.035
Behavioural Flexibility	2.007	0.166
Work Time	0.216	0.645
Functional Part Engaged	3.167	0.084
Behavioural Selectivity	2.323	0.137

1579

1580 **Appendix 2.** Summary information for possum individuals with *C. parvum* positive scats collected.

Possum ID	Scats Collected	No. of <i>C. parvum</i> positive scats	Positive scat collection date	Puzzle trial? (Y/N)	Date of first puzzle trial
0447108	3	1	06.12.2021	Y	07.02.2022
0458519	6	1	14.04.2023	N	NA
6128227	9	1	06.12.2021	Y	08.11.2021
6137856	3	1	21.12.2021	Y	01.02.2022
6138024	9	1	02.12.2021	Y	31.01.2022
6138321	4	1	25.10.2021	Y	02.02.2022
6138335	1	1	19.01.2022	N	NA

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Chapter 4

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1702

General Discussion

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1705 Chapter 4: General Discussion

1706 This thesis investigated intrinsic traits and behaviours predicted to be important to problem-solving
1707 performance in the Common Brushtail Possum (*Trichosurus vulpecula*). I first tested for covariation
1708 among the intrinsic traits that were predicted to be important, and I defined key traits of my study
1709 population (chapter 2). I tested for direct and indirect effects of these traits on problem-solving
1710 performance, measured through approach (i.e. mechanistic behaviours) and performance (i.e.,
1711 likelihood to solve the presented puzzle and time taken to solve the puzzle) (chapter 3). Finally, I
1712 assessed whether these free-ranging possums have the capacity for short-term learning and long-term
1713 memory recall (chapter 3).

1714 In chapter 2, I found that male and female possums differed significantly but slightly in their body
1715 weight. Males were in slightly better body condition than females, but all possums were in reasonable
1716 health as measured by blood parameters. Individuals varied in several personality traits including
1717 exploration, boldness, vigilance, mobility, and activity. Some of these traits were highly correlated,
1718 resulting in a behavioural syndrome. The variation in personality among individuals was not linked to
1719 sex or body condition. Some individuals carried the pathogen, *Cryptosporidium parvum*. Probability of
1720 *C. parvum* carriage did not differ by sex, however, more exploratory individuals were more likely to
1721 carry the parasite.

1722 in chapter 3, I found that the personality trait, boldness, indirectly influenced the likelihood to solve
1723 the puzzle. Vigilance and body condition had direct and indirect effects on the time taken to solve the
1724 puzzle. The mechanistic behaviour, selectivity, had a significant direct effect on both likelihood of
1725 solving and time taken to solve the puzzle. This study population showed evidence of both short-term
1726 learning and long-term memory. Possums improved their time taken to solve in their second
1727 successful attempt at the puzzle within a session (i.e. within several days/weeks), indicating short-
1728 term learning; and possums with lower body condition improved more. There was an interactive effect
1729 of cohort and the personality trait, exploration, on the time to solve the puzzle. Possums from the

1730 “Old cohort” (i.e., experienced individuals who had last interacted with the puzzle 1-2 years prior)
1731 solved the puzzle quickly irrespective of their exploration personality trait. In contrast, in the “New
1732 cohort” (i.e., possums who were novel to the puzzle) only less exploratory possums solved as fast as
1733 the Old cohort while more exploratory possums took longer to solve the puzzle. Parasite carriage did
1734 affect the mechanistic behaviours possums used for problem-solving. Individuals carrying *C. parvum*
1735 demonstrated less behavioural diversity, using less engaged behaviours, and spent significantly less
1736 proportion of time engaged with the functional part of the puzzle.

1737 As the results found in each of my chapters have been discussed already in chapters 2 and 3, in this
1738 chapter I explore some of the broader implications of my research and future directions.

1739 Cognitive significance of solving novel problems

1740 Most problem-solving and cognitive research has been on eutherians (Johnson-Ulrich et al., 2018;
1741 Rowell & Rymer, 2022), birds (Jelbert et al., 2014; Medina-Garcia et al., 2017), and rarely reptiles (Leal
1742 & Powell, 2012; Storks & Leal, 2020); with very few on marsupials (Harris et al., 2023; Wat et al., 2020).
1743 Overall, possums in this study demonstrated an ability to solve a puzzle, learn the solution and
1744 improve, and recall the solution to the puzzle over a year later. These findings reflect the cognitive
1745 ability of this species. Future studies could explore this further. For example, cognition could be tested
1746 with more difficult puzzles. In my study, possums had to pull the puzzle drawer towards themselves
1747 to access the food reward – an intuitive movement because it brings the reward closer. A puzzle in
1748 which animals had to push the drawer away to solve it should be more challenging as it is
1749 counterintuitive. Differences in task difficulty may reveal additional individual differences, as seen in
1750 a previous study on common brushtail possums (Wat et al., 2020): some individuals were able to solve
1751 a simple task—pushing a door to escape, which on this case is the intuitive movement to exit —while
1752 others struggled with a more difficult task that required pulling the door toward themselves to escape.
1753 Other studies in cognition have used tool-use to measure cognitive ability, particularly in birds and

1754 primates (Spagnoletti et al., 2012; Troscianko & Rutz, 2015). Similarly, future studies could test
1755 whether possums can use tools to access a food reward.

1756 Ecological significance of problem-solving, learning and memory

1757 Problem-solving has important implications for the survival of animals, particularly in ever and rapidly
1758 changing environments, such as urban landscapes. Possums in my study were able to improve their
1759 time to solve a puzzle with repeated trials within a session, indicating short-term learning. The ability
1760 to learn quickly allows the animal to adapt to novel challenges. Fast learners may access new resources
1761 more quickly, giving them a competitive advantage over slow learners.

1762 Possums that had experience with the puzzle were able to recall the solution a year later, providing
1763 the first evidence of long-term memory in a free-ranging marsupial. Similarly, free-ranging raccoons
1764 (*Procyon lotor*) have also demonstrated the ability to retain knowledge of a learned behaviour,
1765 remembering the solution to a puzzle in consecutive years (Lazure & Weladji, 2024a). Long-term
1766 memory may give the animal the ability to recall and return to previous foraging opportunities,
1767 particularly those that are intermittent, e.g. seasonal foods. The retention of memory over a long time
1768 is particularly important for species that migrate or hibernate, as they will have long periods during
1769 which learned behaviours are not used (Mateo & Johnston, 2000). There is also evidence of long-term
1770 memory in birds; wild North Island robins (*Petroica longipes*) were able to recall a learned foraging
1771 task after close to 2 years (Shaw & Harvey, 2020). The authors suggest that the ability to retain learned
1772 behaviours over the long-term could be ideal for conservation management strategies. Both learning
1773 and memory can provide ecological benefits for those animals that succeed with problem-solving.

1774 Fitness implications of intra-specific differences in problem-solving ability

1775 In this study, not all possums were able to solve the puzzle, yet they were all healthy and living in the
1776 urban environment. This indicates there are different ways of accessing food. Those individuals that
1777 were able to solve the problem may be adept at accessing artificial food sources provided by humans

1778 that require some form of problem-solving; while those who did not solve may have to look elsewhere.
1779 We might predict, then, that there are dietary differences among individuals, some with more
1780 diversity and eating artificial foods, while others rely on natural food. Future research could explore
1781 the dietary composition of urban-dwelling possums to determine whether reliance on natural versus
1782 artificial food sources is associated with differences in problem-solving ability. It would also be
1783 interesting to test whether any such patterns are linked to differences in fitness of individuals, or,
1784 whether they just demonstrate different foraging approaches individuals can take within the same
1785 landscape, since in my study, all possums were healthy irrespective of whether they could solve the
1786 puzzle, or how long it took them.

1787 Problem-solving performance: urban versus rural

1788 The puzzle used for this study was suited to the possums living in an urban environment as these
1789 individuals would be familiar with artificial materials, having lived in a landscape where they regularly
1790 encounter human-made objects. Comparing possums living in urban versus rural environments could
1791 further our understanding of whether the ability to problem-solve is inherent for the species or
1792 individual. However, the familiarity that urban possums have with artificial objects would likely give
1793 them an unfair advantage over those residing in more natural bushland habitats, where such materials
1794 are unfamiliar. To fairly compare problem-solving abilities across populations, future studies need to
1795 create a problem that both urban and rural species are likely to have had exposure to. This may mean
1796 making the puzzle out of natural materials such as wood.

1797 Research into differences in problem-solving abilities between animals in urban and rural
1798 environments must account for how each context affects that particular species (Johnson-Ulrich &
1799 Forss, 2025). This is essential to determine whether the species thrives in urban landscapes because
1800 of its naturally strong cognitive abilities or because it has developed enhanced cognition through
1801 exposure to novel challenges in urban settings. Characteristics of urban environments, such as human
1802 disturbance and population size, decreased time to solve a puzzle by Eurasian red squirrels (*Sciurus*

1803 *vulgaris*), suggesting that problem-solving abilities were affected by the environmental conditions
1804 (Chow, Uchida, et al., 2021). Exploring differences between urban and rural possum populations may
1805 lead us to understanding whether possums are inherently skilled problem solvers, allowing them the
1806 skills to be successful in urban environments. If there is a difference in the problem-solving ability of
1807 populations, we may infer that individuals with greater problem-solving abilities are more likely to
1808 thrive and relocate to urban areas.

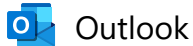
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RE: Thesis Submission to Library

From Clare McArthur <clare.mcarthur@sydney.edu.au>
Date Thu 4/09/2025 1:12 PM
To Angelica Geisler-Edge <angelica.geisler-edge@sydney.edu.au>

Hi Angelica
Confirmed!
And congratulations again on such a wonderful result!
Cheers
c

CLARE MCARTHUR

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From: Angelica Geisler-Edge <angelica.geisler-edge@sydney.edu.au>
Sent: Thursday, 4 September 2025 10:20 AM
To: Clare McArthur <clare.mcarthur@sydney.edu.au>
Subject: Thesis Submission to Library

Hi Clare,

I have removed signatures from the attached copy of my thesis. Can you confirm that my thesis is now appropriate for submission to the library?

Thanks!

Cheers,
Angelica