

# The Application Of Animal Personality In Conservation Biology: Investigating A New Tool In North Island Robin (*Petroica longipes*)

BY

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## Abstract

Conservation biology is an applied and multidisciplinary scientific discipline focused on promoting biodiversity and preserving species at risk of extinction. Animal personality (defined as consistent behaviour within and variation among individual animals) has frequently been linked to survival, reproduction, movement, and other environmental interactions. Therefore, it has been suggested that incorporating animal personality helps mitigate conservation problems. However, the extent to which this has been attempted and the feasibility of doing so still require evaluation. Therefore, I aimed to examine the full extent of how animal personality has been incorporated into conservation, test how feasible measuring personality in real conservation contexts is and assess the applications of personality from a conservation perspective.

First, I performed a systematic review of the peer-reviewed literature on conservation biology and animal personality. Second, to address the lack of appropriate and practical applications of personality in real-world conservation contexts, I adapted existing conservation management protocols for a conservation dependent species, the North Island robin, hereafter referred to by its Māori name toutouwai. Toutouwai is a threatened species that fit the typical characteristics of New Zealand's avifauna in that they are naïve to mammals, including humans. Thus, toutouwai are highly susceptible to invasive mammalian predators but willingly engage in behavioural tasks in the wild. Using this system I adapted standard conservation monitoring procedures, and an anti-predator training procedure to take personality measures of individuals. This system makes for a unique opportunity to study personality in a real-world conservation setting.

From the review, I found that personality has been applied to a broad range of conservation contexts but is not well executed with approximately half of all studies falling short of appropriate methods for quantifying personality. Furthermore, there was a lack of conservation-focused content or applications in the studies that measured personality appropriately, indicating personality as a conservation tool is at an infant stage. From my tests implementing personality into conservation, I found that incorporating personality through adapting conservation management procedures and anti-predator interventions in the wild is feasible under ideal conditions. However, both tests highlight the need for focused research on ecological function and may be prohibitive for most conservationists to expend resources on currently. Overall, personality has a place in conservation but probably in fewer contexts than has been previously suggested

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# Chapter 1: General introduction

## Conservation behaviour

Conservation biology is an applied science with the overarching goal of preserving biodiversity through the development of principles and tools (McCarthy & Possingham, 2007; Soulé, 1985). Conservationists often face problems that require fast action, despite having limited knowledge, time, and resources (Catalano et al., 2019; Soulé, 1985). While the traditional ‘crisis discipline’ and ‘conservation triage’ approach has led to several conservation successes, it has also led to many well-known but often repeated failures (Catalano et al., 2019). Examples of conservation failure include mesopredator release due to pest control programs (Caut et al., 2007; Ruscoe et al., 2011; Trewby et al., 2008), as well as health, survival, reproductive and behavioural problems from both supplementary feeding (Blanco et al., 2011; Hunter et al., 2017) and captive rearing programs (Griffith et al., 1989; Letty et al., 2007; Snyder et al., 1995; Wolf et al., 1996). As a result, conservation biologists have adopted an ‘adaptive management’ model that puts greater emphasis on planning, prioritisation, evaluation, and the continual evolution of conservation techniques (Armstrong et al., 2007; Berger-Tal et al., 2011; McCarthy & Possingham, 2007; Westgate et al., 2013). The adaptive management framework has allowed for the integration of new ideas and methods from fields such as behavioural ecology (Angeloni et al., 2008; Buchholz, 2007; Curio, 1996; Swaisgood, 2007).

It may now seem obvious that animal behaviour should be considered when enacting conservation management decisions, but there was little publication on the topic until the late 1990s (Beissinger, 1997; Caro, 1999; Curio, 1996; Sutherland, 1998). These early works often pointed to a limited amount of research showing that a lack of behavioural knowledge had led to failures in breeding programs (Curio, 1996; Oliver, 1993; Snyder et al., 1995) and wildlife release and reintroductions (Beck et al., 1994; Curio, 1996). When the behaviour has been considered, there have been improvements to many conservation projects (Baskin, 1993; Cannon, 1996; Curio, 1996; Lindburg & Fitch-Snyder, 1994; Wallace, 1994). As the application of behavioural tools to conservation became more common, this new interdisciplinary field was established as conservation behaviour (Blumstein & Fernández-Juricic, 2004).

Conservation behaviourists have made improvements to current conservation practices, including reducing the effects of human imprinting in captive-reared animals (Snyder et al.,

1995), improving the design of artificial refuges such as burrows (Ebrahimi et al., 2012) and nest boxes (Lambrechts et al., 2012), alongside the improvement of standard pest management tools (Bravener & McLaughlin, 2013; Cook & Dean, 1996; Morgan, 1990; Phillips & Winchell, 2011). Furthermore, conservation behaviour has aided in the development of novel tools to mitigate predation (de Azevedo et al., 2017; Griffin et al., 2000; Jolly, Kelly, et al., 2018; Moseby et al., 2012), minimise human-wildlife conflict (Hausberger et al., 2018), and design predator exclusion fences (Hayward et al., 2009; Innes et al., 2011). Over time, behavioural ecologists have been vindicated by showing that behavioural tools are feasible and provide value for conservationists, with increasing examples of successes from this approach (Angeloni et al., 2008; Berger-Tal et al., 2016; Brooker et al., 2016; Buchholz, 2007; Caro, 2007; Fernández-Juricic & Schulte, 2016; Swaisgood, 2007). However, new behavioural tools are often considered beneficial for conservationists before a comprehensive demonstration of how the tools might be applied has been made, with a recent example coming from comparative cognition researchers (Greggor et al., 2014a, 2014b; Schakner et al., 2014). Similarly, another behavioural field that currently falls into this category is animal personality, with many suggesting that personality can be helpful in conservation but few examples of personality being applied in conservation contexts (Brooker et al., 2016; Cordero-Rivera, 2017; Gherardi et al., 2012; McDougall et al., 2006; Mittelbach et al., 2014; Réale et al., 2007).

### Animal personality

The definition of animal personality has changed over time (Carter et al., 2013). However, the consensus is that it refers to the repeatable part of an individual's behaviour (Dingemanse & Wright, 2020), with variation in personality is defined as being among-individual variation in behaviour across repeated observations (Dingemanse & Wright, 2020). Personality theorists argue that an individual animal's response can be consistent over time and/or context, but that the range of possible responses across varying stimuli is limited (Brooker et al., 2016; Carter et al., 2013; Dingemanse, Kazem, et al., 2010; Andrew, Sih et al., 2004). Ultimately this theory suggests that there should be predictable, measurable and consistent differences among individuals in their behaviour (Dingemanse & Wright, 2020), with situations determining *who* is optimal rather than simply what behaviours are optimal (Carter et al., 2013).

Personality appears to be a fundamental aspect of behaviour, quantified in species ranging across taxonomic groups, including fish (Mittelbach et al., 2014), birds (Bell, 2007), mammals (Wolf & Weissing, 2012), invertebrates (Modlmeier et al., 2015), amphibians

(Kelleher et al., 2018), and reptiles (Gosling, 2008). Moreover, personality appears to be an important aspect to consider when trying to understand the ecology and evolution of species (Réale et al., 2007). Accordingly, personality has been linked to foraging (DiRienzo & Montiglio, 2016; von Merten & Siemers, 2012; Wang et al., 2015), habitat use (Burkhalter et al., 2015; Minderman et al., 2010; Modlmeier et al., 2014), migration (Chapman et al., 2011; Found & St. Clair, 2016; Odermatt et al., 2017), dispersal (Kanda & Hatzel, 2015; Saino et al., 2014; Wey et al., 2015), parenting (Barbasch & Buston, 2018; Naguib et al., 2013; Traisnel & Pichegru, 2018), mating (Frumkin et al., 2016; Martin-Wintle et al., 2017), predation risk (Belgrad & Griffen, 2016; Jaatinen et al., 2014) and response to environmental stochasticity (Biro et al., 2010; Herborn et al., 2014; Nakayama et al., 2016; Selmann et al., 2014). Moreover, personality has been argued to influence other aspects of an individual's behaviour, such as learning (Mazza et al., 2018; Peeke & Bell, 2012; Sommer-Trembo et al., 2016) and problem-solving (Lermite et al., 2017; Morand-Ferron et al., 2011). There are several pathways suggested for how individual variation in personality might maintain itself across a population including; genetic mutations giving rise to different behavioural suites, strong tradeoffs driving different behavioural strategies, spatiotemporal functions selecting for certain personalities at certain times and state-dependent feedback loops where individuals physiological condition effects how that individual interacts with the environment which effects that individuals ongoing physiological condition driving consistency in behaviour (Kight et al., 2013). In this way, personalities can be thought of as behavioural specialisations that contribute to population-level variation. However, while the exact mechanisms for the evolutionary maintenance of personality are still theoretical, there is evidence to suggest variation in personality does still have important evolutionary consequences giving rise to differences in; population demography, density, resilience and productivity, individual distribution, disease transmission, speciation, interspecies interaction and broader community level process (Merrick & Koprowski, 2017; Wolf & Weissing, 2012). As personality is so widespread in the animal kingdom and linked to important life history and behaviour, many reviewers have suggested animal personality could be useful not only in conservation but also in conjunction with other conservation behaviour interventions (McDougall et al., 2006; Merrick & Koprowski, 2017; Wolf & Weissing, 2012).

Personality has been proposed as having use in various conservation contexts, both captive and wild (Brooker et al., 2016; Kelleher et al., 2018; McDougall et al., 2006; Merrick & Koprowski, 2017; Wolf & Weissing, 2012). The argument for why personality is useful for

conservation is that personality traits are subject to selective pressures, so there can be rapid changes in population structures based on conservation management decisions, inadvertently or purposefully, selecting for certain traits (McDougall et al., 2006; Merrick & Koprowski, 2017; Wolf & Weissing, 2012). A typical example is that the pressure of being suitable for captivity will select more docile, less aggressive individuals and not select risk-averse or shy individuals. The selective pressures of captivity will bias the population, which could have deleterious consequences for captive breeding by creating a non-representative population and translocation programmes by reducing survivability upon release (Kelleher et al., 2018; McDougall et al., 2006; Merrick & Koprowski, 2017). Another typical example is that detection trapping and monitoring techniques may be biased toward the boldest, most active, or highly exploratory individuals as they are the ones that can be caught or seen (Merrick & Koprowski, 2017). The trapping and monitoring bias could limit our understanding of population size, structure, or associated life-history traits, influencing management decisions' effectiveness (McDougall et al., 2006; Merrick & Koprowski, 2017). Other examples where personality could be useful for conservation include; more explorative individuals might disperse away from protected areas (Kelleher et al., 2018; Merrick & Koprowski, 2017), and more aggressive or sociable individuals might be more susceptible to contact based diseases (Kelleher et al., 2018; McDougall et al., 2006; Merrick & Koprowski, 2017), invasive species control methods may select for shyer harder to capture individuals (Merrick & Koprowski, 2017) and, anthropogenic disturbances could select for shyer or less sociable individuals due to harvesting (Brooker et al., 2016; McDougall et al., 2006; Merrick & Koprowski, 2017), or conversely select for bolder more explorative individuals due to disturbances like light and noise (Merrick & Koprowski, 2017).

The theoretical usefulness of personality to conservation appears strong; however, examples of personality research in real conservation contexts are limited (Kelleher et al., 2018; McDougall et al., 2006; Merrick & Koprowski, 2017) with much of the justification for personality as a conservation tool coming from inferences of studies in model systems (Conrad et al., 2011; Dingemanse et al., 2002, 2003, 2007; Dingemanse, Dochtermann, et al., 2010; Réale et al., 2000; Réale & Festa-Bianchet, 2003). Furthermore, where conservation specific examples are given, the terminology used to describe personality is inconsistent, and several methods are deployed to quantify personality. For example, the various terms used previously have included individuality (Armitage, 1986; Darden et al., 2003), temperament (Martin & Réale, 2008; Réale et al., 2007), behavioural type (Spiegel et al., 2015), and coping style (Vetter

et al., 2016), as well as personality (Haage, Maran, et al., 2017; Wielebnowski, 1999). In terms of the methodology used to quantify personality, approaches used have included subjective ratings of personality (Bremner-Harrison et al., 2004; Martin-Wintle et al., 2017; Wielebnowski, 1999), single behaviour measures (Austin et al., 2004), or repeated measures designs (Haage, Maran, et al., 2017; Spiegel et al., 2015). However, only the latter approach meets what is currently considered the minimum requirement for acceptable studies of personality (Dingemanse & Wright, 2020). Moreover, while the review articles that point toward personality as a conservation tool clearly explain its relevance in conceptual terms, they often fall short when describing how conservationists might implement their ideas. Indeed, definitional, methodological and applicability issues appear to be a problem inherent to the field of personality itself (Beekman & Jordan, 2017; Dingemanse & Wright, 2020), which has important consequences for how personality could be applied to conservation.

Although there is now relative consensus on how personality is defined, that has not always been the case (Dingemanse & Wright, 2020). Different research fields have used different terms for the same broad definition (Carter et al., 2013; MacKay & Haskell, 2015; Réale et al., 2007). Some examples include 'temperament' in genetic/animal husbandry fields (Réale et al., 2007), 'cognitive/coping style' in comparative psychology/animal behaviour (Bell et al., 2009; Andrew Sih et al., 2004), and 'behavioural type' commonly used by behavioural ecologists (Carter et al., 2013; Andrew Sih & Del Giudice, 2012). The literature is further confused with some authors using terms interchangeably between publications (Dall et al., 2012; Andrew Sih, 2013; Andrew Sih et al., 2011; Spiegel et al., 2017), or not defining terms within an article, requiring the reader to interpret the author's meaning (Dingemanse & Wright, 2020). The lack of standardisation makes comparisons across studies difficult, as each study must be re-interpreted under the current best-practice personality framework (Dingemanse & Wright, 2020). The same issues associated with terminology are also true for how personality has been quantified in the past, with some studies lacking what is now considered a bare minimum for personality research, namely, repeated behavioural measures of the same individual (Carter et al., 2013; Dingemanse & Wright, 2020).

At its core, personality research should be measuring the repeatability of behaviour, but this presents methodological constraints on the applications of personality to conservation. Not all conservation contexts will be amenable or suitable for repeated measures designs. For example, lethal fishing and pest trapping programmes for invasive species aim to remove animals after one interaction. Furthermore, tests that measure personality, for the most part,

can only be performed where it is possible to make contextual changes to an individual's environment, be it the presentation of a novel object, environment, or threat stimuli (Carter et al., 2013). Again, there are likely many conservation contexts where task presentation is impossible, let alone can be performed repeatedly. Finally, the lack of empirical studies performed in real conservation contexts is an issue that applies to both personality and conservation behaviour tools more generally. Instead, reviewers advocating for incorporating personality into conservation will point to studies that suggest some relationships should be considered, but few are from real conservation contexts or wild studies (Fernández-Juricic & Schulte, 2016; Merrick & Koprowski, 2017). While not all areas of conservation concern involve wild animals, those that utilise captivity are usually last resort methods (Curio, 1996). For personality and other conservation behaviour tools to have the most impact and provide the most value to conservationists, we need to establish whether and how they can be applied to real, wild conservation contexts (Curio, 1996).

In summary, as it currently stands, those interested in applying personality to conservation will easily find reviews describing the benefits. However, the sources these reviews rely on do not paint a complete picture of what has been done in actual conservation contexts (Merrick & Koprowski, 2017). Moreover, most of the available reviews lack detailed descriptions of how a conservationist might implement personality into a conservation program or how a conservation behaviourist might integrate personality into another conservation behaviour-based intervention. As it applies to conservation, personality must be thoroughly reviewed to detail how personality has been measured alongside its contribution to conservation projects. Moreover, having a complete understanding of the conservation personality interface would benefit both conservationists and behaviourists as it would provide informed, up to date case studies on how to apply personality in a conservation context.

## Study system

Despite the recommendation by researchers that personality would be useful if incorporated into conservation projects, the extent of implementation and outcomes specific to conservation contexts are not well understood (Merrick & Koprowski, 2017). Ultimately, if personality can help solve the growing problems faced in conservation projects, it should be tested in systems representative of a real-world context.

The incorporation of personality may be beneficial to improve the goals of 'mainland island' conservation projects. Conservation islands were originally developed in New Zealand due to introduced mammalian predators causing the extinction and decline of many native

species (Keitt et al., 2011; Russell et al., 2015). Initially, offshore islands were used as they had limited pathways for reinvasion (Keitt et al., 2011) and could be completely cleared of predators, both introduced and native (Darby, 2003; Innes et al., 2010). Derived from offshore island conservation, 'mainland islands' encompass an attempt to mitigate habitat fragmentation and the effect of invasive species (Innes et al., 2011). Specific areas, usually consisting of established or restoring native ecosystems, are selected for intensive predator trapping/removal and habitat improvement (Innes et al., 2011; Scofield et al., 2011), creating an island of protection within the broader landscape that is analogous to an offshore conservation island. As conservation island programmes progressed, new technologies were invented to improve the island like effect in mainland areas, culminating in developing the mammal-exclusion fence (Innes et al., 2011). First implemented at Zealandia Wildlife Sanctuary (Rastandeh et al., 2018). This fencing design enables the eradication/exclusion of New Zealand's introduced mammalian pest species (excluding mice) without needing suitable landscape features to act as barriers to reinvasion or intensive long-term pest management. Fenced mainland islands are sometimes surrounded by lower priority, lower quality habitats. There is an expectation that when the area inside the fence reaches carrying capacity, wildlife will disperse out of the island to these lower quality habitats, often described as a 'Halo' effect (Miskelly, 2018). Mainland islands, both fenced and unfenced, have now been replicated worldwide and are staple management tools used to protect at-risk species (Hayward et al., 2009; Keitt et al., 2011; Young et al., 2013).

Zealandia, the first mainland island to incorporate a predator exclusion fence, is adjacent to several suburbs and nature reserves of Wellington, New Zealand (Fig. 1). Over twenty years ago, Zealandia began translocating endangered and at-risk species from around the country into the safety of its fence (Miskelly, 2018; Miskelly & Powlesland, 2013). For the most part, these translocations have been resoundingly successful, with populations of many vulnerable species exploding over a relatively short time (Miskelly, 2018). The limited space inside the fence means that many animals from several species are now spilling over into neighbouring areas, effectively (re) introducing themselves to an urban ecosystem where they have been regionally extinct for decades (Linklater et al., 2018; Miskelly, 2018). However, dispersing animals face a significant challenge moving from highly protected to much riskier environments over what is essentially a meaningless barrier to flying animals.



Fig. 1. (a) Map of Zealandia (shaded white) and area of toutouwai research (black polygon) in the context of surrounding Wellington suburbs & reserves. (b) Zealandia, suburbs & reserves in relation to the Wellington region. (c) The Wellington region in relation to New Zealand.

A pressing concern for native animals is predation by introduced mammalian predators (Miskelly, 2018; Russell et al., 2015). One of the primary threats to animals dispersing from Zealandia is the free-roaming domestic cat (*Felis catus*; hereafter 'cat') (Woolley & Hartley, 2019). Unfortunately, despite plans to tackle introduced predators in Wellington, the areas surrounding Zealandia are currently not comparable to the sanctuary's protection (Greater Wellington Regional Council, 2012; Miskelly, 2018). While most of the conservation concerns, such as invasive mammalian predators and habitat restoration, are being targeted by local (Wellington City Council, 2012) and regional (Greater Wellington Regional Council, 2012) councils in public reserves, Wellington City Council has only recently assigned a position to co-ordinate urban cat management. Early management frameworks are limited and unlikely to eliminate cats' threat to dispersing wildlife (Greater Wellington Regional Council, 2012; Wellington City Council, 2012). Furthermore, cats are a global problem not solely confined to urban centres (Duffy & Capece, 2012; Loss et al., 2013; Moseby et al., 2018), and similar problems will likely be faced by other conservation islands or urban rewilding projects (Jolly, Webb, et al., 2018; Moseby et al., 2011).

A potential solution to this problem is to initiate the conservation behaviour intervention of aversion training with personality assessments. Aversion training utilises associative learning, the ability to associate one or multiple cues with a stimulus, to condition



an animal into avoiding potentially harmful situations (Jolly, Kelly, et al., 2018). Aversion training has several potential conservation applications, such as discouraging individuals from ingesting certain types of food (Jolly, Kelly, et al., 2018). All types of aversion training, including anti-predator training, typically follow a classical conditioning protocol. Under this protocol, an animal is taught to associate a known noxious stimulus, termed the unconditioned stimulus (i.e. pain, simulated predator attack, or alarm calls), with a novel predator cue, termed the conditioned stimulus, to elicit a novel or conditioned response (i.e. predator recognition and avoidance behaviour)(Griffin et al., 2000). In general, aversion training has been limited to captivity (Greggor et al., 2014a; Rowell et al., 2020). Aversion training has typically been applied to conservation in anti-predator or anti-prey training prior to release as a part of translocation or reintroduction programs (Armstrong et al., 2015; Jolly, Kelly, et al., 2018; Moseby et al., 2012). Although commonly suggested as a tool for conservationists (Griffin et al., 2000; Hume, 1995), a recent review has found a relatively low adoption of anti-predator training studies over time, alongside a poor success rate (Rowell et al., 2020). Personality has been shown to influence anti-predator behaviour (Ciuti et al., 2012; West et al., 2019) and learning (Carter et al., 2014; D'Ettorre et al., 2017), so it is not unreasonable to assume it might be essential to understand the influence of personality in anti-predator training protocols. By incorporating personality into this conservation behaviour intervention, we may gain better insights into anti-predator training as a tool, alongside maximising resource use by generating personality information that can be used elsewhere at the same time.

#### North Island robin/toutouwai (*Petroica longipes*)

One of the frequently dispersing species from Zealandia that is highly susceptible to cat predation is the North Island robin (*Petroica longipes*), hereafter referred to by the Māori name toutouwai (Fig 2.). Toutouwai are small, insectivorous passerines endemic to the North Island of New Zealand (Richard, 2007). Toutouwai populations have been declining post-European arrival and the ensuing introduction of mammalian predators and habitat clearance, with their conservation status now 'At Risk-Declining' (Robertson et al., 2013). In areas with standard predator control, toutouwai and the closely related South Island robin (*Petroica australis*), hereafter referred to by the Māori name kakarūwai, can be found in low numbers (Powlesland, 1980; Richard, 2007). When protected by full predator exclusion zones like Zealandia, large populations can establish over short periods (Empson & Fastier, 2013; McGavin, 2009; Muralidhar et al., 2019). Toutouwai have several characteristics that make them interesting in studying the conservation applications of personality.



Fig. 2. Male (left) and female (right) toutouwai investigating a camera bag.

Their most charismatic yet disadvantageous qualities are their naivet  toward mammals, including humans (Barnett et al., 2013; Jones, 1999; Whitwell et al., 2012). This curious nature means they will voluntarily engage in behavioural and cognitive tasks in the wild (Clark & Shaw, 2018; MacKinlay & Shaw, 2019; Shaw et al., 2017, 2019). Moreover, as a territorial species, they are amenable to repeated testing in the same location across multiple years (Shaw et al., 2019). In addition, they also form long term pair bonds, typically for a minimum of one breeding season, and have multiple breeding attempts a year (Armstrong et al., 2000).

The life-history traits of toutouwai mean detailed reproductive measures can be taken throughout multiple breeding attempts/seasons, alongside relatively accurate relationship histories, without the need for genetic analysis (Armstrong et al., 2000; Shaw et al., 2019). They can also be banded with multiple coloured bands, ensuring individual identity within and between different populations without recapturing animals (Armstrong et al., 2000; Empson & Fastier, 2013). Moreover, there has been previous work under the personality umbrella in toutouwai (Barnett et al., 2013; He et al., 2017) and attempts at the conservation behaviour intervention of anti-predator training in the closely related kakaruwai (Maloney & McLean, 1995; McLean et al., 1999). There have also been several studies on kakaruwai that show populations exposed to introduced mammals can learn to respond with anti-predator behaviours over time, but that this learned behaviour disappears over a short period of time when no longer

exposed (Jamieson & Ludwig, 2012; Muralidhar et al., 2019). These studies show there is the capacity for kakaruwai to learn about introduced mammalian predators being threats on their own, indicating a pathway for teaching kakaruwai more directly. Taken together, these traits and previous research increase the feasibility of testing the implementation of personality protocols in a real conservation context.

As stated above, personality has been investigated in toutouwai, but only in one experiment published across two articles; Barnett et al. (2013) and He et al. (2017). Both papers examined latency to attack a mealworm at the feet of a human observer. While the ultimate personality claims of both these studies are debatable due to the non-standard methodology used in terms of both experimental design and statistical analyses (Carter et al., 2013; Dingemanse & Wright, 2020), at their core, both studies found reliable evidence of behaviour that was repeatable in individuals. This is a promising start for studies aiming to investigate personality in toutouwai, as it is proof that behavioural repeatability can be measured in the wild, a core component necessary for implementing personality into real conservation interventions.

There have been two attempts at anti-predator training in kakaruwai. Maloney and Mclean (1995) attempted anti-predator training in the wild, training nesting females to respond to a model stoat with a dead conspecific in its mouth, by either 1) pairing with a model robin in a mobbing posture with alarm call playback, 2) a model blackbird in a mobbing posture with blackbird alarm call playback, 3) no bird model but robin alarm calls or 4) no bird model but robin distress calls. They found that trained females had improved anti-predator responses to a stoat placed next to the nest. In addition, conspecific models paired with alarm calls, or simply just alarm calls, elicited the largest response. In a later study, Mclean, Holzer & Studholme (1999) investigated anti-predator training in South Island robins in the same system as Maloney and Mclean (1995) but focused on whether social learning improved captive anti-predator training. Robin family units (paired adults and juvenile offspring) were exposed to a model predator, either a cat or ferret (*Mustela furo*), pulled on a string by a researcher while a mix of robin alarm (normal anti-predator response) and distress calls (produced when held in banders hand) was played. This was repeated at least twice and up to a maximum of four times for each family unit. Following completion of training protocols, juveniles were captured, and their predator recognition was assessed in an aviary. The researchers claim that there was little difference between whether animals were trained in the wild or in captivity. While this study used repeated measures, it did not look at how individuals responded to training using a

personality framework. These two studies are some of the first and only to investigate anti-predator training in the wild, and they show that a repeated measures model of anti-predator training is possible, which would also allow opportunities for personality quantification.

In summary, the behavioural characteristics of toutouwai, the ease of monitoring, and their status as a species of conservation concern make them an ideal candidate to investigate the applications of personality as a conservation tool. Previous research into toutouwai personality and the amenability of toutouwai to engage in behavioural tasks suggests that typical personality tests should measure personality, alongside simple tasks, in the wild. Moreover, the work with anti-predator training in the closely related kakaruwai suggests wild anti-predator training using conspecific alarm calling as an aversive stimulus as a conservation intervention should be possible. Furthermore, repeated measures testing during anti-predator training in kakaruwai suggests that personality measures can also be taken during this conservation intervention.

## Thesis overview

This thesis aims to examine the full extent of how animal personality has been incorporated into conservation, test how feasible measuring personality in real conservation contexts is and assess the applications of personality from a conservation perspective. This thesis consists of three data chapters. In **Chapter 2**, I perform a systematic review to determine how personality has been incorporated in conservation to date. I examined primary research articles available in the web of science directory, reviewing articles for their personality and conservation content, alongside summarising their overall findings. I describe what makes for a high-quality personality study, highlight the most relevant work in the field, and suggest how personality could best be incorporated into conservation. **Chapter 3** investigates the feasibility of incorporating personality into a real conservation context, using a population of toutouwai located in an urban conservation reserve. I incorporate personality measurement into standard population monitoring procedures to determine how easily personality could be implemented by conservation practitioners, which directly influences its usefulness as a tool. In **Chapter 4**, I develop and implement an anti-predator training intervention that serves as a personality assessment tool. I adapt previously established anti-predator training protocols to train toutouwai to associate a conspecific alarm call with a novel predator (feral cat) in the wild while also incorporating personality measures into the protocol. Finally, in the general discussion (**Chapter 5**), I highlight how taken together these studies suggest that there is indeed potential for personality to be incorporated in traditional behavioural studies, alongside regular conservation management of species. However, implementing personality as a tool requires specific methodological practices that may be too onerous for conservation practitioners.

Each data chapter is written as a separate paper addressing an aspect of the overall aim of the thesis. I am (or will be) the lead author on all three papers, with my advisor Rachael Shaw being a co-author for all papers. One of these papers (**Chapter 2**) has been accepted for publication. **Chapter 2** has had minor modifications from its submission state to incorporate reviewer feedback and provide consistent formatting.

## Chapter 2: A systematic review of animal personality in conservation biology

### Abstract

Several prominent reviews have suggested that animal personality research may have applied uses in the past two decades, particularly in conservation. However, this suggestion has yet to be evaluated by assessing empirical studies incorporating animal personality and conservation. To address this knowledge gap, I performed a systematic review of the peer-reviewed literature relating to conservation biology and animal personality, including several synonymous terms for personality in my literature search. In total, I retrieved 92 research reports that met my search criteria. I summarised the conservation context(s), the testing procedures (including species and sample size), the analytical approach, and the claimed personality traits. Although providing evidence for repeatability in behaviour is crucial for personality, my review found that repeatability quantification was implemented in only half of the reports. Nonetheless, each of the five defined personality traits of activity, aggression, boldness, exploration and sociability have been investigated to some extent in a range of conservations contexts. I highlight the most robust published studies available in the field, summarising each report's key findings and conservation-focused suggestions. Finally, I suggest a best-practice approach for conservationists considering incorporating personality into conservation. Overall personality is at the early stages of implementation as a conservation tool, with most studies being initial forays into using personality as a conservation tool. While it may be feasible to incorporate personality into a conservation program the resources required in terms of data collection and analysis may present a challenge for many conservation programs without superfluous funding.

## Introduction

Animal behaviour, while initially focused on understanding behaviour from evolutionary perspectives at the species or population level (Tinbergen, 2005), has in recent years seen a growing interest in investigating behaviours at an individual level (Dall et al., 2004; Réale et al., 2007; Roche et al., 2016; Andrew Sih et al., 2004). Of particular interest to researchers is the consistency of individual animals' behaviour and the ecological and evolutionary causes/consequences of this behavioural consistency, commonly understood as animal personality (Bell, 2007; Gosling, 2008; Wolf & Weissing, 2012). In contrast to human personality studies, animal personality can only be inferred from behaviour (Carter & Feeney, 2012). This difference has led to the field of 'animal personality' having many synonyms over time, including temperament, coping style, behavioural syndrome/type and individuality (Carter et al., 2013; Gherardi et al., 2012; MacKay & Haskell, 2015; Réale et al., 2007; Roche et al., 2016).

The proliferation of terminology in early studies of personality, alongside methodological inconsistencies, contributed to an initially confused discipline, particularly for researchers outside the field (See; Beekman & Jordan, 2017 for a critique of these historical issues and several responses from other authors outlining how they have been resolved). However, the field of animal personality research has recently become more clearly defined (Dingemanse & Wright, 2020; Roche et al., 2016). A seminal review by Carter et al. (2013) described best practices for conducting personality research, creating a framework that was built on an earlier review of animal personality research by Réale et al. (2007). Réale et al.'s (2007) review made essential contributions to the development of the field, including providing definitions of key personality traits (see Table 1), alongside a list of tests used to determine personality (reproduced in Appendix S1). Carter et al. (2013) expanded on this work by emphasising how to measure personality and examine a personality study for its ecological, convergent, and discriminant validity (described in Table 2) while highlighting potential pitfalls to avoid. Simultaneously, several statisticians reviewed and developed statistical methodologies for investigating personality in animals (Cleasby et al., 2015; Dingemanse & Dochtermann, 2013; Garamszegi, 2016; Nakagawa & Schielzeth, 2010). This body of work crystalised the idea that repeated measures of behaviours are necessary for animal personality studies.

Table 1. Definitions of personality traits originally described as temperament traits in Réale et al. (2007).

Personality trait	Definition
Activity	The general level of activity of an individual.
Aggressiveness	An individual's agonistic reaction towards conspecifics.
Boldness	An individual's reaction to any risky situation, but not new situations. This includes reaction to risky situations, such as predators and humans.
Exploration	An individual's reaction to a new situation. This includes behaviour towards a new habitat, new food, or novel objects.
Sociability	An individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour).

Diversity of personalities can have implications for the ecology and evolution of species (Biro & Stamps, 2008; Smith & Blumstein, 2008; Wolf & Weissing, 2012), with evidence that personality influences key ecological variables such as survival, movement, disease, reproduction, sampling, response to anthropogenic disturbance, habitat use, species interactions, ecological invasions, human-wildlife conflicts and response to environmental change (Merrick & Koprowski, 2017; Wolf & Weissing, 2012). It has been suggested that incorporating personality into experimental biology can help us understand the process of trait evolution and ecology, as well as how individual variation may help predict, maintain, and adapt population responses to environmental changes (Roche et al., 2016; Wolf & Weissing, 2012).

Conservation has been suggested as a field that may benefit from incorporating animal personality, due to its focus on mitigating environmental threats to vulnerable populations (Conrad et al., 2011; McDougall et al., 2006; Merrick & Koprowski, 2017; Soulé, 1985). For example, in reviews of animal personality research, an often-cited application is to help limit bias within conservation programs that trap or capture animals, as there is evidence to suggest bolder animals are more accessible for trapping than shyer ones (Brooker et al., 2016; Merrick & Koprowski, 2017; Mittelbach et al., 2014; Roche et al., 2016). Another frequently suggested application is quantifying the personalities of conservation dependent species prior to their release into the wild, as there is evidence personalities can be related to dispersal (Biro & Stamps, 2008; Kelleher et al., 2018; Merrick & Koprowski, 2017; Mittelbach et al., 2014; Smith & Blumstein, 2008). Indeed, in their review Merrick & Koprowski (2017) make detailed suggestions of how personality can be applied to a multitude of different conservation contexts,



including detection probability and capture success, stress response, movement and space use, habitat selection, mate choice and reproductive success, parasite infections, harvest success, anthropogenic disturbance, wildlife control, invasive species ecology, reintroductions/translocations, and captive breeding programs. However, in these reviews many suggestions for how personality can be applied to conservation are based on inferences from broader personality literature, rather than actual conservation contexts. Moreover, these suggestions for applying animal personality to conservation management build on earlier debates surrounding 'conservation behaviour' that predate our modern understanding of best-practice animal personality research (Buchholz, 2007; Caro, 2007; McDougall et al., 2006).

Conservation is a multidisciplinary science encompassing diverse fields, including species-specific breeding programs, population biology, international law and community group organisation (reviewed by Griffiths & Dos Santos, 2012; see Appendix S2). Conservation practitioners often have minimal margin for error in designing and implementing interventions (Snyder et al., 1995; Soulé, 1985). Any diversion of resources into a strategy with unknown outcomes could have devastating consequences, risking detrimental impacts on intended conservation goals, stakeholder involvement, continued funding, or even economic and political support (Catalano et al., 2019; Shaw et al., 2021; Soulé, 1985). Conservationists considering incorporating animal personality into their management interventions could easily misstep if they only have access to outdated terminology and methodological processes (Buchholz, 2007; Caro, 2007; Carter et al., 2013; McDougall et al., 2006; Réale et al., 2007). The initial lack of a unified framework or terminology in animal personality research may have made the field inaccessible to naïve readers (Beekman & Jordan, 2017; Jungwirth et al., 2017). Building on these early critiques, a recent editorial in *Ethology* by Dingemanse & Wright (2020) provides a consensus on measuring personality moving forward within the field and therefore the state of previous personality research remains questionable. Exacerbating all of the above issues, the extent to which animal personality has been incorporated into conservation has yet to be quantified. Instead, most reviews only highlight a handful of positive examples (Brooker et al., 2016; Kelleher et al., 2018; Mittelbach et al., 2014; Roche et al., 2016; Wolf & Weissing, 2012). To ensure that conservationists looking to incorporate personality into their practice make the most of the resources at their disposal, it is imperative to evaluate the extent to which animal personality and conservation have already been integrated and to define best practices for such studies.

To evaluate how animal personality has been incorporated into conservation biology

and provide a practical entry point for conservationists interested in incorporating personality in their management decisions I performed a systematic review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) methodological guidelines (Page et al., 2021). PRISMA systematic review protocols provide an objective and transparent way to summarise literature in a reproducible way. PRISMA is particularly valuable in this case because it can overcome the selective reporting or research biases that may have been present in previous reviews of personality. It also allows the assessment of studies that vary in their methodology/terminology, by using standardised definitions in search terms. This enables readers of a systematic review to evaluate the review methodology for themselves, rather than relying on the review authors' subjective interpretations of the literature. Overall, adopting the PRISMA framework for this review allows us to understand the breadth of how animal personality has been used in conservation biology as objectively and comprehensively as possible.

I summarised primary research articles using the PRISMA method to answer the question: how has personality been incorporated into conservation biology so far? I aimed to answer this question by detailing the breadth of methodological techniques used in each article. To evaluate the rigour of the research from a personality perspective, I assessed each research article based on the Carter et al. (2013) guidelines for personality studies (summarised in Table 2). I also categorised articles based on the conservation contexts in which personality tests (defined in S1) have been used, summarised the reasons personality was investigated, as well as the key findings and authors' suggestions concerning personality as a conservation tool. Finally, I used this information to create a shortlist of the articles that have successfully integrated animal personality and conservation, both in terms of the methodology used to evaluate personality and the degree of focus on conservation application. This final shortlist is intended as a helpful resource for conservationists who may be unfamiliar with personality but interested in potential applications for their conservation context.

Table 2. The criteria for determining whether a study assesses repeatability and validity, as defined as best practice, and described in further detail by Carter et al. (2013).

Validity	Criteria
Repeatability	There is an estimate of the repeatability of the trait(s).
Convergent validity	There is a positive correlation between performance in two tests that are hypothesised to measure the same trait.
Discriminant validity	There is a negative or no correlation between performance in two tests that are hypothesised to measure different traits.
Ecological, physiological validity	There is a test of the relationship between the behavioural trait and physiological and/or ecological traits/contexts. Physiological/ecological traits fit into five defined types: reproduction, growth, health, survival and 'Other'.

## Methods

I conducted the systematic review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses, or (PRISMA) framework using the ecology and evolutionary biology extension (O'Dea et al., 2021). Before conducting the literature search, several lists of definitions and criteria were made from Carter et al.'s (2013) review to ensure that when categorising and reporting information from each journal article, I interpreted it using a single set of definitions and criteria (summarised in Table 3). For example, if the authors described a trait as 'excitability', but in the definition guidelines, it fits within the definition of 'boldness', I reported it in the review as 'boldness'. This approach has the additional benefit of enabling a more reproducible methodology for future reviews while also limiting potential biases arising from the somewhat confused state of the animal personality literature. However, it should also be noted that all assessments were made by myself alone and therefore subject to their ability to interpret the original authors' work, alongside their understanding and knowledge of statistical analyses. However, using a pre-determined guide for all categorisations and summarising the literature (Table 3) should help eliminate objective bias to some extent (O'Dea et al., 2021).

I used the Web of Science search engine to access databases of articles available to Victoria University of Wellington, New Zealand. I was only interested in primary research articles that integrated animal personality and conservation biology. To focus on personality studies in the field of animal conservation, I used the following single string of Boolean

operators that I modified from a previous review of the publication of personality studies across taxa (Gherardi et al., 2012):

TS = ((conservation AND animal\*) AND (personalit\* OR ((behavior\* OR behaviour\*) AND syndrome\*) OR temperament\* OR (coping AND style\*) OR individualit\*)) Refined by: DOCUMENT TYPES: (ARTICLE OR PROCEEDINGS PAPER OR EARLY ACCESS) Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI, CCR-EXPANDED, IC Timespan=All years

This search was conducted on 05/05/2021 and initially returned 174 journal articles (hereafter referred to as reports following the definition of Page et al. (2021)), all of which were sought for retrieval and assessed for eligibility. This process was performed manually for each article, and a flow diagram detailing the retrieval process can be viewed in Appendix S3. Five reports in this search could not be accessed and were excluded as inaccessible. The 169 remaining reports were read in their entirety, and a further 31 reports that were literature reviews were excluded. A further 25 exclusions were made for reports that were not directly related to animal personality or conservation, as they were focused on human personality (n = 10), repeatability in animal vocalisation (n= 8), genetics without personality testing (n = 5), technical veterinary research (n = 1) or plant biology (n =1).

After these exclusions, 113 reports remained, and data were extracted from the text of the report. First, objective variables were summarised, including authors names, journal of publication, year of publication, the country where the study took place, species studied, condition of testing (wild or captive), test sample size and whether there was an assessment of repeatability. Next, the slightly more subjective categorisations of the articles were made using the definitions and criteria established prior to beginning the literature search (Table 3). Further exclusions were made for reports that did not include material aligning with any of the objective or subjective categories (n = 21) and reports that did not include any form of repeatability assessment (n = 44).

Table 3. Report assessment categorisation guide for this systematic review of studies incorporating animal personality and conservation biology.

Report component	Category	Criteria for inclusion in a category
Conservation context	See list of 13 conservation contexts in appendix S2	Where the report met definitions for >1 of the contexts in appendix S2, the most extensively discussed context was assigned.
Personality test	See list of 18 categories in appendix S1	Assigned based on meeting the description for a test type given in appendix S1, regardless of the name given to the test in the original paper.
Repeatability and validity	Repeatability, convergent validity, discriminant validity, ecological/physiological validity	If the definitions given in table 2 were met the report was marked as yes for that category. If there was evidence for ecological/physiological validity we assigned which type it was by assessing the ecological/physiological context that personality was compared to.
Personality trait	Activity, aggressiveness, boldness, exploration, sociability	If a report met the repeatability criterion, this was assigned based on criteria described in table 1, regardless of the label for the trait that was used in the original paper.
Relationship between personality and ecological and/or physiological traits	None	Where there the authors indicated there was no statistically significant relationship found
	Positive	Where the authors reported a statistically significant relationship with higher degrees of the personality trait meaning higher eco/physio trait e.g. boldness increased survival
	Negative	Where the authors reported a statistically significant relationship that higher degrees of the personality trait meant lower eco/physio trait e.g. boldness decreased survival
	Other	Where there was a relationship that could not be described using positive/negative terms.
Conservation content	Low	Less than a paragraph in the discussion
	Medium	Approximately a paragraph in the discussion
	High	Specific conservation section /Specific recommendations to conservationists

The remaining 48 reports that included an attempt to quantify repeatability were further summarised. This summary included the statistical method used for estimating repeatability, the personality traits identified, the ecological/physiological trait(s) that personality was compared to, the relationships found in those comparisons, and whether the report confirmed ecological, convergent and/or discriminant validity or not and the amount of conservation content included in the report (see Table 3 for further details). I categorised reports as high quality if they showed ecological validity alongside convergent and/or discriminant validity for the personality traits assessed. The discussion section of reports with either or both convergent or discriminant validity testing was examined. The reason for investigating personality, the study's key findings, the suggestions of reasons for findings and/or suggestions of future use of findings concerning conservation were summarised. Finally, I categorised reports as highly relevant to conservation based on the amount of conservation content they included. Reports were identified as the highest quality examples of research interfacing animal personality and conservation biology if they scored both the highest in terms of personality study quality and had the most conservation relevance.

After summarising the literature, I examined the patterns in publication year, sample size, taxa examined, testing condition, type of personality test and conservation context of reports that included repeatability assessment with those that did not. For reports that assessed repeatability, I collated the types of personality tests for reports that assessed repeatability and organised them by testing conditions and conservation context. I separately collated each ecological/physiological trait measured against personality traits.

To investigate why so many reports did not have repeatability measures we performed row-wise Fishers Exact tests to determine if there was a difference in the proportions of reports that assessed repeatability versus those that did not across time, by taxonomic class, conservation context or personality test. To determine if there was a difference in the proportion of captive to wild testing conditions in reports that assessed repeatability and those that did not, I performed the Chi-Square goodness of fit test. Finally, I performed a Two-samples Wilcoxon test and calculated the Wilcoxon effect size of the difference in sample sizes between reports that assessed repeatability and those that did not. All significance tests were calculated with an alpha of 0.05.

The initial summaries were made using Google sheets, data cleaning, and error checking performed in Microsoft Excel. Statistical tests and figure creation were made using

RStudio (RStudio Team, 2021) using the packages *reshape2* (Wickham, 2007) and *rstatix* (Kassambara, 2021) for tests and *ggplot2* (Wickham, 2016), and *cowplot* for figures (Wilke, 2020). Tables were produced using Microsoft Word. The entire dataset of 174 articles, together with their inclusion/exclusion status and categorisation, is available in Appendix S4 and a complete reference list in Appendix S5.

## Results

Our search resulted in 174 total returns, but only 92 met my eligibility criteria and were assessed by this review. Publication of reports increased slowly from 1999 to 2014, peaking in 2015, with more than half of the reports in this review being published between 2015-2021 (Fig. 3a). Study sample sizes ranged from 3 to 1748 with a median of 41, mode of 20 and mean of  $100 \pm 208$ . Most reports in this review had sample sizes  $N < 100$  (Fig. 3b). The species studied ranged across all classes of vertebrates and two classes of invertebrates (Insecta, Chromadorea), with the most frequently studied group, mammals, making up over a third of the reports in this review (Fig. 3c). Testing personality in captivity was the most common testing condition (Fig. 3d).

When examining the rates of wild testing within each taxonomic class, birds were the only class to have more wild testing ( $N_{\text{Captive}} = 9$ ,  $N_{\text{wild}} = 12$ ). In contrast, remarkably more captive testing was performed with mammals ( $N_{\text{Captive}} = 23$ ,  $N_{\text{wild}} = 15$ ), fish ( $N_{\text{Captive}} = 13$ ,  $N_{\text{wild}} = 2$ ), and reptiles ( $N_{\text{Captive}} = 7$ ,  $N_{\text{wild}} = 3$ ). There was no wild testing of amphibians' ( $N_{\text{Captive}} = 5$ ,  $N_{\text{wild}} = 0$ ) and invertebrates ( $N_{\text{Captive}} = 3$ ,  $N_{\text{wild}} = 0$ ). The most common test performed was the novel object test, followed closely by movement tracking and novel environment tests (defined in Table S1.), with these tests making up more than a third of all tests used across the reviewed reports (Fig. 4a). Tonic immobility, separation and proximity to conspecific tests were not used in any of the reviewed reports. The most common conservation context cited in a third of the reports was population biology, with community-based conservation, conservation education, economics, habitat management, wildlife law & policy and wildlife trade not appearing in any report (Fig. 4b).

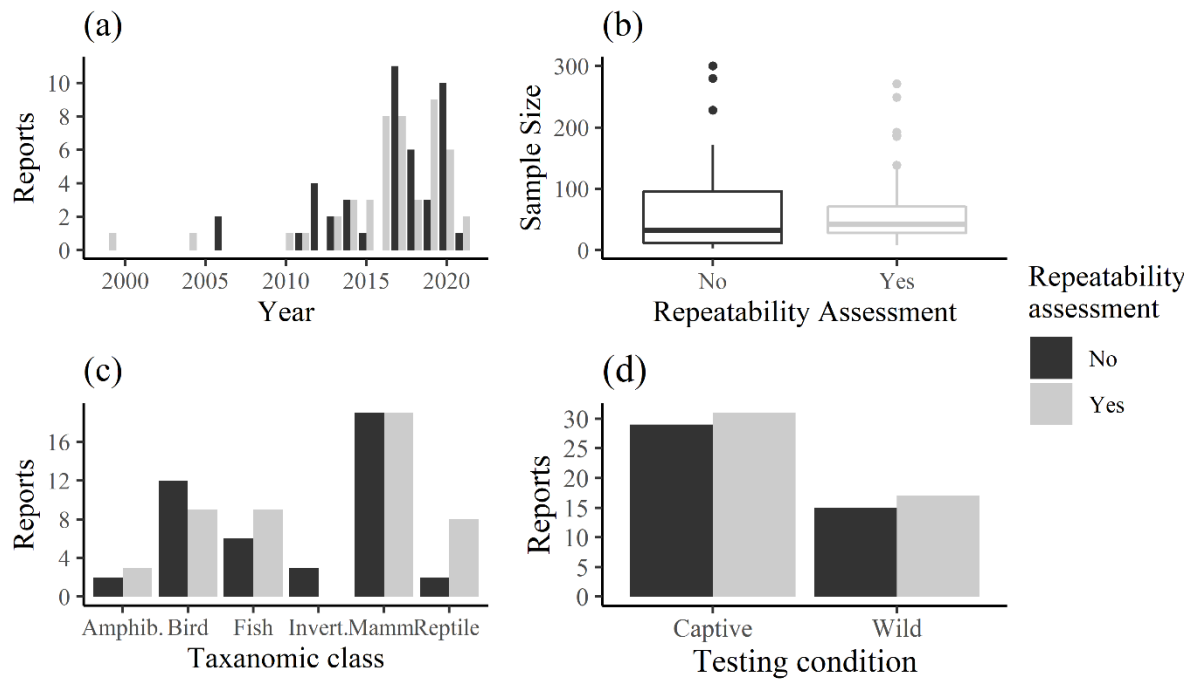


Fig. 3. (a) Bar chart illustrating the publication of personality conservation reports over time. Bars coloured black represent reports where there was no attempt to assess the repeatability of behavioural measures, bars in grey represent reports where there was an attempt to assess the repeatability of behavioural measures. (b) Boxplot displaying the difference in sample sizes of personality conservation reports. (c) Bar chart illustrating the number of personality conservation reports published across different animal taxa. (d) Bar chart illustrating the differences in personality conservation reports between wild and captive testing



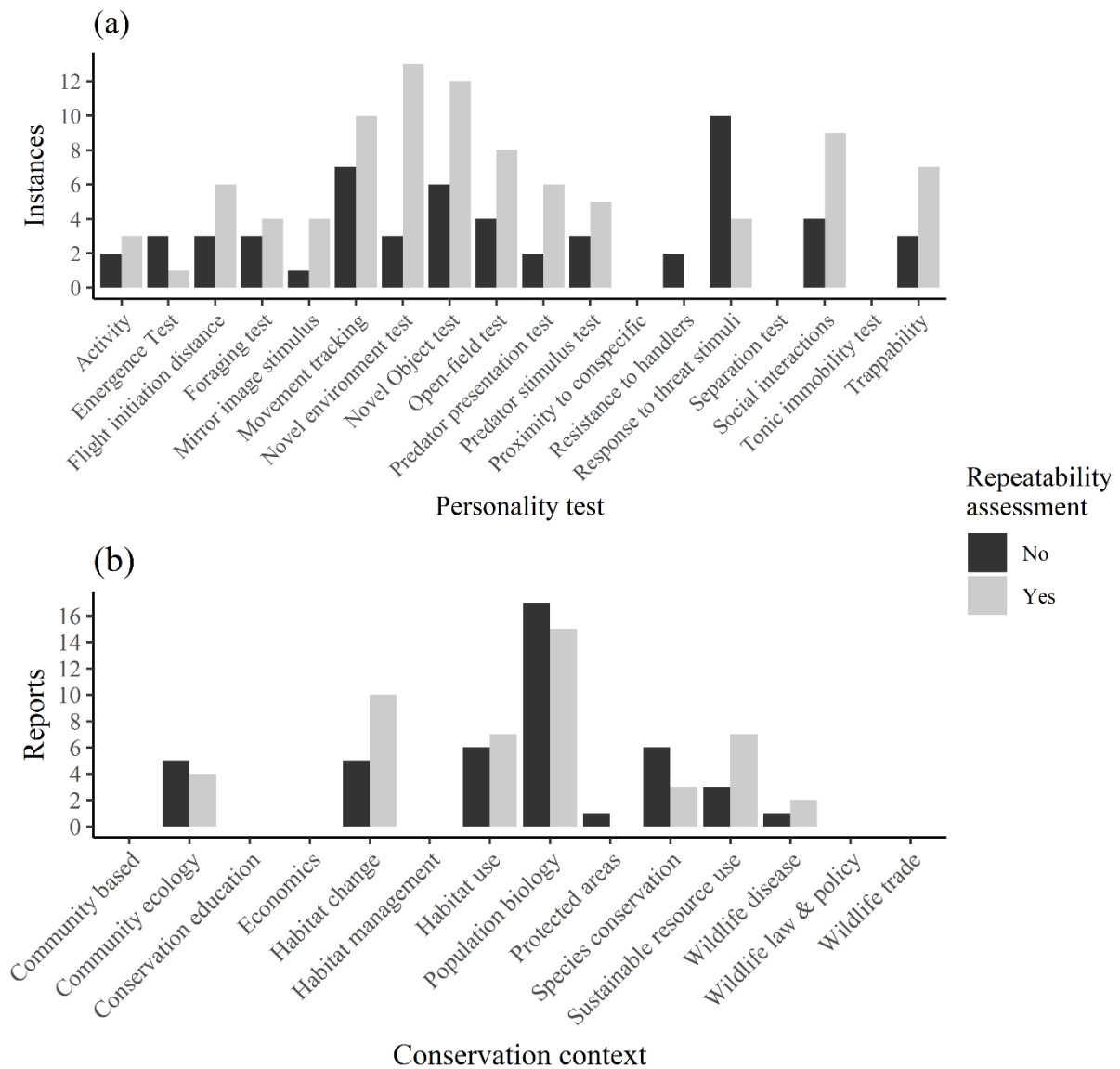


Fig. 4. (a) Bar chart illustrating the instances of personality tests being used across reports interfacing animal personality and conservation captured by systematic review. One report may have had more than one type of personality test. (b) Bar chart illustrating the instances of conservation contexts cited in reports interfacing animal personality and conservation captured by systematic review.

Comparison between reports that assessed repeatability of behaviour and reports that did not.

Of the 92 reports that met my overall eligibility criteria, only 48 assessed the repeatability of behaviours (these reports are listed in Appendix S6), meeting the minimum criteria for measuring personality (Carter et al., 2013). The proportion of reports with repeatability assessments did not significantly differ from those without in any year, taxonomic class, conservation context or personality test (Appendix S7). The proportion of reports with repeatability assessment did not significantly differ from those without in wild or captive testing condition  $\chi^2(1, N = 92) = 0.018, p = 0.984$  (Fig. 3d). The sample sizes reports that assessed repeatability (median = 46, range = 8 - 1748) did not differ from those that did not (median = 34, range = 3 - 340;  $W = 905.5, p = 0.241, n = 92$ ; Wilcoxon effect size = 0.123, Fig. 3b).

Analysis of the 48 reports that assessed the repeatability of behaviour.

Correlation-based methods were the most common method of determining repeatability across reports ( $N_{reports} = 22$ ), followed by mixed-effects modelling ( $N_{reports} = 12$ ) and intra-class correlation coefficients ( $N_{reports} = 9$ ) with the rest using other methods such as Bayesian modelling ( $N_{reports} = 5$ ). In terms of evaluating repeatability, Boldness was the most common personality trait investigated ( $N_{instance} = 27$ ), followed by Activity ( $N_{instance} = 16$ ), Exploration ( $N_{instances} = 13$ ), Sociability ( $N_{instances} = 5$ ) and aggression ( $N_{instances} = 3$ ). All but three of the reports that assessed repeatability compared the personality trait investigated to some ecological/physiological trait, meeting the definition of ecological validity (Carter et al., 2013). A list of tests used by reports that assessed repeatability sorted by testing condition and conservation context can be seen in Appendix S8. The most common ecological/physiological trait category was other behaviour ( $N_{instances} = 57$ ), followed by reproduction ( $N_{instances} = 33$ ), growth ( $N_{instances} = 23$ ), survival ( $N_{instances} = 20$ ), and health ( $N_{instances} = 8$ ). All specific ecological/physiological traits investigated and their relationships to personality traits can be seen in Appendix S9. For reports that assessed repeatability Twenty-eight out of these 45 ecologically valid reports confirmed convergent and/or discriminant validity in their reporting, and therefore had their key finding(s) and conservation applications summarised in Table 4. Nineteen of these 45 valid reports were also in the highest category of conservation content. Overall, 18 reports had the highest possible scores in terms of both conservation content and personality assessment; these studies are listed and summarised in Table 5.

Table 4. Summary of key findings and suggestions/interpretations of the use of personality in conservation from the 28 validated reports. Reports are organised alphabetically by authors.

Report	Species	Reason for investigating personality	Key personality finding(s)	Conservation application
Allard et al. 2019	Blanding's turtles ( <i>Emydoidea blandingii</i> )	Use in a reintroduction program	Survival positively correlated with exploration but no correlation with boldness or aggression. Body mass and travel distance positively correlated with exploration but no correlation with boldness or aggression. Detectability was not correlated with any personality type. Evidence of personality dependent habitat selection based on level of boldness/exploration, which may have impacted survival	Personality-based selection protocols could be important for reintroduction programs and habitat matching
Andersson, Laikre, and Bergvall 2014	domestic rabbit ( <i>Oryctolagus cuniculus domesticus</i> )	Use in captivity and relation to observer ratings	Exploration and activity were more prominent in males and juveniles	Individuals can be screened for behavioural types
Arroyo, Mouquet, and Bretagnolle 2017	Montagu's harrier ( <i>Circus pygargus</i> )	Relationship to human disturbance/reproduction	Shyer individuals had more reproductive failures. Evidence of selection for bolder individuals from human disturbance	Minimising human contact in conservation programs should be considered, but the risks should be weighed by practitioners. Human disturbance could lead to population-level changes in behaviour.
Baker et al. 2016	kangaroo rat ( <i>Dipodomys stephensi</i> )	Relationship to social behaviour and predation	Exploration negatively correlated with faecal cortisol concentration	Personality-based screenings might be useful for translocation procedures and may enable the maintenance of behavioural diversity in a population and improvement of captive conditions.
Bremner-Harrison et al. 2018	San Joaquin kit fox ( <i>Vulpes macrotis</i> )	Testing methods for measuring personality in free-ranging animals and assessing	Boldness varied across familial groups. Each test is able to quantify personality, but tests differed in their required resource intensity	Quantifying personality in free-ranging animals can be done through different methods but decisions on which test to use

	<i>mutica</i> )	value to managers		should be made based on available resources, specific questions, and the goal of the conservation program
Castanheira et al. 2016	gilthead seabream ( <i>Sparus aurata</i> )	Effect of a social group on personality	Boldness is mediated by social context	Personality could be used to develop different rearing conditions in aquaculture or breeding/selection programs to increase sustainability and welfare.
Dutra et al. 2016	saffron finch ( <i>Sicalis flaveola</i> )	Use in anti-predator training (Captive reared/captured individuals)	No relationship between boldness and anti-predator response or sex	Captive reared/captured individuals may be biased in their personality expression and not representative of wild populations.
Germano et al. 2017	desert tortoises ( <i>Gopherus agassizii</i> )	Use in translocation	More exploratory individuals had higher survival and used refugia more. Exploration was dependent on body size.	Targeted personality assessment prior to translocation could improve initial survival but may bottleneck the population.
Haage, Maran, et al. 2017	European mink ( <i>Mustela lutreola</i> )	Use in reintroduction programs	Survival post-release was positively related to boldness.	Selection for reintroduction based on personality types may be useful but may decrease genetic variation in the population. Incorporating anti-predator training that focuses on shy individuals may improve translocation/reintroduction programs.
Hammond et al. 2020	mountain yellow-legged frog ( <i>Rana muscosa</i> )	Use in translocation and monitoring	Activity and exploration are positively associated with visual detection post-release	Quantifying personality differences prior to release may be important for species that cannot accommodate tracking devices. If detection is biased by personality type, it may lead to underestimates of survival post-release for less active/less exploratory individuals.
Heinen-Kay et al. 2016	Bahamas mosquitofish ( <i>Gambusia hubbsi</i> )	Relationship to group-wide predation level	Exploration is higher in low-predation populations and appears to be heritable. Exploration positively correlates with detection.	Personality may be important for understanding responses to environmental stressors such as human-induced climate change. The selection of complex behaviours

may lead to evolutionary divergences.

Kowalski et al. 2019	common vole ( <i>Microtus arvalis</i> )	Relationship to movement behaviours (wildlife corridors)	Movement through corridors was not explained by the exploration score	Landscape features are potentially more important than individual behaviour regarding movement, particularly in wildlife corridors
Madden and Whiteside 2014	pheasant ( <i>Phasianus colchicus</i> )	Relationship to selection by hunters	Bolder individuals were less likely to survive. No relationship between boldness and body condition.	Shooting may impose selection for increased shyness, which could affect other aspects of the population and make shooting more difficult.
Maes, Van Damme, and Matthysen 2013	natterjack toad ( <i>Bufo calamita</i> )	Relationship to movement, habitat use. Comparison between captive and natural populations	Faster moving individuals had higher activity. No correlation between feeding latency and activity. Captive raised individuals are more active than wild raised.	Wild animals may differ from captive-reared individuals, so should be incorporated into personality testing. Personality does not exclusively explain movement behaviours so be cautious in interpretation.
Martin-Wintle et al. 2017	giant panda ( <i>Ailuropoda melanoleuca</i> )	Use in captive breeding	Disassortative mating for activity is associated with better reproductive outcomes. Assortative mating for boldness is associated with better reproductive outcomes. If both partners were bold, a pair was more likely to mate and produce offspring when the male was more aggressive than the female	Personality pairing can be useful in captive breeding programs and authors provide a guide for optimal pairings
May, Page, and Fleming 2016	brushtail possum ( <i>Trichosurus vulpecula</i> )	Use in translocation	Increased boldness is associated with riskier sleeping habitat and body mass gains.	Shyness is selected against in captive breeding which may influence post-release survival. Personality screening could be useful in future translocations.
Michelangeli, Wong, and Chapple 2016	delicate skink ( <i>Lampropholis delicata</i> )	Testing the trapping bias hypothesis	No relationship between the three different trapping methods and personality traits of boldness, activity, exploration, and sociability.	Trapping bias may be only relevant for passive trapping methods

Nogueira et al. 2017	collared peccary ( <i>Pecari tajacu</i> ) white lipped peccary ( <i>Tayassu pecari</i> )	Relationship to hormones Comparison between related species	Positive correlation between exploration and plasma glucocorticoid concentrations White lipped peccary more explorative than collared peccary	Human selection and environmental change may favour certain personality traits which could reduce behavioural variability in populations. This may contribute to the variation in the conservation status of collared and white lipped peccary as white lipped peccary are more explorative
Nogueira et al. 2021	paca ( <i>Cuniculus paca</i> )	Use in captivity and relationship to observer ratings	More active individuals displayed more abnormal behaviours	Targeted hunting may select certain personality types in the population
Schwarz et al. 2021	Galápagos sea lion ( <i>Zalophus worlabeeki</i> )	Movement/foraging	Activity was not correlated with age, body condition or body mass. Activity type related to habitat preference.	Habitat use/grouping may be mediated by activity type. As habitats change individuals with differing personalities may vary in their ability to adapt.
Silva et al. 2014	Nile tilapia ( <i>Oreochromis niloticus</i> )	Relation to hormonal activity	Activity negatively correlated with serotonergic activity in the hypothalamus	Selection programs aimed at improving feeding motivation may benefit from personality assessment.
Turner et al. 2020	spotted hyena ( <i>Crocuta crocuta</i> )	Relationship to anthropogenic disturbance	Individuals from low-disturbance areas were bolder. Shyer individuals had greater survival. No effect of social rank or sex on boldness	The anthropogenic disturbance may favour shy individuals.
Villegas-Ríos et al. 2017	Atlantic cod ( <i>Gadus morhua</i> )	Comparison between populations	Activity and boldness differed between populations. Boldness is negatively correlated with body condition.	Personality differences are due to environmental variation and findings may be important for understanding population responses to natural and human-induced selection
Ward-Fear, Brown, and Shine 2020	yellow-spotted monitor ( <i>Varanus</i> )	Use in conditioned taste aversion training protocol	Boldness predicted response to a training protocol and subsequent survival. Shyer individuals more likely to survive	There may be selection on behavioural type due to invasive species and from the use of conditioned taste aversion training protocols

*panoptes*)

Webber and Willis 2020	little brown bat ( <i>Myotis lucifugus</i> )	Relationship to social behaviours	Individuals with similar activity scores roosted together	Personality may influence disease transmission as individuals with similar activity congregate more. This could lead to population-level change if the disease spreads by contact.
Wielebnowski 1999	cheetah ( <i>Acinonyx jubatus</i> )	Use in captivity and relationship to keeper ratings	Ratings correlated to behavioural measures. Non-breeding cheetahs shyer than breeders and female cheetahs shyer than males	Understanding personality may be important for coping in captive environments and improving breeding programs
Williams et al. 2019	African elephant ( <i>Loxodonta africana</i> ), Asian elephant ( <i>Elphas maximus</i> )	Use in captive social groups and relationship to keeper ratings	Keeper scores matched behavioural ratings. Sociability is not related to individual origin, sex, species, or relatedness to others. Sociability is positively correlated with positive social interactions.	Changes to species-specific captive management guidelines based on personality
Wong et al. 2017	wide-band anemone fish ( <i>Amphiprion latezonatus</i> )	Comparison between related species	Personality was present in one species but not the other	Personality could explain interspecific differences in the ability to respond to environmental change

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Table 5. Reports identified as having both high-quality personality and high content conservation information

Species	Conservation context	Personality test(s)	N	Personality trait(s)	Source
Mountain yellow-legged frog <i>Rana muscosa</i>	Population biology	Movement tracking	185	Activity, exploration	(Hammond et al., 2021)
little brownbats <i>Myotis lucifugus</i>	Wildlife disease	Movement tracking	34	Activity	(Webber & Willis, 2020)
giant panda <i>Ailuropoda melanoleuca</i>	Species conservation	Open-field	29	Aggression, activity, boldness, sociability	(Martin-Wintle et al., 2017)
African elephant <i>Loxodonta africana</i>	Species conservation	Movement tracking	29	Sociability	(Williams et al., 2019)
Asian elephant <i>Elphas maximus</i>					
Montagu's harrier <i>Circus pygargus</i>	Habitat change	Activity, movement tracking	30	Boldness	(Arroyo et al., 2017)
delicate skink <i>Lampropholis delicata</i>	Community ecology	Movement tracking	63	Activity, exploration, sociability, boldness	(Michelangeli et al., 2016)
kangaroo rat <i>Dipodomys stephensi</i>	Population biology	Movement tracking	46	Exploration	(L. Baker et al., 2016)
Blanding's turtles <i>Emydoidea blandingii</i>	Population biology	Mirror image stimulus, predator stimulus test	23	Exploration	(Allard et al., 2019)
European mink <i>Mustela lutreola</i>	Population biology	Novel environment, threat stimulus, predator presentation	10	Boldness	(Haage, Maran, et al., 2017)



		foraging, flight initiation distance			
domestic rabbit <i>Oryctolagus cuniculus domesticus</i>	Sustainable resource use	Trappability	61	Exploration, activity	(Andersson et al., 2014)
cheetah <i>Acinonyx jubatus</i>	Species conservation	Open-field test	8	Boldness	(Wielebnowski, 1999)
Atlantic cod <i>Gadus morhua</i>	Sustainable resource use	Response to threat stimuli, flight initiation distance	303	Activity, boldness	(Villegas-Ríos et al., 2017)
Yellow-spotted monitor <i>Varanus panoptes</i>	Community ecology	Response to threat stimuli, flight initiation distance	46	Boldness	(Ward-Fear et al., 2020)
Bahamas mosquitofish <i>Gambusia hubbsi</i>	Habitat change	Trappability	249	Exploration	(Heinen-Kay et al., 2016)
brushtail possum <i>Trichosurus vulpecula</i>	Population biology	Conspecific interaction, response to threat stimuli, movement tracking, novel environment, flight initiation distance	20	Boldness	(May et al., 2016)
desert tortoise <i>Gopherus agassizii</i>	Population biology	Trappability, resistance to handlers	59	Exploration	(Germano et al., 2017)
pheasant <i>Phasianus colchicus</i>	Sustainable resource use	Foraging, novel object, predator presentation	21	Boldness	(Madden & Whiteside, 2014)
collared peccary <i>Pecari tajacu</i>	Habitat change	Novel object, novel environment, predator presentation	20	Exploration	(Nogueira et al., 2017)

## Discussion

This study investigated how personality has been incorporated into conservation using a systematic review of the literature, following PRISMA guidelines (O'Dea et al., 2021). Using a modified keyword search term, we identified 92 primary research articles in a well-used scientific article indexer, Web of Science. However, little more than half of these reports accurately assessed personality by assessing repeatability of behaviour in their personality test. Of the 48 reports that reported personality correctly, 28 also confirmed their personality measures using discriminant or convergent techniques. Of these 28, 18 had a high degree of information specifically for conservationists. We believe these 18 reports represent the best introduction to integrating animal personality and conservation.

Many reports included in this review claimed to measure personality and incorporate it within some conservation context, most of which were published after 2014. This is notable because, in theory, most already had access to Carter et al.'s (2013) seminal review on animal personality. Therefore, a best practice in terms of methodological and statistical approaches to studying personality had already been established prior to the publication of most papers in this review, provided they had access to the journals that published this research. Furthermore, reports published after 2017 could access the Beekman & Jordan (2017) discussion. These post-2017 studies, therefore, have a distinct advantage because the field of personality research had the opportunity to tailor their research following the best practice guidelines set out in the responses. Therefore, it was an astonishing result that nearly half of the eligible reports of this review did not assess repeatability.

Why were there so many reports lacking repeatability quantification?

I attempted to pinpoint why there was such a dearth of reports that assessed repeatability. My literature summary revealed no clear pattern of repeatability assessment being included more frequently (i.e., in more than half of all papers published) in the most recent years, as one might expect. Moreover, I found no difference in the proportion of repeatability assessment between years, taxonomic class, conservation context, personality tests or testing conditions. Although there was a slightly higher minimum sample size in studies that included repeatability estimates, there was no difference in sample sizes between reports that assessed repeatability and those that did not. Some authors may not have included repeatability due to the systems investigated using rare or non-territorial/long travelling animals and therefore having limited handling time for ethical or practical reasons, which may explain why most threat stimuli and handling tests did not include repeatability (Richardson et

al., 2019). Furthermore, some reports were looking at the population level and did not take measures at the individual level (Tudorache et al., 2015; Turner et al., 2015; White et al., 2017). However, several reports managed to assess personality at the individual level and then compare differences in the population (Castanheira et al., 2016; Villegas-Ríos et al., 2017; Wong et al., 2017). It appears that the difference between those that did repeatability testing and those that did not come down to the authors' decision. Despite this, if there is no evidence for repeatability in behaviour, then personality terminology should not be used (Dingemanse & Wright, 2020), as acknowledged by at least one report where they deferred to 'personality proxy' rather than outright personality (Richardson et al., 2019).

It is possible that my methodology for gathering reports biased my findings toward more outdated or misguided work, as my search terms included older synonyms for personality. Additionally, the search terms that we used may have failed to capture some studies that investigated personality as it was defined in our methodology. For example, an overlooked study could have used terms such as Neophobia instead of Exploration, without directly referencing personality. Furthermore, my search may not have encompassed all possible conservation contexts due to the broad interdisciplinary nature of the field, or we may have undersampled relevant studies due to using only one indexing system for our search. Nonetheless, my search terms were sufficiently broad to still retrieve several studies that ultimately did not meet my inclusion criteria. Moreover, I used standardised terms and definitions when evaluating each report. As such, I am confident that my methodological process did not overly bias my assessment toward finding studies that did not assess repeatability, and we are confident we gathered a representative sample of the relevant literature. Instead, I suggest that it is more likely that the confusing nature of the animal personality field may have led some authors followed older or alternative guides when defining personality in their studies due to the confusing nature of the animal personality field and/or following inappropriate methodology from previous studies. Furthermore, as discussed by Dingemanse & Wright. (2020), many authors appear to cite Réale et al. (2007) inappropriately, defining personality as a class of behaviours, irrespective of repeated measures of each distinct behaviour. Because so many reports in this review did not assess repeatability, I chose to only discuss in detail those that did meet this minimum criterion for assessing personality, to ensure that any conservationist wanting to understand what has so far been incorporated from animal personality has access to best practice examples.

How has personality been incorporated into conservation biology?

Our search revealed the widespread use of personality tests across several conservation contexts that focus on animal biology in the wild and captivity. However, captive testing was the dominant testing condition across reports, mirroring other disciplines within animal behaviour research (Greggor et al., 2014a, 2016; McDougall et al., 2006; Roche et al., 2016; Andrew Sih et al., 2015) and personality generally (Bell et al., 2009; Roche et al., 2016). The issues with overreliance on captive testing, and the need to understand animal behaviour in situ, have been discussed extensively elsewhere (Greggor et al., 2014a, 2016; Pritchard et al., 2016), but it should be noted that wild testing is of particular importance to animal personality. For example, Bell et al. (2009) found that repeatability estimates were higher in field-based studies than in the lab. Repeatability of behaviour is at the core of animal personality (Dingemanse & Wright, 2020), so quantifying repeatability in wild contexts, where there may be more room for between individual variance to be expressed (Bell et al., 2009), will likely improve the applicability of personality research to conservation. Despite this, I recognise that in many cases species of conservation concern are often limited in population size, accessibility, or are in a crisis state (Soulé, 1985). This, alongside the difficulties performing experiments with wild animals (Dawkins, 2007; Pritchard et al., 2016) may also contribute to captive testing being more frequent in the reports in this review.

The most prevalent personality test was the novel object test, as it was used in every conservation context except species conservation, community ecology and wildlife disease. This was closely followed by the novel environment test. This pattern is unsurprising as these are among the best defined and most used tests across the broader personality literature (Carter et al., 2013; Merrick & Koprowski, 2017; Roche et al., 2016). Both tests are relatively simple to implement repeatedly and are the only way to measure Boldness and Exploration as personality traits (Carter et al., 2013; Réale et al., 2007). Furthermore, both can be conducted at short, medium, and long-time scales, through direct observation, video recordings or GPS/electronic tracking, making them ideal for implementation in conservation contexts both in the wild and in captivity (Réale et al., 2007). Due to the widespread implementation and flexibility of novel object/environment tests, they should be a top priority for future studies attempting to measure personality in conservation contexts.

Perhaps one of the most interesting findings of this review is that there is no evidence that a specific personality trait will have the same relationship across species and/or contexts. This finding is highlighted when examining studies that examined boldness. Boldness was

investigated in reports within each ecological/physiological category and was found to have either positive, negative or no relationships to the ecological/physiological traits in question (Appendix S9). For example, boldness was not related to survival in desert tortoises or Blanding's turtles, yet was positively related to survival in European mink, and negatively related to survival in swift fox, pheasants, spotted hyenas, yellow-spotted monitors and brushtail possums (as summarised in Table 4; Allard et al., 2019; Bremner-Harrison et al., 2004; Germano et al., 2017; Haage, Maran, et al., 2017; Madden & Whiteside, 2014; May et al., 2016; J. W. Turner et al., 2020; Ward-Fear et al., 2019, 2020). Similar variation in the nature of ecological links to personality measures was apparent for boldness and body condition measures with no relationship in Blanding's turtles and pheasants, positive relationships in desert tortoises and brushtail possums, and negative relationships in Atlantic cod (Allard et al., 2019; Germano et al., 2017; May et al., 2016; Villegas-Ríos et al., 2017). This suggests that personality's role in conservation is more complicated than the traditional unidirectional relationships suggestions made by reviewers, such as shyer individuals will always have lower rates of trapping (Brooker et al., 2016; Mittelbach et al., 2014; Roche et al., 2016). However, boldness was the only personality trait that had several examples of the same or similar ecological variables being tested across species with methodological and statistical rigour. Further investigation under recently outlined methodological and statistical frameworks will hopefully enable us to make sense of these conflicting results (Dingemanse & Wright, 2020). Ultimately, personality associations found for a particular conservation context may not necessarily be reproducible in other contexts, populations or species. Perhaps this is an obvious conclusion, but it is something that both personality researchers interested in applying their research and conservationists looking to incorporate personality should be aware of.

#### Advice for conservation practitioners

Despite the breadth of research on the interface of animal personality and conservation, interpreting the implications that personality could have for conservation is not possible without carefully examining the methodology and statistics used to support a report's conclusion. An important outcome of this review is the identification of reports that meet all of Carter et al. (2013) 's recommendations for personality research while also having substantial conservation content. In this context, Tables 4 and 5 provide a preliminary reading list for conservation practitioners considering applying personality to their work. These relatively few studies set a benchmark for best practice in personality measurement in a conservation context. Among these reports, the most common motivations for studying

personality were for use in translocation/reintroduction programs or to improve captive management and behavioural training programs. These studies provide evidence from actual conservation contexts that there are important ecological consequences dependent on personality type. Examples include survival, detection and habitat use post-translocation, as well as mate paring and social structures in captivity. However, as each study investigated personality in slightly different contexts and compared different behaviours, as yet there is no consensus on what to expect for specific personality traits. Overall, the authors of these studies share the view that personality may be helpful in conservation programs to select individuals that will be optimised to specific environmental conditions or paired with certain conspecifics. Furthermore, among these reports, there are multiple suggestions that as the environment is changed or there is human interference (i.e. hunting, monitoring), there is the potential for certain personality types to be selected, and this may have severe consequences for conservation dependant species. However, with our review identifying only 18 reports that are highly relevant to conservation and that also follow best practices for measuring personality, it is clear that more research is necessary to reveal the full extent of how personality could contribute to conservation. Ultimately, before embarking on any new research, the feasibility of incorporating personality should be assessed to ensure that accurate and valuable information can be obtained, without negatively affecting ongoing conservation management. Therefore, below we provide some final recommendations for conservationists interested in incorporating personality into their projects.

First, we recommend that conservation practitioners and researchers follow the guidelines of Wolak *et al.* (2012) when designing their personality research to achieve the optimal combination of sample size and tests per individual within their study system. Additionally, Garamszegi (2016) provides an excellent guide and resources on what to do if the analysis of behaviour is constrained due to practical or ethical reasons. Conservationists may want to quantify and record behaviour as part of procedures already at the core of their work. For example, conducting visual observation measures using novel space testing is a relatively simple and effective way of quantifying personality, particularly if the species is kept in captivity for any period, i.e., during a translocation event. Two excellent examples of how this may be implemented are Allard *et al.*'s (2019) study of Blanding's turtles and Hammond *et al.*'s (2020) study of Mountain yellow-legged frogs.

I also advise looking for opportunities to record behaviours repeatedly across time and/or context without altering what would already be occurring, as this is one of the easiest

and most cost-effective ways for conservationists to incorporate personality into their programs. Many of the reports in this review tested animals as part of ongoing conservation programs, such as an ongoing reintroduction program for European mink (Haage, Angerbjörn, et al., 2017), conditioned taste aversion training with yellow-spotted monitors (Ward-Fear et al., 2019, 2020) and regular breeding season monitoring of Montagu's harrier nesting (Mougeot & Arroyo, 2017). Due to the longitudinal nature of these projects, multiple measures of individuals were able to be made over time; and the repeatability of behaviours could be examined easily. However, depending on what personality traits and species are being tested, incorporating behavioural measures in this way may not be the most robust method (Carter et al., 2013). Yet if study species are held in captivity as part of a conservation intervention (e.g., captive breeding or translocation), it may create the opportunity to collect personality information using multiple tests. Once the repeatability of a personality trait has been sufficiently quantified, it may then be possible to establish more straightforward behavioural measures that can be used as a proxy for personality (e.g. Ward-Fear et al. 2019). These simple measures could then be added to existing protocols to screen animals, allowing for management decisions to be made without entire personality testing protocols needing to be implemented. However, this type of proxy establishment should only come after appropriately quantifying personality in the managed population, as this review highlights that personality traits do not always show the same ecological relationships across conservation contexts and species.

In terms of statistical methodologies, most reports summarised follow the protocols of Nakagawa & Schielzeth, with correlational, mixed modelling or intra-class correlation coefficient tests. It may not be possible in all conservation contexts to meet the assumptions of such tests (Wolak et al., 2012), but other approaches are valid and may carry less strict assumptions (see Allegue et al., 2017; Cleasby et al., 2015; Garamszegi, 2016). Alternatively, Bayesian approaches are available for those that shy away from frequentist statistics (see Villegas-Ríos et al., 2017). Whatever statistical approach is chosen, there must be some form of repeated measures testing and analyses to meet the Carter et al. (2013) guidelines. Establishing the validity of tests is an essential aspect of personality quantification (see Table 2 for definitions) but not as critical as repeatability testing. A standard methodology used for convergent and discriminant validity testing is factor analysis, where it is possible to examine the relationships between repeatable traits. However, correlation analysis can be sufficient (Carter et al., 2013). In summary, for those conservationists who are interested in exploring the interface of conservation and personality in their practice, I suggest starting by reading Carter

et al. (2013), drawing on the examples in the best practice reports identified by this review (Table 4, 5) and following the statistical guides mentioned above.

## Conclusion

This systematic review reveals that personality has been broadly applied to conservation biology, with personality tests being used in many conservation contexts. However, in most cases, personality has not been very well incorporated into conservation biology, with very few examples meeting the requirements of personality research. Nevertheless, we were able to identify several rigorous integrated personality reports and use these as the basis for providing recommendations on how conservationists might integrate personality into a conservation program. I hope any conservationist who follows these recommendations will be well prepared to quantify personality, ultimately improving our understanding of how integrating animal personality may benefit conservation biology. However, it is clear a great deal of time and resources are needed to perform personality quantification so it may not be as feasible across all conservation contexts.



## Chapter 3: Adapting conservation management procedures to quantify animal personality in North Island robin/toutouwai (*Petroica longipes*)

### Abstract

Animal personality researchers often describe how their research could be used to aid conservation efforts. However, the application of methodology or tools from animal personality to real conservation contexts is missing or appears to be impractical. Furthermore, studies at the interface of animal personality and conservation lack information on the best practices for how to identify personality in a way that is targeted for conservation practitioners. To address these issues and show how one might successfully integrate personality into conservation, I adapted existing conservation management protocols for a conservation dependent species, the North Island robin, hereafter referred to by its Māori name toutouwai. To identify personality traits, I utilised two different approaches: measuring a single behaviour over multiple contexts and measuring multiple behaviours over a single context. I found that latency to acquire a mealworm was robust, albeit ambiguous, personality measure in toutouwai and nest defence behaviours were repeatable in females. I then attempted to identify a functional benefit of these personality measures by modelling their relationship to reproductive output measures. There was no relationship between personality and reproductive success. This study confirms that incorporating personality through adapting conservation management procedures is feasible in an ideal context, highlights the limitations of implementing personality across conservation contexts, and emphasises the need for focused research on ecological function. Overall, this chapter guides how a conservationist might identify opportunities, incorporate methods, and quantify personality in an actual conservation context.

## Introduction

Conservation is an applied science with the goal of conserving, maintaining, and promoting biodiversity that incorporates information from a wide range of academic disciplines (McCarthy & Possingham, 2007; Robinson, 2006; Soulé, 1985; Westgate et al., 2013; Young, 2000). Studies investigating animal behaviour commonly discuss how their findings might contribute to conservation (Brooker et al., 2016; Caro & Sherman, 2011; Tobias & Pigot, 2019). Unfortunately, conservationists are often limited in their resources and face a considerable opportunity cost to learn about and implement the suggested behavioural interventions, when established methods with relatively well-known consequences already exist (Catalano et al., 2019; Dunlop et al., 2012; Hiers et al., 2016). These issues are compounded when trying to implement methods from fields that require a great deal of background knowledge, skill, or replication in endangered species as diversion of scarce resources can cause the failure of a conservation project (Catalano et al., 2019; Greggor et al., 2014b; Meek et al., 2015; Schakner et al., 2014; Shaw et al., 2021). Ideally, for behavioural researchers to make a practical contribution to conservation interventions, the tools they propose should be able to be readily implemented in real-world conservation contexts.

In particular, animal personality is a behavioural discipline that has been frequently described as having the potential to aid in conservation (Brooker et al., 2016; Gherardi et al., 2012; Kelleher et al., 2018; McDougall et al., 2006; Mittelbach et al., 2014; Réale et al., 2007). However, when it comes to the practical application of animal personality to conservation, there is cause for concern (Chapter 2). Personality research in the conservation space is often poorly executed, with approximately half of the studies at this intersection of fields failing to meet the minimum standards of personality quantification (Chapter 2). Studies that do quantify personality are further split, with some studies opting for the analysis of a single behaviour across time and/or context (Carlson & Langkilde, 2013; Michelangeli et al., 2016; Ward-Fear et al., 2020), with others measuring multiple behaviours during tasks and analysing relationships with factor analysis (Allard et al., 2019; Hammond et al., 2021; May et al., 2016). The differences between these two methods are stark, with each presenting challenges to conservationists that must be assessed. Single behaviour methods are likely to be advantageous for conservation practitioners, as one behaviour can be measured relatively easily over time with large sample sizes, without requiring the video analysis that is almost necessary for multiple behaviour methodology. Alternatively, multi behaviour analysis is far more statistically and methodologically rigorous as single behaviours are more prone to confounding

variables like hunger or motivation that limit the accuracy of recording personality in an individual (Dingemanse & Wright, 2020), but requires vastly more time on the data collection and analysis side. Despite the flaws, single behaviour personality methods have been successful in quantifying personality traits that impact areas of conservation concern, including habitat use, capture likelihood, survival, and reproduction (Carrete et al., 2016; Holtmann et al., 2017; Michelangeli et al., 2016; Spiegel et al., 2015; Ward-Fear et al., 2019, 2020; Ward-Fear et al., 2018). Moreover, what is most important is that in both single and multi-behaviour personality quantification, it is insufficient to quantify personality alone; there should be an attempt to try to connect personality to the ecology of the species (Carter et al., 2013; Dingemanse & Wright, 2020; Réale et al., 2007).

Connecting personality to the ecology of a species is essential from both behavioural research and conservation perspectives. By linking personality to the ecology of a species, the relationship can provide information that conservationists can act on. For example, experimental tests of exploratory behaviour in great tits (*Parus major*), were related to dispersal distance in the wild (Dingemanse et al., 2003). This suggests that the personality of an individual influence the observed ecology of a species that would be of interest to conservationists. Suppose a conservation manager was concerned with great tit dispersal after a translocation event. In that case, they could use exploration tests to identify individuals who are likely to have desired dispersal characteristics limiting reliance on chance. Linking personality and ecology can also help integrate personality within ecological frameworks (Réale et al., 2007) and test the assumptions/predictions of personality theory (Dingemanse & Wright, 2020). For example, the link between exploration and dispersal was established by the great tit experiment. This could be a universal relationship, or it could be specific to that species or even population. In future studies where exploration is measured, dispersal can also be measured, and the results can feedback into the overarching personality theory driving future assumptions and predictions (Dingemanse & Wright, 2020).

For personality to be readily incorporated into conservation interventions, the techniques used to quantify personality must be feasible and meaningful for conservationists. Ideally, quantification methods should also complement the work conservationists already do, as they are often stretched in terms of time in resources (Catalano et al., 2019). Therefore, I examined if personality could be quantified from simple tasks given to individual toutouwai during the establishment of a study population and standard breeding season monitoring. Toutouwai represents an ideal system to investigate the incorporation of personality into a

conservation program due to several unique aspects of their ecology. Toutouwai is a highly territorial, surprisingly curious, conservation dependant passerine endemic to the North Island of New Zealand (Collen et al., 2014). Toutouwai is often one of the first species translocated or reintroduced to areas that have undergone pest eradication (Collen et al., 2014). They are easily individually identifiable through the use of coloured leg bands, they can easily be trained to approach observers, and they can be easily monitored for survival/reproduction post-translocation (Armstrong et al., 2000; Collen et al., 2014; Shaw et al., 2015). These traits make them useful regarding the success of predator suppression over time, as an indicator for more cryptic harder to monitor species, and also make them ideally suited to wild behavioural testing which is necessary for the quantification of personality (Powlesland, 1997b). Overall, this study aimed to use both single behaviour & multiple behaviour methods to quantify personality in a way that could be incorporated into current conservation management protocols. In addition, I attempted to link personality to the species ecology by investigating the relationship between personality and previously established reproductive measures (Shaw et al., 2019) taken through the breeding season. Ultimately, I aimed to assess how and why personality could be incorporated into the current management protocols of a conservation dependent species.

## Methods

### Study site & species

Toutouwai have been resident in Zealandia since translocations in 2000 and 2001, with the population steadily increasing from 76 birds to between 500-765 birds by 2009 (McGavin, 2009). A research population of individually colour banded individuals that have been habituated to mealworms (*Tenebrio molitor*; hereafter referred to as MW) has been operating consistently since 2014 (Shaw et al., 2015) in an approximately 25 ha location and has been subject to extensive cognitive testing (Clark & Shaw, 2018; MacKinlay & Shaw, 2019; Shaw, 2017; Shaw et al., 2015, 2019; Shaw & Harvey, 2020; Shaw & Schmelz, 2017). Therefore, to avoid potential confounds of repeated behavioural testing, an adjacent banded population was established in 2018. This new research population was directly adjacent to the previous, approximately the same size, but closer to the sanctuary fence line (Fig. 5). This population was established using the same protocols as Shaw et al. (2015), with minor modifications to record behavioural data during the banding process (see below). Between 10/07/2018 and 30/12/2018, 67 toutouwai were banded. The management of this population followed previously established protocols (Powlesland, 1997a; Shaw et al., 2015), with the caveat of limiting interaction with the animals as much as possible. This study, including population

establishment and personality measures, took place between July 2018 & May 2020.

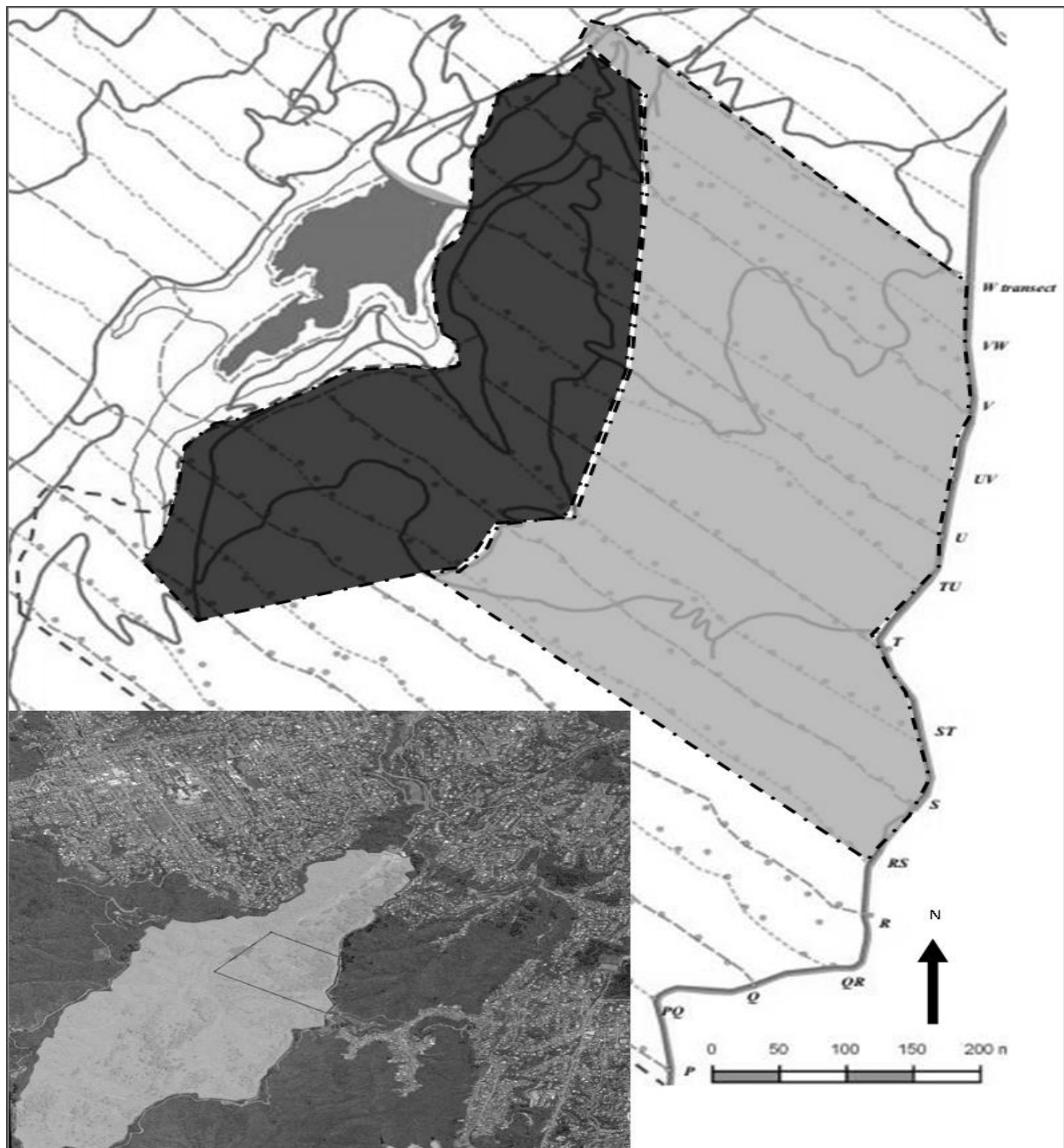


Fig. 5. Map of Zealandia toutouwai research areas with regional context. The picture bottom left shows the full extent of Zealandia as it relates to the suburbs of Wellington highlighted in grey. The black polygon indicates the toutouwai research areas. In the larger picture, the areas with line and dot borders outline the research areas more precisely. The area with the black fill is the original research area, and the grey fill is the newly established research area. The solid lines are pathways accessible to visitors. The letter labels represent the beginning of transects that run across the sanctuary. Circles along these lines are bait stations. The dashed line at the outer edges of each research area is the permitted working space.

## Permissions/Animal Ethics

This study was approved under Victoria University of Wellington Animal Ethics Committee AEC26212, performed under the New Zealand Department of Conservation Wildlife Authority 69292-RES, and with the permission of Zealandia's Conservation and Research Manager.

## Test methodologies

### *Banding Task*

Forty-one toutouwai had behavioural recordings made during standard banding procedures. The person carrying out banding (Annette Harvey – Level 3 for Passerines under the NZ National Bird Banding Scheme) recorded the latencies (in seconds) for acquiring the first thrown MW (Banding condition 1), acquiring a MW at the bander's feet (Banding condition 2), acquiring a MW next to the drop trap (Banding condition 3), and entering the drop trap for the first time (Banding condition 4). Latency measures began upon the throwing of the MW.

### *MW Throw Task*

Between July and November in 2018, September and November 2019, and May 2020, the study population was monitored to identify territory locations, partnerships, and breeding status. I followed a grid of transects established by Zealandia as part of their pest mitigation program for this monitoring (Fig 5). These transects run East-West across the sanctuary, are 50m apart and have markers every 25m along their length. I stopped at each marker and waited for five minutes, clapping at each minute interval until a bird arrived or the time expired. When a toutouwai appeared, I readied a stopwatch on my smartphone and threw a MW as close to the toutouwai as possible while simultaneously beginning the stopwatch (MW Throw condition 1). The toutouwai was given up to one minute to acquire the MW; if the toutouwai did not acquire the MW within a minute, a second worm was thrown as close as possible to the toutouwai. If the toutouwai did not acquire the second MW, a third and final MW was thrown as close as possible to the toutouwai. If the second thrown MW was acquired, the individual latency of the success was recorded plus the 60s of the failed attempt. If the third MW thrown was acquired, the individual latency of the success was recorded plus the 120s of the failed attempts. If the MW was not acquired within the time limit of the third thrown MW, the test was aborted, and the individual was excluded from further testing. Provided the toutouwai did acquire a MW within three attempts, it passed through to the following test condition. The same

latency recording protocol was applied, but rather than throwing the MW at the toutouwai in each attempt, I threw the MW halfway between myself and the toutouwai (MW Throw condition 2). Finally, provided the toutouwai acquired a MW during the first and second conditions, I dropped the MW at my feet (MW Throw condition 3). Latency was recorded as per the same protocol as conditions one and two; however, If the toutouwai did not acquire a MW in this condition, the toutouwai was given a maximum latency value (180 s), and the test ended. Latencies to acquire the MWs were recorded from the stopwatch to a field notebook, and then inputted into Google Sheets at the end of the day. In total, 87 toutouwai completed all three conditions of the MW throw test at least once.

### *Foraging Tray Task*

Between 23/10/2018 and 12/11/2018, I gave 25 male toutouwai a foraging task designed to measure personality. However, of the original 25, only 21 were measured at least twice in this task. The foraging task consisted of a core multi-behaviour measurement task, with three single behaviour measurements of latency (s) to acquire a MW taken before, during and after the multi-behaviour.

Prior to the multi-behaviour foraging task, I attempted to weigh subjects by placing a scale with a MW held in place with a bulldog clip on the ground in the bird's territory. After securing the MW in place, if required, I attracted the subject by clapping and then throwing a small stick at the scales. The subjects had four minutes to acquire the MW from the scales; the measurement ended once the MW was wholly removed. Unfortunately, this method was typically unsuccessful in providing an accurate weight due to subjects not standing entirely on the scale and removing the MW too quickly for the weight to be recorded.

Immediately after weight measurement was attempted, the multi-behaviour foraging task was performed. For this, I placed a 30cm radius black plastic tray in the middle of the territory. I then hid the tray under a blanket to load 12 live mealworms to bulldog clips equipped to the bottom of the plastic tray and covered it with leaf litter from the subject's territory while out of view of the toutouwai. The tray was positioned with two Go-pros, one close to the tray ~10cm and one ~1.5m away. If the subject had left at the end of the weight measurement, I then clapped to attract them back, after which the tray was uncovered, and I positioned myself with an iPad ~2m from the tray. If required, I attracted the subject by clapping, and once they were within 1 m of the tray, I threw a MW onto the tray to begin the test, which lasted for 20 min. This test approximates an open field task, as the toutouwai had free reign to explore the tray and move throughout their territory during the test. I recorded latency (s) to acquire the

first MW, latency (s) to acquire MW's throughout the task, duration (s) spent moving, time (s) spent with head down, perching duration (s), and time (s) spent on, next to (<1m) and far (>1 m) from the tray. Occurrences of behaviours were also recorded, including the number of MW acquired, movement occurrences (number of hops & flights), number of times head went down, number of perches, and number of times entering zones (<1m, >1m and on the tray). These behaviours were chosen as they are easily quantifiable as distinct actions, are similar to behaviours used in other examinations of personality (acquire food, movement, distance from the focal point) (Réale et al., 2007), or are related to vigilance (head-up vs down).

The latency (s) to acquire the MW was recorded, this being Foraging Condition 1. Latency (s) to acquire the first MW from the multi-behaviour foraging tasks was used to measure Foraging condition 2. Following the completion and packing away of the foraging task, weight measurement was attempted following the same protocols as in the beginning. The latency (s) to acquire MW during this weight measurement attempt was recorded as Foraging condition 3.

#### *Nest Disturbance Task*

Between 16/10/2018 and 10/11/2018, I measured the response to a short period of nest disturbance for 18 females. Only females participated in this task, as female toutouwai do all the incubation and chick brooding (Powlesland et al., 2000). Of these 18 birds, 13 were able to be measured twice. Nests were first disturbed during the last ten days of eggs being present, with a repeated disturbance within the first five days of chick presence. However, in three cases, the second disturbance occurred prior to chick presence, while eggs were still present. The nest disturbance consisted of holding a small mechanic's mirror attached to a large stick/pole over a nest that a female was incubating for 10 s. This would usually be done as part of routine monitoring when the female is not on the nest, to visually check nest contents when the nest is located above head height. The mirror was held at the height of 10 cm above the nest. After 10 s had elapsed, I removed the mirror and moved 3 m from the nest. I recorded the behaviours performed by females during the presentation of the mirror and her latency (s) to return to the nest. The behaviours recorded included duration (s) spent moving, time (s) spent with head down, perch duration (s), defensive behaviours (broken wing display, pecks at mirror, alarm calling) and time (s) spent within 30cm, within 1m and >1m from the nest. Occurrences of behaviours were also recorded movement occurrences (number of hops & flights), number of defensive behaviours, number of times head went down, number of perches, and number of times entering zones (<1m, >1m and within 30cm of the nest). These behaviours



were chosen as they represent behaviours used in other examinations of personality (movement, distance from focal point), are related to vigilance (head-up vs down), or have been observed during real predation events before (defensive behaviours).

### Statistical analysis

All statistical analyses were performed using RStudio (RStudio Team, 2021) in three stages. First I calculated adjusted repeatabilities for the latency to acquire MW across contexts. Next, I calculated repeatedly measured behaviours in the multi-behaviour task and performed Exploratory Factor Analysis (EFA) on the repeatable behaviours identified. Finally, I determined if there was a correlation between the resulting Factor Scores and average latency to acquire a MW across all contexts and trials to determine the relationship between these personality measures, and performed model averaging to determine the effect of quantified personality measures on reproduction. The specifics of these three stages are detailed below.

#### *Latency to acquire MW*

The first step in quantifying personality is to assess whether the behaviour is repeatable. Repeatability,  $R$ , describes the relative partitioning of variance into within-group and between-group sources which are generally referred to as Intra-class correlation (ICC). Behaviours that show relatively low within-individual variance compared to high among-individual variance are more repeatable (Bell et al., 2009). Repeatability estimation in personality studies is typically used to quantify if behaviours are stable within individuals over time, the core criteria for determining personality traits. Adjusted repeatabilities differ from typical repeatability in that they fit fixed effects into the model,  $R^2$ , allowing for a more precise estimation of repeatability that accounts for the testing methodology and physiology of the test species. The closer to 1 an  $R$  estimation is the higher the repeatability of the behaviour in individuals, with meta-analysis indicating average repeatability estimates of 0.37 and values greater than 0.5 considered highly repeatable (Bell et al., 2009), while  $R^2$  can provide an estimate for how much the fixed effects alone account for variation in behaviour as a percentage estimate.

Latency (s) to acquire MW was used as a single key repeatably measured behaviour in the Banding, MW throw and foraging tasks. During banding, there was four latency to approach measures (Banding condition 1-4), while during the MW throw (MW throw condition 1-3) and foraging task (Foraging condition 1-3), there were three respectively. Within each task, this meets the minimum threshold of two repeated measures necessary to determine repeatability. I followed the Nakagawa & Schielzeth, 2010 guideline using the rptR package (Stoffel et al., 2019), calculating adjusted repeatability for latency to approach in each of the Banding, MW

throw and Tray tasks, with test condition, tarsus, sex and trial (where applicable) as the fixed factors. I further quantified if latency to approach was repeatable across context by calculating adjusted repeatability across the three tasks, following suggested guidelines (Nakagawa & Schielzeth, 2010), again with the condition, tarsus, sex and trial (where applicable) as the fixed factors.

#### *Multi-Behaviour personality quantification*

A more comprehensive way to quantify personality is to measure multiple behaviours, determine if they are repeatable, and quantify their relationships with one another using factor analysis (Dingemanse & Wright, 2020). To determine if simple tasks measuring multiple behaviours could be used to quantify personality, I also recorded multiple behaviours in both the foraging tray task and nest disturbance task (discussed above). Adjusted repeatability was again assessed using the rptR package. Repeatable behaviours were averaged across trials and were then assessed using Exploratory Factor Analysis (Budaev, 2010). The suitability of the data for EFA was assessed by Bartlett's test for Sphericity and Kaiser-Meyer-Olkin (KMO) test for Sampling Adequacy, and where possible, Factor Scores were calculated.

#### *Ecological validity of personality measures*

To determine if the behaviour(s) identified from cross-contextual repeatability testing and EFA Bartlett score were ecologically valid measures, I examined their relationship to reproductive output in the breeding season directly following personality testing. I used previously established units of reproductive output in toutouwai and a model averaging approach using the dredge function of the MuMIn package to determine this separately in males and females (Bartoń, 2020). Although the previous work examined the reproductive measures of toutouwai at the level of the nest (Shaw et al., 2019), a disproportionate number of individuals only produced one nest during the time they were monitored. Therefore, I opted for General Linear Models (GLM), examining the season's total clutch and fledgling production as response variables. The first models had total clutches produced in the season as the response variable and breeding season onset, nest failure in the season, adult survival, and average latency to acquire a MW as the dependent variables. The second model had total independent young as the response variable and breeding season onset, adult survival, and average latency to acquire a MW as dependent variables. I also ran a GLM with breeding onset as the response variable and adult survival and average latency to acquire a MW as dependent variables ( $N_{\text{male}} = 25$ ,  $N_{\text{female}} = 19$ ). This model was not averaged as there were only two dependent variables. For all of these models, the sample size was ( $N_{\text{male}} = 25$ ,  $N_{\text{female}} = 19$ ). Finally, I ran analyses

that used these same models for females only but substituted nest personality (captured in the EFA factor score) for average latency to acquire a MW (for these models  $N_{\text{female}} = 17$ ).

## Results

### Latency to acquire MW as a personality measure

#### *Banding Task*

The 41 toutouwai tested latency to acquire the MW was highly repeatable across the four test conditions when including condition as a fixed factor (Table 6).

#### *MW Throw Task*

The MW throw task was completed once by 88, twice by 40 and three times by 21 individuals. Latency to acquire the MW was repeatable when including condition and observation as fixed factors (Table 6).

#### *Tray Task*

In total, 22 toutouwai went through two trials of the Tray task, with subjects in each observation having three conditions of latency to acquire a MW. Latency to acquire the first MW was repeatable when calculating adjusted repeatability, including trial and test conditions as fixed factors (Table 6).

#### *Cross-context latency to acquire MW*

In total, 114 toutouwai had at least one measure of latency to acquire MW across the three tasks. Latency to acquire a MW was repeatable across contexts when including condition and observation as fixed factors (Table 6). Average latency to acquire a MW was taken forward for EFA but failed to meet KMO requirements, so it was excluded from the EFA.

Table 6. Adjusted repeatability estimates for banding, MW throw, tray, and all tasks of latency to acquire MW. Repeatability estimates for fixed factors are also included with the label (Fixed).

Behaviour	R	SE	CI	P	R <sup>2</sup> (Fixed)	SE (Fixed)	CI (Fixed)
Latency to acquire MW across banding	0.575	0.076	0.423-0.707	4.06e-15	0.499	0.131	0.344-0.856
Latency to acquire MW across MW throw task	0.178	0.055	0.082-0.290	5.41e-05	0.190	0.048	0.137-0.330
Latency to acquire MW across tray task	0.203	0.115	0-0.443	0.029	0.017	0.041	0.001-0.154
Latency to acquire MW across all tasks	0.239	0.046	0.153-0.331	3.16e-13	0.632	0.073	0.522-0.807

## Multi-behaviour personality measure

### *Tray Task*

In total, 22 male toutouwai went through two observations of the tray task. None of the behavioural measures were repeatable even when accounting for observation as a fixed factor (Table 7). This meant no further Factor Analysis could be conducted with confidence for behavioural measures taken during the tray task.

Table 7. Adjusted repeatability estimates for each behaviour measured in the tray task. Repeatability estimates for fixed factors included with label (Fixed)

Behaviour	R	SE	CI	P	R <sup>2</sup> (Fixed)	SE (Fixed)	CI (Fixed)
Latency to acquire MW	0.003	0.143	0-0.475	1	0.103	0.122	0.001-0.465
Number of MW acquired	0.204	0.186	0-0.601	0.204	0.202	0.156	0.043-0.651
Head Down Duration	0.215	0.185	0-0.640	0.190	0.228	0.163	0.052-0.667
Head Down occurrences	0.141	0.172	0-0.565	0.298	0.388	0.230	0.117-0.973
On tray duration	0.293	0.189	0-0.679	0.104	0.136	0.130	0.018-0.517
On tray occurrences	0	0.139	0-0.455	0.500	0.074	0.111	0.006-0.414
>1m away duration	0.242	0.182	0-0.632	0.156	0.444	0.245	0.166-1.104
>1m away occurrences	0	0.146	0-0.474	0.500	0.063	0.109	0.006-0.421
Active duration	0	0.136	0-0.440	1	0.061	0.105	0.004-0.384
Active occurrences	0	0.141	0-0.442	1	0.162	0.160	0.024-0.650
Zones occurrences	0	0.139	0-0.442	0.500	0.097	0.120	0.008-0.469

### *Nest Disturbance Task*

In total, 13 female toutouwai had two observations of the nest disturbance task. Only time spent within 30cm of the nest, occurrences within 30cm of the nest, time spent using broken wing behaviours and zones crossed were repeatable when including observation as a fixed factor (Table 8). The repeatable behaviours were taken forward for Factor Analysis. The data were structured into a correlation matrix and assessed by KMO and Bartlett's Test of Sphericity, passing both; KMO (0.648), and Bartlett's Test of Sphericity ( $X^2(6) = 63.55$ ,  $p = <0.001$ ). All behaviours had high communalities and loaded onto one factor  $>0.7$ , accounting for 76% of the variance in behaviour. Factor scores were then calculated using Bartlett's method (Budaev, 2010), and FAC1 was categorised as Nest boldness.

Table 8. Adjusted repeatability estimates for each behaviour measured in the tray task. Significantly repeatable behaviours are in bold. Repeatability estimates for fixed factors are included with the label (Fixed)

Behaviour	R	SE	CI	P	R2(Fixed)	SE (Fixed)	CI (Fixed)
Head Down duration	0	0.171	0-0.563	1	0.081	0.16	0-0.585
Head Down occurrences	0.022	0.179	0-0.598	0.469	0.129	0.175	0.001-0.634
<b>Within 30cm of nest duration</b>	<b>0.464</b>	<b>0.211</b>	<b>0-0.814</b>	<b>0.038</b>	<b>0.046</b>	<b>0.083</b>	<b>0-0.3</b>
<b>Within 30cm of nest occurrences</b>	<b>0.504</b>	<b>0.212</b>	<b>0-0.827</b>	<b>0.026</b>	<b>0.027</b>	<b>0.063</b>	<b>0-0.228</b>
>1m away from nest duration	0	0.17	0-0.557	1	0	0.07	0-0.231
>1m away from nest occurrences	0.4	0.213	0-0.777	0.066	0.027	0.069	0-0.236
Active duration	0.429	0.222	0-0.819	0.052	0.053	0.092	0-0.32
Active occurrences	0.399	0.218	0-0.779	0.066	0.039	0.085	0-0.309
<b>Defence behaviour duration</b>	<b>0.459</b>	<b>0.214</b>	<b>0-0.816</b>	<b>0.040</b>	<b>0.027</b>	<b>0.069</b>	<b>0-0.243</b>
Defence behaviour occurrences	0.275	0.215	0-0.695	0.156	0.018	0.078	0-0.276
<b>Zone occurrences</b>	<b>0.523</b>	<b>0.207</b>	<b>0.023-0.85</b>	<b>0.0208</b>	<b>0.037</b>	<b>0.065</b>	<b>0-0.23</b>

### *Latency to acquire MW and nest boldness*

If latency to acquire MW and nest boldness were measuring the same aspect of personality, the expectation is that there would be a positive correlation. In contrast, if they measured different aspects, it would be negative. However, there was no correlation between average latency to acquire a MW and nest boldness in this study ( $r(11) = 0.38$ ,  $p = 0.184$ ).

### *Ecological validity of personality measures*

#### *Latency to acquire MW*

Average latency to acquire a MW was unable to be verified as an ecologically valid personality measure in this study, as total clutches produced in a season were not influenced by any variable included in the models for males or females (Table 9, 10). Total independent young produced in a season were shown to be dependent on breeding season onset in females (Table 10), with earlier onset meaning more independent young. Total independent young were not dependent on any of the other variables (Table 9, 10). There was a general trend for breeding season onset to be relatively important, but in most cases had confidence intervals overlapping zero (Table 9, 10). This indicates that the average latency to acquire a MW is unrelated to these reproductive measures in toutouwai.

Table 9. GLM results with breeding onset as the response variable and adult survival and average latency to acquire a MW as dependent variables. Estimate, Unconditional standard error (SE), T value and P-value are reported.

Sex	Behaviour measure	Parameter	Estimate	Unconditional SE	T value	P
Male	Breeding onset	(Intercept)	3.23	0.200	16.094	1.18e-13
		Survived Season	-0.214	0.217	-0.988	0.334
		Average latency to acquire MW	-0.001	0.001	-0.197	0.845
Female	Breeding onset	(Intercept)	3.206	0.120	16.069	2.71e-11
		Survived Season	-0.033	0.239	-0.140	0.890
		Average latency to acquire MW	-0.001	0.001	-0.831	0.418
	Breeding season onset	(Intercept)	2.808	0.231	12.167	7.83e-09
		Survived Season	0.084	0.329	0.256	0.802
		Nest personality	-0.172	0.142	-1.215	0.244

Table 10. Multi-model average results for the models of reproductive success and average latency to acquire a MW. For each predictor, the estimate, unconditional standard error (SE), confidence interval and Relative importance are listed. Predictors that influence the response variable (Confidence intervals that do not cross zero) are in bold. Models were run separately for males and females

Sex	Behaviour measure	Parameter	Estimate	Unconditional SE	Confidence interval	Relative importance
Male	Total clutches	(Intercept)	0.712	0.350	(0.002 – 1.422)	
		Breeding onset	-0.020	0.014	(-0.050, 0.010)	0.43
		Nest failure in season	0.165	0.317	(-0.500, 0.822)	0.24
		Adult survival	-0.093	0.324	(-0.763, 0.580)	0.23
		Average latency to acquire MW	-0.001	0.002	(-0.005, 0.004)	0.22
	Total independent young	(Intercept)	0.552	0.570	(-0.592, 1.697)	
		Breeding onset	-0.031	0.016	(-0.128, 1.476)	0.65
		Adult survival	0.674	0.387	(-0.128, 1.476)	0.59
		Average latency to acquire MW	-0.002	0.002	(-0.007, 0.003)	0.26
Female	Total clutches	(Intercept)	0.779	0.377	(0.004, 1.554)	
		Breeding onset	-0.022	0.016	(-0.056, 0.011)	0.41
		Nest failure in season	0.144	0.360	(-0.616, 0.910)	0.21
		Adult survival	0.093	0.354	(-0.656, 0.841)	0.20
		Average latency to acquire MW	-0.001	0.001	(-0.002, 0.002)	0.20
	Total independent young	(Intercept)	0.817	0.552	(-0.309, 1.942)	
		<b>Breeding onset</b>	<b>-0.043</b>	<b>0.020</b>	<b>(-0.084, -0.002)</b>	<b>0.75</b>
		Adult survival	0.477	0.438	(-0.452, 1.405)	0.31
		Average latency to acquire MW	-0.001	0.001	(-0.003, 0.002)	0.22



### *Nest boldness*

Nest boldness was unable to be verified as an ecologically valid personality measure in this study. Total clutches produced in the season were not influenced by any variable included in the models for males (Table 11). Total independent young were shown to be dependent on breeding season onset in females, with earlier onset meaning more independent young. Total independent young were not dependent on any other variable (Table 11).

Table 11. Multi-model average results for the models of reproductive success and nest boldness score. For each predictor, the estimate, unconditional standard error (SE), confidence interval and Relative importance are listed. Predictors that influence the response variable (Confidence intervals that do not cross zero) are in bold.

Behaviour measure	Parameter	Estimate	Unconditional SE	Confidence interval	Relative importance
Total	(Intercept)	0.799	0.322	(0.131, 1.470)	
clutches	Breeding onset	-0.024	0.017	(-0.064, 0.016)	0.37
	Nest failure in season	-0.036	0.365	(-0.815, 0.746)	0.20
	Survived season	0.104	0.364	(-0.674, 0.881)	0.20
	Nest boldness	-0.020	0.187	(-0.420, 0.379)	0.19
Total	(Intercept)	1.004	0.461	(0.054, 1.954)	
independent young	<b>Breeding onset</b>	<b>-0.051</b>	<b>0.023</b>	<b>(-0.010, -0.001)</b>	<b>0.80</b>
	Survived season	0.480	0.420	(-0.413, 1.372)	0.31
	Nest boldness	0.019	0.235	(-0.480, 0.520)	0.19

## Discussion

This research aimed to determine how and why personality can be successfully incorporated into the current protocols of a conservation-dependent species. Using toutouwai as an example, I showed that both single behaviour and multiple behaviour techniques could be deployed to measure personality in a conservation context. However, single behaviour (latency to acquire MW) and more complex multiple behaviour Factor Score results (nest boldness) were not correlated and unable to be verified as ecologically valid measures. While it appears feasible for personality methodology to be easily incorporated into the current conservation management of a toutouwai, the benefits of doing so more broadly require further discussion.

### Latency to acquire a MW as a personality measure

Latency to acquire a MW is a repeatable behaviour within and across contexts in toutouwai, meeting the standard requirements to be considered a personality trait (Carter et al., 2013). Despite this, there are some issues with interpreting what personality facet this behaviour is related to. As previously discussed, the test type used likely is a driver for the personality being measured (Carter et al., 2013; Réale et al., 2007), but what were the test types used during the measurement of latency to acquire a MW? The banding and MW throw tasks could reasonably be considered risk-taking/threat stimuli or novel object exploration. The argument for risk-taking/threat stimuli is that the subject must take risks in each condition presented in the banding task, coming closer to a bander, eventually being trapped, and in the MW throw task coming within touching distance of a person. However, depending on how the toutouwai interprets the person in the MW throw task and the use of novel objects in the form of a trap in the banding task, the subject could be simply exploring their environment. When examining the other context where latency to acquire MW was measured, the foraging tray task, it is clear that this was likely an exploratory context as there was no real risk in the situation. Furthermore, there may be a bias in the individuals being tested as each context requires voluntary participation prior to a time limit being reached which may have been selected for only the boldest or most inquisitive individuals. Although failure to participate was very rare due to the characteristics of toutouwai this should be carefully considered if attempting recreation in another species. Overall the behaviour remained repeatable despite the potential for ambiguity in what personality facet was being measured across the contexts. The overall repeatability indicates that latency to acquire a MW represents a key aspect of an individual's personality as regardless of being measured in different tasks and contexts within

those tasks, it is consistently repeatable. Furthermore, it is such a simple behaviour to measure that it can easily be incorporated into current monitoring practices in toutouwai and taken from almost any behavioural task involving food rewards. Ultimately, further measurement of this behaviour and its relationship to toutouwai ecology is required to determine how useful it will be to conservationists as a personality measure.

#### Multiple behaviour tasks to measure personality

The only multi-behaviour task able to quantify personality through EFA was the nest disturbance task. The most likely reason the nest disturbance task was able to measure repeatability of behaviour and the foraging tray task did not come down to the intensity of stimulus provided during the task. The nest disturbance task was rather intrusive, while the foraging tray task was very passive. Identifying appropriately stimulating tasks will be particularly important for those planning on measuring the personality of wild animals due to the multitude of distractions natural environments provide to subjects. Suppose the stimulus is not engaging enough for the subject. In that case, they may return to behaviours they would otherwise be engaged in or be more easily distracted by other stimuli in their environment, making behavioural recordings during the task unreliable. In typical multi behaviour assessments of personality, participant engagement is less of a concern because individuals can be tested in captivity meaning individuals have nowhere else to go and are only provided stimuli to gain their attention (Allard et al., 2019; Germano et al., 2017; Hammond et al., 2021). In cases where there has been wild multi behaviour testing the stimuli used have been quite intense such as trapping or human handling (Arroyo et al., 2017; May et al., 2016), or where there as been passive observations of behaviour over long periods of time that lessens the importance of infrequent environmental stimuli (Hertel et al., 2019). Across these studies, there is also a wide variety of relationships with no universal findings, as discussed in Chapter 2. The impact of stimuli on personality tests should be further investigated. If very strong stimuli are required to record personality over short periods in the wild, only certain aspects of an animal's personality will be measured in that condition. Suppose more passive aspects of an individual's personality are not able to be reliably measured in the wild and can only be derived from captive measures. In that case, the meaningfulness of those aspects of personality for conservation purposes is questionable. Alternatively, if long time intervals between tests can mitigate the need for strong stimuli, initial sample sizes will need to be very high to account for a loss of subjects over time, and other environmental conditions may need to be taken into account such as time of the year i.e. breeding seasons. Overall, multi-behaviour personality

tasks are the most robust way of measuring personality (Carter et al., 2013; Dingemanse & Wright, 2020), but further experimentation with the effect of task stimuli is required.

#### Ecological validity of personality measures

The personality measures derived by this study were not correlated and are unrelated to any of the reproductive measures investigated. While it is clear there are differences between individual toutouwai in their latency to acquire a MW under various contexts, and in female nest defence behaviour, selection on these personality measures in relation to reproduction appears to be non-existent or contextually/environmentally constrained (McCowan et al., 2015). Because there is variation in the population, it may be that only under specific contexts/environmental conditions that this variation matters, with the Zealandia population currently existing under what could be considered 'normal' conditions. A test for this hypothesis would be to examine the same personality measures in a population undergoing increased invasive mammalian predation, ideally from a translocated population where personality measures could be taken under 'normal' environmental conditions. However, there may be other reasons why there was no relationship between the personality and reproductive measures of this study.

#### Nest boldness

The finding that nest boldness was unrelated to reproductive measures is surprising, as the behaviours measured during the task could be assumed to contribute to a successful nesting attempt. Toutouwai spends ~18 days incubating eggs and ~21 days with chicks in the nest (Armstrong et al., 2000). During this time, the offspring are vulnerable to predation, with the protection and provisioning of the nest entirely incumbent on the parents, primarily the female (Armstrong et al., 2000). Each of the behavioural measures that contributed to the nest boldness score, time spent and the number of occurrences within 30cm of the nest, time spent using broken wing behaviours and zones crossed are measures that indicate the degree of nest defence, i.e., more time spent trying to distract a potential predator by guiding it away from the nest. A potential explanation for the lack of relationship is that these behaviours are ineffective in deterring nest predation in this population; therefore, they are unrelated to nest failure. If true, how females respond to nest disturbance would not have a significant impact on reproductive measures.

The typical predators of toutouwai in Zealandia are New Zealand falcon/karearea (*Falco novaeseelandiae*) and Morepork/ruru (*Ninox novaeseelandiae*) with mice (*Mus musculus*) perhaps predating eggs from nests (Brown et al., 2008; Miskelly, 2018). The

behaviours exhibited by toutouwai in reaction to the mirror may not have reflected a female's type of behaviour to a known predator. In the closely related South Island robin/kakaruwai (*Petroica australis*), there is some evidence to suggest different degrees of the anti-predator response of adults is dependent on the type of introduced predator (Muralidhar et al., 2019), and other species have shown discrimination in anti-predator response to different nest predators (Olendorf & Robinson, 2008; Trnka & Prokop, 2012). If the nest boldness measured here is more of a generic response to disturbance rather than an actual predator response, this would explain the lack of a relationship. However, there is also a peculiarity with the Zealandia population that could contribute to the lack of a relationship. Zealandia has relatively large populations of several species in a small space (Miskelly, 2018), leading to interspecific interactions not observed before. There is evidence of agonistic interspecific interactions by several species on toutouwai nests including, several observations of kākā (*Nestor meridionalis*) taking eggs and/or destroying toutouwai nests, little spotted kiwi/kiwi pukupuku (*Apteryx owenii*) destroying toutouwai nests on the ground, and saddleback/ tīeke (*Philesturnus rufusater*) disturbing the nests of several toutouwai (pers coms). There is little to no sign of adult defence of the nest in each of the videos and observations associated with these events. Suppose these atypical events are more common than currently considered, and there is no effective defence the toutouwai can provide. In that case, this may also explain the lack of relationship between nest boldness and offspring production. Unfortunately, the proportion of nest failures caused by typical predators versus the proportion of nest failures caused by atypical species or environmental causes in this system cannot be known due to the difficulty in determining the reason for a nest being empty without remains being present or video of the event.

Nest boldness could be a beneficial measure for conservationists to incorporate into translocation procedures for toutouwai. I suspect that if the nest disturbance task were modified to use typical predator models and reproductive output measures analysed in a system where predator-induced nest failure can be accurately quantified, there would be a more direct relationship. An ideal test will be determining if the nest boldness scores of females prior to translocation predict reproductive output post translocation in a less predator-controlled environment. However, careful consideration should be given as this is a relatively invasive procedure, the time necessary to code and analyse video may be prohibitive without sufficient resources and there has been a lack of relationship to reproductive output in this study.

## Latency to acquire a MW

The measure of average latency to acquire a MW was also unrelated to reproduction in this population. While ostensibly a boldness measure, there is some ambiguity in what latency to acquire a MW relates to, perhaps being a measure of exploration instead. This ambiguity may explain why there was no relationship to reproductive measures in this population, as previous research with zebra finch (*Taeniopygia guttata*) with unclear personality tests also failed to show a relationship with reproduction (McCowan et al., 2015). Despite this explanation, there is reason to question why there would be an assumption of a relationship between boldness/exploration and reproduction in toutouwai. In this study, I measured a behaviour suspecting it to be a personality trait (latency to acquire a MW) and measured an important ecological variable (reproductive output), but there may not be a direct link or selection present. Instead, there may be intermediary behaviours or variables overlooked in this study that link personality to reproduction. For example, in fishing spiders' (*Dolomedes triton*), aggression is linked to fecundity through positive correlations between adult size, feeding rates and egg sac mass, not through a direct correlation (Johnson & Sih, 2005).

Overall, the lack of relationship between personality measures and reproduction in this study adds to the argument I started in Chapter 2 and emphasised by prominent reviews (Carter et al., 2013; Dingemanse & Wright, 2020; Réale et al., 2007) that we should not rely on findings from previous studies in other species when it comes to justifying why personality is important, that validating the ecological/physiological links to the species in question is the most appropriate way forward. Future examinations of personality, in general, should look to link behaviours that are repeatable during tasks, with ecologically important behaviours, alongside taking multiple measures for ecological validity rather than relying on the findings of previous work. A thorough examination of all reasonable potential relationships is required but should not go so far as to become data dredging. This will require researchers intimately familiar with their study systems developing hypotheses in conjunction with personality researchers. It is not enough to suggest the usefulness of personality for conservation. The only way it will truly work as a tool is to collaborate between those who know their system and those who know their personality.

## Recommendations for conservationists

This research reveals that it is possible to incorporate personality quantification methods into current management methodologies, with most of the extra burden coming from data gathering and statistical analysis. However, not every system will be able to adapt the

same procedures as I used with toutouwai, so what should conservationists who want to incorporate personality measures be looking for in their system? The first step would be to identify any points in their current management protocols where multiple observations of the same individuals are already being performed or contexts where multiple measures could be taken. Examples could include visits to feeders, entry/exit of hides (artificial or natural), capture for processing (health check-ups, blood draws), or visitation by researchers. In systems with more limited opportunities for direct observation (e.g., seabirds, elusive predators), it may be possible to deploy activity loggers like GPS systems to record behaviour. This may limit the type of personality able to be quantified in the system, but there are several examples of using movement tracking (logging the movement of animal behaviour over time/context) in combination with landscape analysis to quantify personality in several species (Bubac et al., 2018; Campioni et al., 2016; Hertel et al., 2019).

Once the opportunity for repeated observations has been established, the next step is to determine what behaviour(s) should be recorded. Ideally, this should be grounded in two factors: knowledge of the study species and how personality is quantified. Researchers/conservationists working within their system will likely know best when determining what behaviours can reliably be recorded and quantified and their ecological functions. What is less common knowledge is how personality is quantified, perhaps due to the myriad ways it has been done in the past. I suggest the pathway forward is to find personality researchers and actively collaborate with them. If this is untenable, conservationists should work to the guidelines outlined by Carter et al. (2013). This would involve thinking about the contexts where behaviours can be repeatably measured, the types of tests that could be used and the type of personality they might measure. What may seem like a simple observation could be representing a novel object test or a social interaction test. For example, feeding stations are areas where multiple individuals can visit and interact with each other; if the individuals can be identified and behaviours recorded, it may be possible to get individual measures of aggression. Alternatively, if a feeder is being upgraded or changed, the introduction of new features could represent a novel object test. Furthermore, altering the situations where repeated measures can take place can allow for changes in test type, which means the ability to measure different personality traits. For example, introducing a model predator to a foraging station or hide can alter the test from social interaction or open field test to a predator stimuli test, allowing for the measurement of boldness. Even in the rare case where a conservation context does not lend itself to complex personality quantification, repeated

measures of individuals over time may help track conservation interventions' effect and inform adaptive management. Next, conservation practitioners can consider what ecological variables are important from a conservation perspective (e.g., survival, reproduction) and what personality traits might reasonably be related to those measures. Through careful planning and consideration, personality measures can be simply and effectively implemented, creating the ability to improve conservation practice. Finally, determine the level of resources available that can be wasted on a potentially fruitless endeavour. Incorporating personality into conservation is not guaranteed to be successful, as demonstrated in this study, but will undoubtedly require hundreds of work hours to be methodologically appropriate. The largest time sink will be on coding videos of behaviour and on the statistical analysis side. If the project cannot sustain hundreds of hours of wasted time then it is not justified. Unfortunately, this will likely limit potential applications to conservation contexts in wealthier more resourced locations and where risk-taking can be better tolerated i.e. not in critically endangered species. Hopefully, work in these less critical areas can later be translated to where findings may be of more use.

## Conclusion

Incorporating personality into already established conservation management strategies is complex and does not necessarily require a massive increase in resources. This research shows that single and multi-behaviour tasks can be incorporated directly into already established management protocols and produce robust, if ambiguous, personality measures. Despite the ambiguity and lack of ecological validity, latency to acquire a MW measure and the nest disturbance task be incorporated into standard monitoring and translocation procedures for toutouwai due to their relative ease of implementation. While considering the broader conservation landscape, it is difficult to suggest that all conservationists immediately implement something similar in their context. The ecological function of personality is what makes personality a tool for conservationists; without ecological links, then no matter how easy or little impact the steps recording personality are, it will increase costs. Conservationists should not risk wasting resources until there are tangible benefits; however, behaviourists may be freer to fail. A collaborative approach where behaviourists can investigate the ecological function of personality measures alongside the typical conservation management of the species may be able to bridge the gap. However, conservationists know their systems better than any outsider. It may be worth the extra investment of incorporating personality prior to the ecological function being pinned down for the benefit of having the data to look back on. Ultimately, I would not encourage conservationists to consider implementing personality into



their management without the prior establishment of meaningful ecological validity and only doing so if there is no or negligible increase in expending resources as with toutouwai.

## Chapter 4: Integration of animal personality to in situ anti-predator training

### Abstract

Anti-predator training is a behavioural tool developed to train naïve animals about predators they will face upon release after a translocation. There has been mixed success of anti-predator training as a tool generally and little implementation in wild contexts, i.e., *in situ*. In situ applications of anti-predator training could benefit from incorporating animal personality, allowing for more individualised analysis of success, or as additional variables for analysis with other measures of concern for conservationists. The New Zealand mainland island system and toutouwai that occupy many of these islands make for an ideal system to study the integration of animal personality to in-situ anti-predator training. I subjected a population of 21 toutouwai to an in-situ antipredator training program also designed to be used as a method for quantifying personality at Zealandia, a mainland island in Wellington, New Zealand. The anti-predator training protocol was not successful in eliciting the desired behavioural changes in toutouwai. However, I robustly quantified the personality traits of boldness and exploration from that training protocol. I found that an individual's exploration score did predict the change in behaviour associated with vigilance after training, but not any other behaviour. Furthermore, an individual's boldness score was not related to this vigilance behaviour, or indeed any other. This result contradicts previous findings and the expectation that boldness should be associated with a test that elicits risk-taking. Overall these results may be explained by problems with the anti-predator training protocol, and broader issues with how personality is generally studied. This study provides a proof-of-concept template for further research, provides evidence that personality can be incorporated within other behavioural tools, and provides discussion on the limitations of personalities usefulness in conservation.

## Introduction

At the end of the last century, behavioural ecology began to have a more prominent role in conservation biology (Anthony & Blumstein, 2000; Caro, 1999; Martin, 1998). Behavioural ecology is a key component of modern conservation biology research (Buchholz, 2007; Caro & Berger, 2019; Greggor et al., 2014a, 2016; Tobias & Pigot, 2019). Insights from behavioural ecology can solve complex problems, such as reducing human imprinting in captive-reared animals (Greggor et al., 2014a), improving the design of artificial refugia, e.g., burrows (Ebrahimi et al., 2012), and predator-proof fences (Connolly et al., 2009), alongside informing researchers of the impact human activity has on many species (Caro, 2016). However, examples of applying behavioural tools for conservation in wild contexts, i.e., in situ, are relatively limited compared to applications of tools in captivity, i.e., ex situ (Caro, 2016; Greggor et al., 2014a). For example, captive breeding and translocation programs are ex-situ contexts where the uses of behavioural tools such as enrichment stimuli, pre-release foraging/predator training, and behavioural selection for mating/release purposes are part of many conservation management plans (Armstrong et al., 2015; Caro, 2016). Alternatively, behavioural tools that apply to in situ contexts where animals are not brought into captivity, such as habitat fragmentation, exploitation, pollution, invasive species, and climate change, exist but are not common (Caro, 2016). Some notable examples include in situ taste aversion training of lizards (*Varanus panoptes*) to avoid eating invasive deadly cane toads (*Rhinella marina*) (Ward-Fear et al., 2016) and, optimisation of lighting fixtures to avoid the ecological trap of flight-to-light behaviours in mayflies (*Ephoron virgo*) (Mészáros et al., 2021).

One conservation sector that may benefit from implementing in situ applications is mainland island conservation projects (Innes et al., 2011). Mainland islands are a common conservation method across Australasia, being relatively common in New Zealand (Innes et al., 2011; Russell et al., 2015). Derived from offshore island conservation, mainland islands encompass an attempt to mitigate habitat fragmentation and the effect of invasive species (Innes et al., 2011). To limit the effects of predator naivety on native species, established or restoring native habitat is selected for intensive predator trapping/removal and habitat improvement (Innes et al., 2011; Scofield et al., 2011), creating an island in the landscape analogous to an offshore conservation island. These sites are sometimes surrounded by lower priority, lower quality systems where wildlife that has been translocated to the main reserve is expected to grow in size and eventually disperse in what is often described as a 'Halo' effect. Beginning with small populations of remnants and individuals translocated from other areas,

older mainland island sites are now seeing success with dispersing species into surrounding 'Halos' where they have been regionally extinct for decades (Linklater et al., 2018; Miskelly, 2018). However, dispersing animals face a significant challenge moving from highly protective to much riskier environments over small or physically non-existent barriers (Woolley & Hartley, 2019).

A tool sometimes used when translocating conservation dependent animals to an environment with threats is aversion training (Greggor et al., 2019; Griffin et al., 2000; Moseby et al., 2015; Snijders et al., 2021). Aversion training techniques are derived from classical conditioning experiments (Greggor et al., 2019; Griffin, 2008; Griffin & Evans, 2003; Kershenbaum, 2017). Under an aversion training regime, a subject is trained to associate a conditioned (neutral) stimulus with an unconditioned (known) stimulus to change the behaviour of the subject toward the neutral stimulus (Griffin et al., 2000; Kershenbaum, 2017). There are several forms of aversion training, but the most well known and most applied in translocations is anti-predator training (Greggor et al., 2019; Griffin et al., 2000; Rowell et al., 2020; Snijders et al., 2021). Anti-predator training conditions animals to respond adversely to a co-evolved or novel predator by pairing a predator model with an aversive unconditioned stimulus such as physical pain, chasing or alarm calling in captivity (Griffin et al., 2000; Rowell et al., 2020). The typical justification for this type of training is that captive-reared animals are not exposed to predatory situations during their development or are separated from the knowledge pathway their parents would typically provide and are therefore naïve to potential predators (Greggor et al., 2019; Griffin et al., 2000; Kershenbaum, 2017). However, the same is true for species on mainland islands, as protected populations cannot learn about the invasive predators (Muralidhar et al., 2019).

Native species in Australasia are naïve to the many mammalian predators that have been introduced into the region (Holdaway, 1999; Moseby et al., 2015). It has been hypothesised that in situ anti-predator training techniques could be used on these naïve species (Moseby et al., 2015; Rowell et al., 2020), and there is some evidence to support the claim from both model and live predators (Maloney & McLean, 1995; McLean et al., 1999; Moseby et al., 2012; Ross et al., 2019; West et al., 2018). The use of free-roaming live predators in the form of cats under semi-controlled conditions appears to be a possible strategy in the context of Greater Bilby's (*Macrotis lagotis*) (Ross et al., 2019) and Burrowing Bettongs (*Bettongia lesueri*) (Moseby et al., 2018) in Australia. However, New Zealand's historical near-complete lack of mammals (with the exception of bats and sea mammals) means there is no evolutionary

template for endemic birds recognising cats as predators, and a similar experiment would be ethically dubious (Innes et al., 2011; Rowell et al., 2020; Walker et al., 2017). However, training animals in situ using model predators may provide a happy medium between using live predators for in situ and ex-situ aversion training. The ethical considerations and potential community-wide implications of releasing a predator into a mainland island can be avoided while not requiring the expense and disturbance that extracting individuals to captive facilities for ex-situ training would require (Moseby et al., 2015, 2018; Rowell et al., 2020). If shown to be successful such in situ training could be incorporated into the pre-existing infrastructure of New Zealand's mainland island programs and prepare dispersers for the threats they will face over the fence. Implementing anti-predator training in situ on New Zealand's mainland islands offers a solution for conservationists who want to provide the best opportunities to disperse animals while considering available resources and animal welfare.

Some of the earliest in situ anti-predator training of mammalian predator-naïve animals were conducted on the South Island robin (*Petroica australis*; hereafter referred to by Māori name as kakaruwai)(Griffin et al., 2000). Two training regimes were implemented; the first trained female kakaruwai to respond to stoats (*Mustela erminea*)(Maloney & McLean, 1995), and the second trained juvenile kakaruwai to respond to stoats and domestic cats (*Felis catus*) as predators (McLean et al., 1999). Both studies were deployed during the breeding season, utilised in-situ anti-predator training phases and were successful in training naïve animals to elicit comparable behavioural responses to animals naturally co-occurring with stoats (Maloney & McLean, 1995; McLean et al., 1999). However, both examined the efficacy of their training over brief periods (one to three days) and did not use a within subject's design to examine the change in response of trained animals, but instead examined the difference between trained and untrained groups. Furthermore, related research in kakaruwai has shown that individuals exposed to introduced mammalian predators can learn that these introduced species are pests when cohabitating over several generations, but this recognition can be lost rapidly when isolated from the predators (Jamieson & Ludwig, 2012; Muralidhar et al., 2019). This indicates that kakaruwai can learn to interpret mammals as threats provided there is an associated negative stimulus.

Another approach to in situ anti-predator training would be to examine the within-subject behavioural change from before training to after, as this would more directly quantify the effect of training than a comparison to a naïve or untrained population (Greggor et al., 2019). Additionally, testing the maintenance of this training over more than a few days would

aid in assessing the efficacy of this type of protocol for conservation (de Faria et al., 2020; Maloney & McLean, 1995; McLean et al., 1999). There is no use in expending resources training animals if the training wears off after a matter of a few days, the training needs to be remembered until a real-world encounter with the trained predator. Furthermore, directly testing individual adults outside of the breeding season may reduce potential confounds, such as heightened predator response or social learning in previous regimes (Maloney & McLean, 1995; McLean et al., 1999). Using adults outside the breeding season will have further benefits as training times will depend less on specific time points in the breeding season or interfere with reproduction, allowing more freedom in protocol design and potentially less resource cost being taken away from standard breeding season monitoring. Finally, designing a protocol in such a way that accounts for potential differences in how individuals respond to stimuli may help interpret the results of an aversion training protocol or even broader aspects of a species ecology (Brooker et al., 2016; de Azevedo et al., 2017; Lopes et al., 2017; McDougall et al., 2006; Merrick & Koprowski, 2017; Moseby et al., 2012; Ward-Fear et al., 2018).

Behavioural ecologists quantify the differences between individuals and report on the potential consequences of these differences under the term animal personality (Carter et al., 2013; Dingemanse & Wright, 2020). Most recently defined as 'among-individual variation in average behaviour across repeated observations' (Dingemanse & Wright, 2020), animal personality has been argued to be important for conservation in several reviews (Biro & Stamps, 2008; Brooker et al., 2016; Buchholz, 2007; McDougall et al., 2006; Mittelbach et al., 2014; Roche et al., 2016; Smith & Blumstein, 2008). There has been a broad application of personality-based research in conservation contexts, but much of that research has been poorly executed from a personality standpoint (Chapter 2). However, some of the most rigorous examples suggest that understanding the personalities of individuals could have tangible and meaningful results for conservation management decisions (Chapter 2). For example, researchers working on Blanding's turtle's (*Emydoidea blandingii*) translocation found that personality assessments made prior to translocation were related to differential survival and behaviour patterns post-release (Allard et al., 2019). More explorative individuals were more likely to survive and travel longer distances. At the same time, bolder turtles were more likely to be basking at the surface of the water, notably increasing their predation risk. Moving forward, personality information could be used to pre-screen individual turtles, improve the outcome of their translocation procedures, and maximise individual animal welfare (Allard et al., 2019). Studies employing less rigorous personality assessments have also demonstrated

that personality information may help inform aversion training programs in two species of birds (de Azevedo et al., 2017; Lopes et al., 2017; Paulino et al., 2018) and a lizard (Ward-Fear et al., 2020). Ultimately, despite the need for more robust personality assessment in conservation contexts, there is evidence that personality information can improve the outcomes of traditional conservation management (Chapter 2) and perhaps aversion-based tools (de Azevedo et al., 2017; Lopes et al., 2017; Paulino et al., 2018; Ward-Fear et al., 2020).

Zealandia is a 225ha mainland conservation island with a mammal-proof fence in the suburbs of Wellington, New Zealand (Miskelly, 2018). The wildlife populations in Zealandia have matured to the extent that several endemic species have begun to spill over into surrounding areas outside the mammalian predator-proof fence (Linklater et al., 2018; Miskelly, 2018). Prior to dispersal animals in Zealandia have no way of learning about introduced predators that exist outside the fence, such as rats (*Rattus sp.*), mustelids (*Mustela sp.*) and a relatively large population of domestic cats (*Felis catus*) resulting from the proximity to human dwellings (Woolley & Hartley, 2019). One way to ensure the welfare of wildlife dispersing from Zealandia and prepare them for the introduced mammalian predators outside the sanctuary would be to subject them to in situ anti-predator training. One of these dispersing species is the North Island robin (*Petroica longipes*; hereafter referred to by its Māori name toutouwai), a close relative of the kakarawai. This system presents an ideal opportunity to test if an in situ anti-predator training protocol can be performed in conjunction with personality quantification in a conservation sector where such tools will eventually be implemented.

I had three distinct goals in this study. First, I assessed the effectiveness of an in situ anti-predator training protocol in wild toutouwai using a taxidermy cat. Second, I examined if reframing the anti-predator training protocol as an animal personality framework can enable robust and valid quantification of personality in toutouwai. Finally, I examined whether personality traits influence how an individual responds to anti-predator training.

## Methods

### Study site & species

Toutouwai have been resident in Zealandia since translocations in 2000 and 2001, with the population steadily increasing from 76 birds to between 500-765 birds by 2009 (McGavin, 2009). A research population of individually colour banded individuals has been operating consistently since 2014 (Shaw et al., 2015) in an approximately 25 ha location and has been subject to extensive cognitive testing (Clark & Shaw, 2018; MacKinlay & Shaw, 2019; Shaw, 2017; Shaw et al., 2015, 2019; Shaw & Harvey, 2020; Shaw & Schmelz, 2017). Therefore, to

avoid potential confounds of repeated behavioural testing, an adjacent banded population was established in 2018. This new research population was directly adjacent to the previous, approximately the same size but closer to the sanctuary fence line. The management of this population followed previously established protocols (Powlesland, 1997a; Shaw et al., 2015), with the caveat of limiting interaction with the animals as much as possible. This study took place between May 2020 and March 2021.

Prior to presenting the anti-predator training protocol to individuals, the research area was surveyed and toutouwai territories were identified by observing the animals' behaviour, including height of perch in the canopy, interactions with conspecifics and time spent on the ground foraging. I chose the optimal location for testing within these territories, considering the centrality of the territory, distance from public pathways, and ground flatness. In all but one case (due to territory boundaries shifting), the same location was used for all conditions and trials for the same individual. Twenty-six individuals were assessed throughout this study ( $N_{\text{males}} = 19$ ,  $N_{\text{females}} = 7$ ). However, only twenty were able to be retested thoroughly post-training ( $N_{\text{males}} = 17$ ,  $N_{\text{females}} = 3$ ) due to interference from conspecifics in the case of females and failure to arrive within an hour in the case of the males. All statistical analyses were performed using RStudio (RStudio Team, 2021).

#### Permissions/Animal Ethics

The initial survey was conducted after New Zealand's first COVID-19 national self-isolation, which lasted between 25<sup>th</sup> March and 27<sup>th</sup> April 2020 under 'Alert Level 3' conditions (M. G. Baker et al., 2020) with approval by Victoria University of Wellington and Zealandia, following all additional Health & Safety requirements. The anti-predator protocol was performed under COVID-19 'Alert level 1' conditions. This study was approved under Victoria University of Wellington Animal Ethics Committee AEC26212, performed under the New Zealand Department of Conservation Wildlife Authority 69292-RES, and with the permission of Zealandia's Conservation and Research Manager.

#### Anti-predator training procedures

The anti-predator protocol consisted of five test conditions (summarised in Fig. 6. a, b, c, d), with subjects given two trials per condition. The test conditions consisted of reveal only (reveal condition), novel object reveal (pillow condition), initial cat reveal (cat condition), aversion training (training condition), trained cat reveal (trained condition). Reveal condition was just the reveal mechanism itself, which consisted of quickly pulling a camouflage pattern tarpaulin back (Fig. 6a). In pillow condition, a pillow with a grey and black cover of similar



size and shape to a domestic cat was revealed when the tarpaulin was pulled back (Fig. 6b). Cat condition revealed an ethically sourced taxidermy black and grey coated cat (Fig. 6c). Training condition revealed the cat model again and also paired it with an unconditioned stimulus of a conspecific alarm call played from a grey UE Boom 2 Bluetooth speaker (Ultimate Ears, Irvine, CA, USA) hidden under the taxidermy cat (Fig. 6d). The trained condition consisted of the final trained cat reveal, using the same taxidermy cat (Fig. 6c). The apparatus setup procedure was the same across all conditions. I arrived at the predetermined location within the subject's territory. Without trying to attract the subject, I positioned two metallic fence posts approximately 1m apart. In between these posts, I cleared the area of large debris and placed a camouflage print piece of tarpaulin  $\sim 50\text{cm}^2$  that had several meters of nylon string attached to each corner.

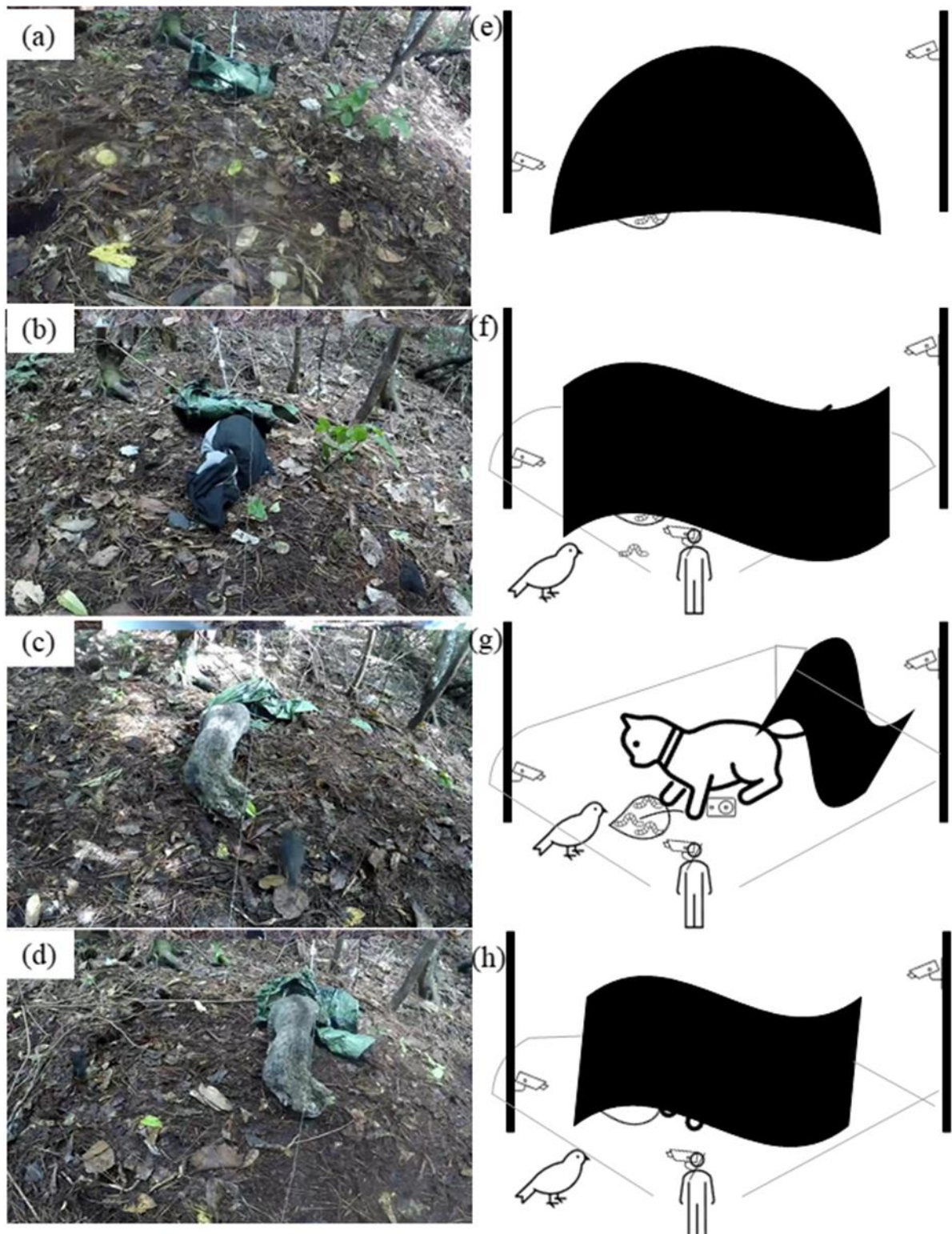


Fig. 6. The anti-predator testing conditions are represented by figures a-d, and the anti-predator set-up and reveal protocols are represented by e-h. (a) screenshot of the reveal condition. (b) screenshot of the pillow condition. (c) screenshot of the cat condition, which is also representative of the post-training condition. (d) screenshot of the training condition, note the speaker cannot be seen as it is underneath the cat. (e) the experimental set-up being set in place underneath a blanket to ensure toutouwai could not see the condition. (f) the pre-reveal set-up and enticement of the subject with a mealworm. (g) the reveal set up for the training condition, the only difference between conditions being what was underneath the cover. (d) the post-reveal set-up.

If applicable, I placed the object for the condition on the ground between the posts, underneath a black bedsheet, so it was out of sight of the subject while I positioned the tarpaulin over the object (Fig 6e). I then wrapped the nylon around the fence posts and unwound the nylon from either end of the tarpaulin to my observation position ~2-3m from the tarpaulin in direct eyesight and downhill if possible. I then returned to the tarpaulin, packed away the bedsheet and positioned two GoPro Hero4 (GoPro, Inc, San Mateo, CA, USA) on the fenceposts, one at the base of the post, the other mid-way up to capture a wider angle. The position of these cameras remained the same across all trials for an individual. I then killed three mealworms (*Tenebrio molitor*; hereafter MW) under the sheet and placed them on an upturned green leaf. In reveal condition, the MW were placed ~30cm from the fencepost with the lowest GoPro. In pillow condition, the MW were placed ~30cm from the fencepost on the side of the pillow that would be visible from my observation position. For conditions three, four and five, the MW were placed at the base of the cat's paw, which was ~30cm from the fencepost on the side that would be visible from my observation position. The subject was usually present at this point, but if not, I attracted the subject by clapping.

Once the subject was present, I started recording on the two-fencepost mounted GoPros and a GoPro mounted on my head. I then moved to the observation position and acquired the subject's attention by clapping and holding a MW between my index finger and thumb pointed at the subject. Once I was confident, I had the subject's attention. I then threw a MW as close to the position of the covered MW as possible, trying to avoid hitting the tarpaulin itself (Fig. 6f). This was to ensure the subject would be in the best position to see what was being revealed. Once the subject acquired the thrown MW, I pulled on the nylon string to pull back the tarpaulin, revealing an object in conditions 2-5 (Fig. 6g). The time taken for the reveal averaged  $3.206 \pm 3.352$  seconds. Once the tarpaulin had been pulled back, I began a timer. After one minute, the tarpaulin was reset back to its original starting position by pulling the nylon attached to the ends of the tarpaulin (recovering the object, if applicable) (Fig. 6h). The observation period then continued for five minutes post-reveal. At the end of the post-reveal period, I packed up the object, ensuring that I was out of sight of the subject.

The anti-predator protocol was administered between 09/07/2020 and 13/09/2020, between 0900 and 1500. Conditions 1-4 were administered on consecutive days, with a morning and an afternoon trial of the same condition occurring on the same day. To facilitate testing each subject twice within a day, a maximum of five individuals were tested per day. After all, 26 individuals had completed conditions 1-4 I returned to administer the trained

condition for the 21 subjects that remained in the study area or had not yet partnered for the breeding season. The minimum time that had elapsed between the training condition and the trained condition was 20 days, and the maximum was 52 days.

For each trial ( $N_{trials} = 246$ ), the videos from all three GoPros were combined and synchronised into a single video using DaVinci Resolve 16 (Blackmagic Design Pty Ltd, Port Melbourne, VIC, AU). Behaviours were coded at a frame-by-frame resolution using the open-source Behavioral Observation Research Interactive Software or BORIS (Friard & Gamba, 2016). The acquisition of a MW and consumption of a MW were coded as single events, respectively. State events were used to capture the duration in seconds and frequency of other behaviours. This included the time that a subject spent with head up, head down, perching, hopping, flying and the distance of the subject from the apparatus. The distances were classed into three categories: close range ( $\leq 50$  cm radius from the centre of fenceposts), medium-range (ca. 1 m from the centre point of fence posts) and far range ( $> 1$  m from the centre point of fence posts) from the apparatus. On the rare occasions that an individual could not be seen in any video frame, no state other than time spent at the far range was recorded.

I used previous anti-predator research to guide my selection of behavioural indicators for assessing the impact of the anti-predator training. Previous research on the closely related kakaruwai indicates that toutouwai reacting to a threat should decrease their time spent close to a predator model, have an increased latency to acquire food next to a predator model, and spend more time perched (Jamieson & Ludwig, 2012; Maloney & McLean, 1995; McLean et al., 1999; Muralidhar et al., 2019). In addition, studies in more distantly related species suggest that an animal reacting to a threat should spend less time with its head down, as this represents a state of decreased vigilance (Bednekoff & Lima, 2005; Quinn et al., 2006; Lima & Bednekoff, 1999; Tisdale & Fernández-Juricic, 2009).

Prior to determining if there was an effect of the training condition on the behavioural measures, I assessed if there was habituation or sensitisation to the reveal process (movement of tarpaulin) across conditions one, two or three (reveal, pillow & cat). This was important to ensure that I was measuring reaction to the object presented rather than the reveal itself. Initially, I assessed the effects of trial, condition, and the interaction of trial & condition on each of the behavioural measures described above (time spent in close range, latency to acquire MW, time perching and time with head down) using a Two-Way Repeated Measures Analysis of Variance (ANOVA). However, all of the response variables contained outliers, and residuals were heteroscedastic. Therefore, I instead utilised Aligned Rank Transformation (ART),

allowing for non-parametric Two-Way repeated measures ANOVA analysis (Wobbrock et al., 2011). Post-hoc analysis of each ART-ANOVA that showed an effect of trial and or condition was performed using ART Contrasts (ART-C) (Elkin et al., 2021). This same process, as described above, was used to assess the effect of training (cat condition vs trained condition) and assess the conspecific alarm call as an unconditioned stimulus (cat condition vs training condition). All ART and ART-C analyses were performed using the ARTool package in R (Kay et al., 2021).

#### Assessing personality during anti-predator training

In order to quantify personality in this study, I re-examined the anti-predator training protocol described in detail above through a personality framework (Carter et al., 2013; Dingemanse & Wright, 2020; Réale et al., 2007). Under a personality framework trials, 1 and 2 in reveal condition (reveal only) approximate a startle test. A startle test presents a stimulus to a subject that could be perceived as threatening (Yuen et al., 2017); in this case, the quick reveal of the tarpaulin cover could be perceived as threatening. To approximate a novel object test, I used trial one in pillow condition (novel object reveal) and trial one in cat condition (initial cat reveal), as a novel object test presents an unknown object to a subject (Carter et al., 2013; Réale et al., 2007). To approximate a threat stimuli test, I used trials 1 and 2 in training condition (aversion training), as a threat stimuli test presents an aversive stimulus to a subject (Carter et al., 2013; Réale et al., 2007). To approximate an open field test, I used the six trials from the reveal, pillow and cat conditions, focusing on the 5 min period after the initial reveal had already occurred and the tarpaulin put back in place. This was done because an open-field test presents an area for a subject to explore freely, without stimuli (Carter et al., 2013; Réale et al., 2007; Yuen et al., 2017). Training condition (aversion training) was excluded from the open field test approximation due to some evidence in this study that the conspecific alarm call had lasting effects on behaviour even after it had stopped playing. For each personality test, I recorded the latency to acquire the first MW, time spent within 50cm of the object, time spent >1m from the object, time spent with head down, time spent moving (hopping + flying), and zones crossed (sum of distance categories occurrences). However, for the open field test, I omitted the latency to acquire the first MW (as no MWs were present).

Following Réale et al.'s (2007) definitions of personality traits, the startle and threat tests constitute contexts where there is a potential risk to an individual, meaning the personality trait of 'boldness' can be measured. By contrast, the novel object and open field tests represent contexts where 'exploration' can be measured. Alternatively, there may be overlap wherein one

of these test types may simultaneously be influenced by and measure two or more personality traits simultaneously (Carter et al., 2013). For example, the personality trait 'activity' as it reflects the general level of activity of an individual (Carter et al., 2013; Réale et al., 2007) may be measurable in both a threat test and a novel object test regardless of the context of the tests. Therefore, for each test type (startle, threat, novel object, and open field), behavioural measures included in factor analysis and expected personality trait alignment(s) were summarised with these two frameworks in mind prior to conducting statistical analysis (Table 14).

Initially, for each of the personality tests described above, the repeatability of every behavioural measure was assessed across trials and within each subject using intraclass correlation coefficient (ICC), following the guidelines of (Nakagawa & Schielzeth, 2010). Agreement repeatability was used for the startle, novel object and threat stimuli tests as there were only two trials. In contrast, adjusted repeatability was used for the open field test, with trial as a fixed factor. Behaviours with positive and statistically significant ICC values were then selected for Exploratory Factor Analysis (EFA). EFA was chosen over the more common PCA as EFA is far more appropriate for identifying latent, unobservable constructs like personality (Budaev, 2010). Although EFA guidelines typically suggest sample sizes > 100 are necessary, this is not empirically based. Much smaller sample sizes can be used provided communalities of variables & factor loadings are high (Allard et al., 2019; Budaev, 2010). A great deal of caution was applied to ensure the appropriate use of EFA when analysing the variables, selecting only those behaviours that had positive ICC values from across the range of tests used while avoiding highly auto-correlated variables. Additionally, behaviours were required to have relatively high communalities (>0.4) and factors loadings > 0.7 (Budaev, 2010). Prior to running the EFA, a subject's behavioural measures were averaged across the trials of each personality test and log-transformed to better approximate a normal distribution. Using the EFATools package in R (Steiner & Grieder, 2020), the data were structured into a correlation matrix and tested using the Kaiser-Meyer-Olkin Measure of Sampling Adequacy (0.789) and Bartlett's Test of Sphericity ( $X^2_{(105)} = 398.55$ ,  $p = <0.001$ ) to ensure it was appropriate to proceed with the EFA. Kaiser-Meyer-Olkin statistic is a measure of the proportion of variance among variables that might have common variance, while Bartlett's sphericity test determines whether all correlations are zero (Budaev, 2010). KMO values greater than 0.6 are considered adequate, and suitability improves as the statistic approaches 1, so a value of 0.789 indicates this matrix is suitable for factor analysis (Budaev, 2010). In this case, Bartlett's test of sphericity rejects the null hypothesis that all correlations are zero,

indicating the matrix is suitable for factor analysis (Budaev, 2010). Behaviours were then loaded into the EFA using Principal axis factoring, as suggested when data violate assumptions of normality (Yong & Pearce, 2013). The number of factors was based on Parallel Analysis using simulated random data sets, and eigenvalues  $>1$ , with a two-factor solution, was confirmed by analysis of the scree plot. The first iteration of the FA had behaviours from the startle and novel object tests with low communalities and factor loadings of  $<0.7$ . These measures were then removed from the dataset, Kaiser-Meyer-Olkin and Bartlett's tests re-run ( $0.826$ ;  $X^2_{(36)} = 226.64$ ,  $p = <0.001$ ), and factor solution was reconfirmed as two-factor and performed with varimax rotation. Factor scores were then calculated for each subject using the Bartlett method, enabling unbiased comparison across factors (Yong & Pearce, 2013).

To determine if personality influenced the outcome of the training protocol, I examined if there was a relationship between factor scores related to personality and the change in behaviour between the final time that a subject saw the cat model before receiving training and the first time it saw the cat model again after training was complete. I, therefore, used the behavioural responses in trial two of the cat condition (initial cat reveal) as a baseline and examined the relative change in the responses in trial one of the trained condition (trained cat reveal).

Having re-examined the anti-predator training protocol through a personality framework, it is possible to test if personality influences anti-predator training uptake. However, the latency to retest the subject after training may have contributed to changes in behaviour as much as personality traits, so I utilised multimodal averaging to determine what the most likely predictor(s) were for the change in behavioural responses post-training. The behavioural responses measured were time spent perching (Perch), time spent with head down (Head Down), latency to acquire the first MW (Acquire MW) and time spent within 50cm of the object (Close). A global model was constructed for each behavioural measure. The behaviour was the dependent variable, and the boldness factor score, exploration factor score, and latency between training and retesting were the predictor variables. Global models were constructed for each of the four behaviours used to determine training success; time spent perching, time spent with head down, latency to acquire mealworm, and time spent close. Dependent variables were Yeo-Johnson transformed to meet the assumptions of linear models. Using the dredge function in the MuMIn package (Bartoń, 2020), the models were evaluated using Akaike Information Criterion corrected for small sample sizes (AICc) to determine the most likely model. Model rankings, information and relative weights were then extracted and

summarised.

## Results

### Anti-predator training procedures

Overall, there was no evidence of sensitisation to the reveal mechanism itself. There was no consistent decrease in time spent with head down, time spent perching, time spent close or increase in latency to acquire a MW over the first three conditions. Accordingly, across all behavioural measures, there was no interaction between trial and condition (Table 12). The only behaviours that provided evidence for sensitisation or habituation were latency to acquire a MW and time spent close (Fig. 7a, b). There was a decrease in the amount of time spent close between the reveal and pillow conditions, indicating sensitisation to the pillow (Table 13). This indicates that the novel pillow was recognised as being different from the reveal mechanism alone, but this relationship did not carry through to the cat condition. Evidence for habituation is greater than that for sensitisation. Latency to acquire a MW decreased between pillow condition trial one & cat condition trial two and across the cat condition trials, which may indicate the pillow was being perceived similarly to the cat initially and then habituated to the cat, leading to a more rapid approach to acquire the MW.

Finally, there was a decrease in time spent close between reveal condition trial one & pillow condition trial one (Table 13), probably driving the overall difference seen between these two conditions generally described as sensitisation above. This result can be ignored as meaningful as the second pillow trial showed increased time spent close to being no different from the second reveal trial. No other behaviour or trial had an effect. Overall, there is weak evidence to indicate there was sensitisation during the first three conditions of the experiment, with more substantial evidence to support habituation to the cat model. Ultimately, these results show that the pillow was probably perceived as different than the reveal mechanism alone, indicating it was sufficient as a novel object. Moreover, the cat model was probably not perceived as being different from the pillow and was quickly habituated to indicating no latent perception of cats as predators in the population and supporting the idea that the cat model represents a novel predator.



Table 12. Two-way repeated measures ANOVA results of Aligned Ranked Transformed (ART) behaviours across conditions during the anti-predator training protocol. Model Reveal vs Pillow vs Cat was used to determine if there was habituation and/or sensitization to the experimental apparatus. Model Cat vs Trained was used to determine the effectiveness of the training on modifying behaviours. Model Cat vs Training was used to determine if there was any effect on behaviours during the training condition relative to the cat condition. Degrees of freedom (DF), Residual degrees of freedom (DFr), F value (F) and P value (P) are reported. Significant results are in bold.

Model	Behaviour	Model term	Df	Df r	F	P
Reveal vs Pillow vs Cat (Habituation + Sensitisation to the experimental apparatus)	Latency to Acquire MW	Condition	2	115	2.566	0.081
		<b>Trial</b>	<b>1</b>	<b>115</b>	<b>4.130</b>	<b>0.044</b>
		Condition:Trial	2	115	2.266	0.108
	Duration Close	<b>Condition</b>	<b>2</b>	<b>115</b>	<b>7.337</b>	<b>0.001</b>
		Trial	1	115	0.871	0.352
		Condition:Trial	2	115	2.896	0.059
	Duration Perching	Condition	2	115	1.545	0.217
		Trial	1	115	2.259	0.135
		Condition:Trial	2	115	0.153	0.857
	Duration Head down	Condition	2	115	2.133	0.123
		Trial	1	115	0.033	0.796
		Condition:Trial	2	115	0.533	0.588
Cat vs Trained (Training effectiveness)	Latency to Acquire MW	Condition	1	57	0.994	0.322
		Trial	1	57	2.675	0.107
		Condition:Trial	1	57	0.117	0.732
	Duration Close	Condition	1	57	0.205	0.652
		Trial	1	57	0.243	0.623
		Condition:Trial	1	57	0.000	0.989
	Duration Perching	Condition	1	57	0.560	0.457
		Trial	1	57	0.582	0.448
		Condition:Trial	1	57	0.746	0.391
	Duration Head down	Condition	1	57	0.142	0.707
		Trial	1	57	0.001	0.990
		Condition:Trial	1	57	0.181	0.671
Cat vs Training (Alarm call assessment)	Latency to Acquire MW	<b>Condition</b>	<b>1</b>	<b>72</b>	<b>6.825</b>	<b>0.010</b>
		<b>Trial</b>	<b>1</b>	<b>72</b>	<b>6.069</b>	<b>0.016</b>
		Condition:Trial	1	72	3.122	0.081
	Duration Close	Condition	1	72	1.191	0.278
		Trial	1	72	2.616	0.110
		Condition:Trial	1	72	0.025	0.874
	Duration Perching	Condition	1	72	0.513	0.476
		Trial	1	72	1.799	0.184
		Condition:Trial	1	72	0.018	0.891
	Duration Head down	Condition	1	72	0.464	0.497
		Trial	1	72	1.220	0.260
		Condition:Trial	1	72	0.862	0.356

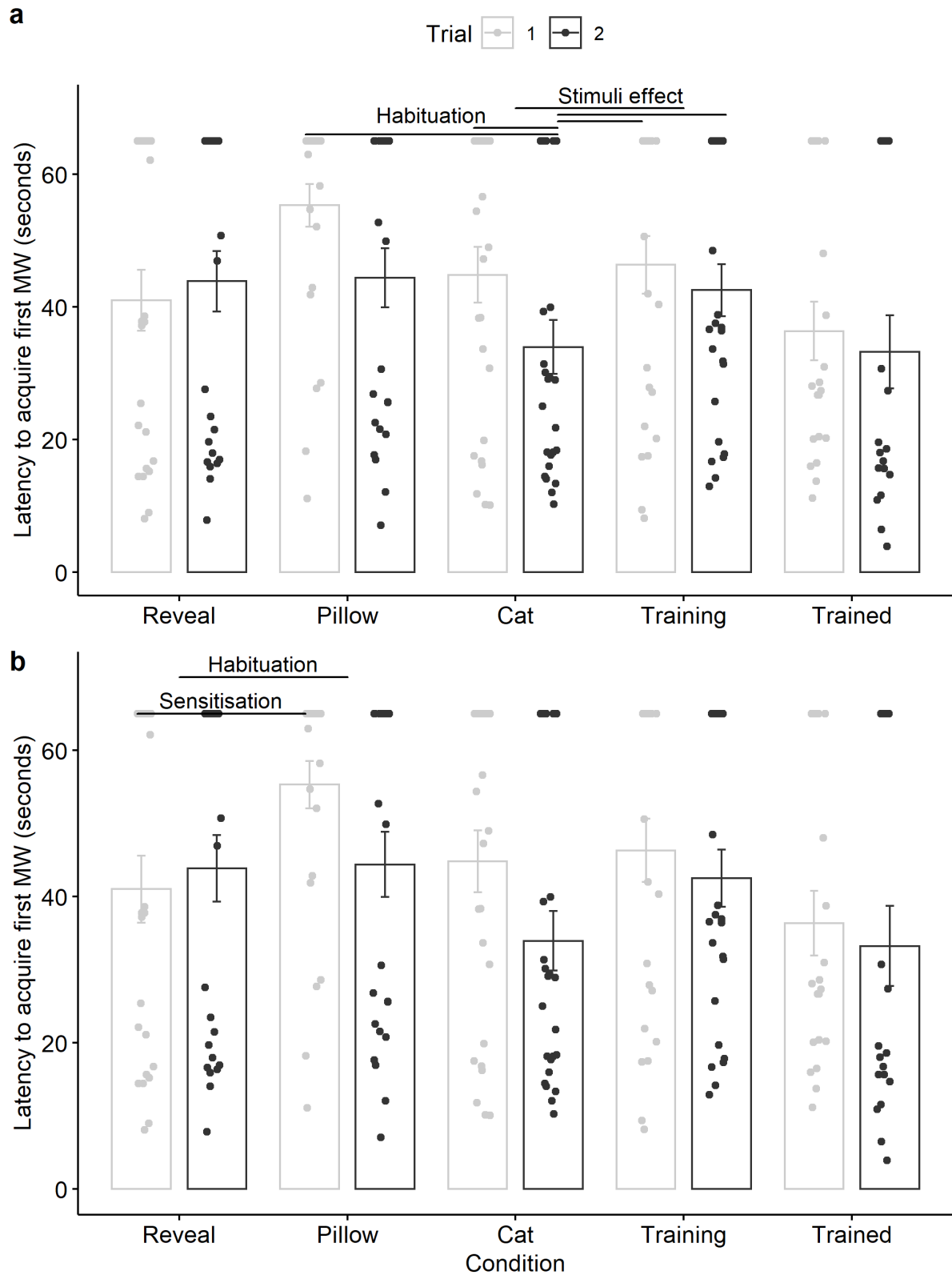


Fig. 7. The summary of results of latency to acquire first MW and time spent close across all anti-predator training conditions and trials. (a) is the mean latency to acquire first mealworm with standard deviation across all toutouwai tested. (b) is the mean time spent close with standard deviation across all toutouwai tested.

Table 13. Significant or near significant Pairwise Aligned Ranked Transformed Comparisons (ART-C) with Tukey adjusted p-values of behaviours measured during conditions of the anti-predator training protocol. Contrast estimate (CE), standard error (SE), degrees of freedom (Df), T ratio, and P-value (P) are included for each condition and trial comparison.

Behaviour		Condition	Trial	Condition	Trial	CE	SE	Df	T Ratio	P
Latency to acquire MW		Reveal	1	Pillow	1	-27.083	9.65	115	-2.807	0.063
		Pillow	1	Cat	2	34.917	9.65	115	-0.039	0.005
		Cat	1	Cat	2	12.88	4.72	72	2.730	0.038
		Cat	2	Training	1	-16.30	4.72	72	-3.454	0.005
		Cat	2	Training	2	-13.14	4.72	72	-2.785	0.033
Time Spent close		Reveal	1	Pillow	1	36.4583	9.65	115	3.778	0.003
		Cat	2	Training	1	3.58	4.61	72	2.597	0.054

Overall, there appears to be no effect on the behaviour of toutouwai from the training regime implemented as there was no population-level change in any behaviour between the first presentation of the taxidermy cat (cat condition) to the cat after a training session (trained condition). There was no interaction between trial and condition, or difference between conditions, or difference between trials for any behaviour (Table 12) when comparing cat condition and trained condition. If there was an effect of training, there should have been an increase from the cat condition to the trained condition in the time spent doing any/all the behaviours.

Comparing the cat only condition to the cat and alarm call condition, there was limited evidence to support an effect of the alarm call as an aversive stimulus in one behaviour, latency to acquire a MW. There was no interaction between trial and condition, but there was an effect of each on its own (Table 12). There was an increase in latency to acquire a MW when the alarm call was played than when it was not (Fig. 7a). However, the expectation was that there would be a decrease in time spent close, time spent with head down and time spent perching was not present. Ultimately this indicates that the alarm call was a milder stimulus than intended and expected.

#### Assessing personality during anti-predator training

Several behavioural measures did not show repeatability after calculating ICC, but at least one behavioural measure from all four personality tests did (Table 14). The first EFA did not meet the standards required for further analysis due to the startle test's low communalities and low loading values, alongside the behaviours from the novel object test having low loading values that were distributed close to evenly across each factor (Table 14). However, the

adjusted EFA that only included behaviours from the open field and threat stimuli tests produced two factors that cumulatively explained 83 % of the variance in toutouwai behaviour, with the first factor (FAC1) accounting for 65.3% of the variance and the second factor (FAC2) accounting for 17.7% of the variance. Based on the categories defined by Réale et al. 2007, I identified FAC1 as Boldness and FAC2 as Exploration. Eleven toutouwai had positive boldness scores, while twelve toutouwai had positive exploration scores, and there was no correlation between scores (Fig. 8).

Table 14. Personality tests with the corresponding anti-predator test conditions/trials they were extracted from, alongside the behavioural variables that were included in EFA, their expected personality alignments, repeatability estimate (R) and first & final factor loadings across factors 1 and 2 (FAC). Factor loadings greater than 0.7 are in bold.

Test Type	Corresponding anti-predator tests	Behavioural Variables		Expected Personality Trait	R	First EFA		Final EFA	
						FAC1	FAC2	FAC2	FAC2
Startle	Reveal condition, trial one & two	Duration Down	Head	Boldness	0.517	0.138	0.322	N/A	N/A
		Occurrences Active		Boldness/Activity	0.626	0.118	0.640	N/A	N/A
Novel Object	Pillow condition trial one & Cat condition trial one	Duration Down	Head	Exploration/ Boldness	0.475	0.433	0.599	N/A	N/A
		Duration Close		Exploration	0.546	0.669	0.369	N/A	N/A
		Occurrences Active		Exploration/Activity	0.539	0.630	0.557	N/A	N/A
		Number of MW Acquired		Exploration	0.558	0.666	0.471	N/A	N/A
Threat Stimulus	Training condition, trial one & two	Duration Down	Head	Boldness	0.464	<b>0.839</b>	0.210	<b>0.852</b>	0.244
		Duration Close		Boldness	0.671	<b>0.844</b>	0.368	<b>0.815</b>	0.402
		Occurrences Active		Boldness/Activity	0.468	<b>0.851</b>	0.232	<b>0.900</b>	0.226
		Number of MW Acquired		Boldness	0.631	<b>0.800</b>	0.397	<b>0.815</b>	0.389
		Zones Crossed		Boldness	0.596	<b>0.903</b>	0.105	<b>0.926</b>	0.088
Open field	Post reveal phase of conditions one, two and three, with trials one & two for each	Duration Down	Head	Exploration/ Boldness	0.408	0.420	<b>0.748</b>	N/A	N/A
		Duration Close		Exploration	0.386	0.367	<b>0.888</b>	0.401	<b>0.815</b>
		Occurrences Active		Exploration/Activity	0.390	0.263	<b>0.821</b>	0.250	<b>0.877</b>
		Zones Crossed		Exploration	0.273	0.140	<b>0.742</b>	0.125	<b>0.906</b>

Does personality influence anti-predator training uptake?

Personality had little impact on the behaviour of toutouwai post-training, with only Exploration predicting the change in time spent with head down (Table 15.16). Individuals with a higher exploration score also showed a more considerable decrease in time spent with their head down (Fig. 9a). Boldness did not predict any post-training change in behaviour (Table 15,16). Training latency predicted the change in time spent close but no other behaviour (Table 15,16). Individuals that were tested later increased their time spent close (Fig. 9b).

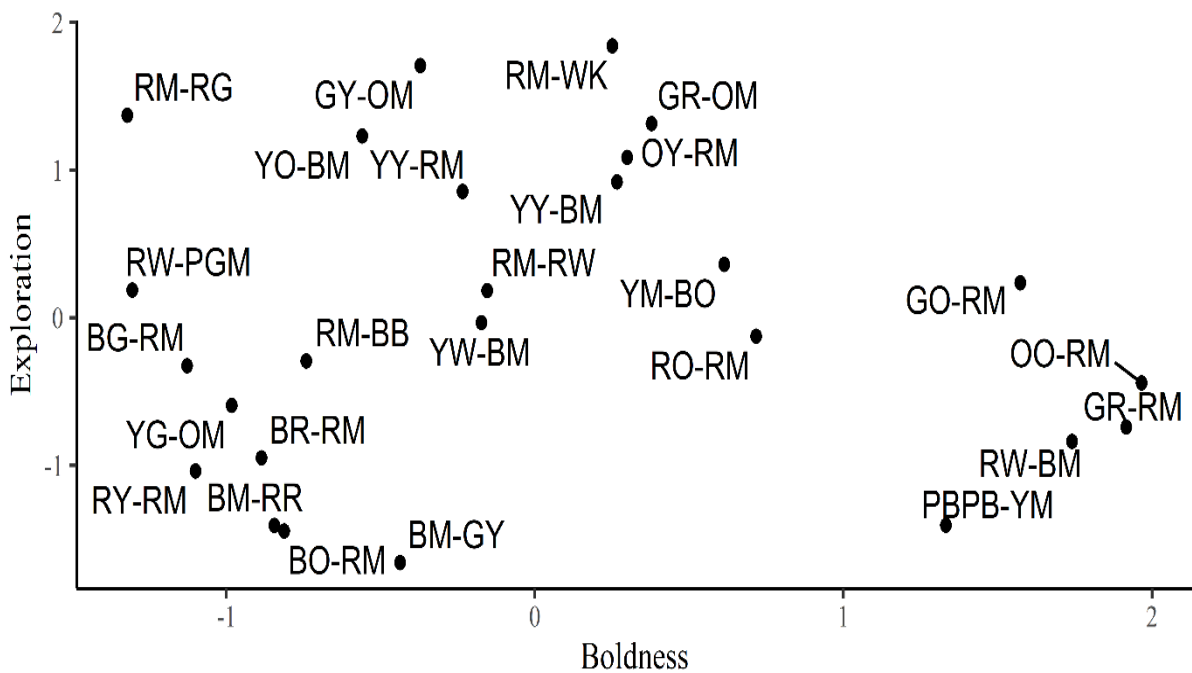


Fig. 8. Scatterplot of Exploration and Boldness scores for individual toutouwai

Table 15. multi-model average results for the behavioural measures taken during anti-predator training, personality scores and training latency (interval between anti-predator training and re-presenting cat model). For each predictor, the estimate, unconditional standard error (SE), confidence interval and Relative importance are listed. Predictors that influence the response variable (Confidence intervals that do not cross zero) are in bold

Behavioural measure	Parameter	Estimate	Unconditional SE	Confidence interval	Relative importance
Perch	(Intercept)	0.263	1.324	(-2.510, 3.031)	
	Exploration	1.258	2.759	(-4.525, 7.042)	0.210
	Boldness	-1.277	2.794	(-7.135, 4.580)	0.210
	Training Latency	0.405	2.812	(-5.488, 6.298)	0.193
Head Down	(Intercept)	-0.523	0.900	(-2.409, 1.362)	
	<b>Exploration</b>	<b>-4.350</b>	<b>1.807</b>	<b>(-8.141, -0.560)</b>	<b>0.80</b>
	Boldness	2.325	1.879	(-1.617, 6.269)	0.33
	Training Latency	1.776	1.906	(-2.222, 5.775)	0.26
Acquire MW	(Intercept)	0.271	3.058	(-6.130, 6.672)	
	Training Latency	-11.664	6.328	(-24.908, 1.580)	0.59
	Boldness	5.705	6.865	(-8.617, 20.028)	0.26
	Exploration	-2.479	6.408	(-15.930, 10.971)	0.19
Close	(Intercept)	0.356	2.750	(-5.408, 6.121)	
	<b>Training Latency</b>	<b>14.580</b>	<b>5.712</b>	<b>(2.618, 26.541)</b>	<b>0.85</b>
	Exploration	-6.242	5.635	(-18.084, 5.599)	0.30
	Boldness	-5.844	6.163	(-18.737, 7.048)	0.27



## Discussion

I had three distinct goals in this study. First, to assess the effectiveness of an in situ anti-predator training protocol in a population of wild toutouwai using a taxidermy cat. Second, to examine if reframing the anti-predator training protocol as an animal personality framework can enable robust and valid quantification of personality in toutouwai. Finally, to determine whether personality traits influence how an individual responds to anti-predator training. I found that the anti-predator training protocol implemented did not have the desired level of effect in changing behaviour toward a taxidermy cat. However, I did show that the longer the period between training and testing, the lower the desired behavioural response became. I used the anti-predator training protocol to quantify personality robustly, a first for this species. However, the personality information was not particularly helpful in interpreting the effect of anti-predator training at the individual level. Despite inconclusive findings, discussion of these results should serve to inform future research directions.

### Anti-predator training procedures

This anti-predator training protocol did not significantly change the overall behavioural responses to a taxidermy cat in a population of wild toutouwai. Some evidence suggests the toutouwai may have too quickly habituated to the predator model, with latency to acquire a MW decreasing between the pillow and cat conditions. If there was habituation, it was broken by the aversive stimulus as latency to acquire a MW did increase when the alarm call was present, indicating that it did cause a behavioural change. However, the effect of the alarm call was small and did not even approach the average response of the first time the pillow was presented. This is surprising as previous work with kakaruwai did indicate that an alarm call presentation on its own would be sufficient to elicit a strong behavioural response (Maloney & McLean, 1995). I interpret this as meaning the alarm call limited further habituation to the cat but did not provide enough of a negative stimulus to alter behaviour even temporarily and may have required the use of movement as well (Maloney & McLean, 1995). These results show that the most likely explanation for the lack of the desired effect on toutouwai behaviour is due to an insufficient aversive stimulus failing to create a negative association with the taxidermy cat. However, these relationships were not present for any of the three other behaviours measured, so the degree to which habituation limited the effect of training overall is questionable, a more likely reason for the failure of training was due to the protocols were unsuccessful was the result of blocking, a phenomenon where animals will only learn about



new stimuli in situations where an association already exists provided the new stimuli provides additional information (Greggor et al., 2020). An association between the cat and food likely developed in the initial stages of the protocol and the later alarm call stimuli were not sufficient to break this association and form a new one. Despite this interpretation, several other factors may have contributed to the lack of behavioural change that could be important to consider for future protocols, particularly the methodological differences between this and past anti-predator protocols. I chose to use adults, on their own outside the breeding season to control for those states potentially confounding the training and because that time and those individuals are easier to work with and there is less potential to interfere with breeding success. However, there is reason to consider that the difference in season and ages trained may have improved the training protocol.

During the breeding season, toutouwai, as with other songbirds, devote much of their time to rearing offspring, with females solely responsible for nest building and incubation (Armstrong et al., 2000; Powlesland et al., 2000), while both males and females provision nestlings and fledglings until their independence (Armstrong et al., 2000; Powlesland et al., 2000; Shaw et al., 2019). Parental investment extends to the point of parents exhibiting potentially self-sacrificial behaviours, such as mimicking broken wings, attacking potential predators and attempting to draw attention away from their nests (Flack, 1976; Maloney & McLean, 1995; Powlesland, 1980). Thus, during the breeding season, a heightened state of vigilance and/or agitation may be responsible for making toutouwai more susceptible to anti-predator training. This hypothesis is supported by observations made by Powlesland (1980) and Flack (1976) that the degree to which individual kakaruwai responded to native and introduced predators depended on breeding conditions, with animals outside the breeding season responding more passively.

The use of conspecifics and the life stage of those animals chosen to be trained may have enhanced training efficacy (Rowell et al., 2020). There is evidence from a wide variety of animals that social learning can transmit complex information such as songs (Mooney, 2009), types of food to eat (Galef, 1993; Jaeggi et al., 2010; Thornton, 2008), and how to use tools (Nagell et al., 1993; Tebbich et al., 2001). Evidence suggests that predator avoidance behaviours are socially learned in many species, being particularly fast in birds (Griffin, 2004). Indeed, one of the core theories in why animals such as toutouwai have an extended parental care period is to teach their offspring behaviours that will improve their fitness (Thornton & Raihani, 2008). Even if social learning is not the main driver of the difference in anti-predator

training, the characteristics of juveniles could be explanatory in itself as juveniles are generally more innovative, flexible, exploratory and persistent learners than adults in some species (Loepelt et al., 2016; Morand-Ferron et al., 2011; Vince, 1958). However, I believe the combination of social learning techniques applied to juvenile kakaruwai in prior studies (Maloney & McLean, 1995; McLean et al., 1999) is probably one of the key reasons their training protocols were so effective.

Perhaps the most insightful aspect of this anti-predator training protocol is in relation to the measuring of training efficacy. In typical anti-predator training studies, the measure of success is survival post-release, there is not often any remeasurement or memory testing of these individuals (Greggor et al., 2019; Griffin et al., 2000; Haage, Maran, et al., 2017). Studies, where the efficacy of a training protocol is quantified, are within a few days to a month after the training was performed (de Azevedo et al., 2017; Maloney & McLean, 1995; McLean et al., 1999). I have shown with at least one behaviour (time spent close) as more time elapses between training and trained testing, there is likely to be a decrease in the desired effects of the training, a finding supported in some recent work in collared peccaries (*Pecari tajacu*) (de Faria et al., 2020). An overabundance of studies that retested over concise time frames (e.g. a few days) may be overinflating the effectiveness of anti-predator training as a tool (Rowell et al., 2020). This is because in most cases where anti-predator training would be applied *ex* or *in situ*, the feasibility that regular reinforcement training sessions could occur is minimal. Therefore, the trained subjects would likely need to encounter the predator they have been trained to avoid within a short time frame for the training to be effective. Alternatively, a landscape of fear concept could be employed where stimuli are placed throughout the environment that could elicit desired behavioural maintenance or response (Arlinghaus et al., 2017; Bleicher, 2017). However, such an approach would require careful monitoring as it could lead to habituation rather than maintenance if not performed correctly (Greggor et al., 2014a; Magurran & Girling, 1986). Considering the use of stronger stimuli may be worthwhile in future attempts at antipredator training in toutouwai, but the feasibility and ethics of doing so should also be considered. More aversive stimuli in an open space may lead to individuals no longer engaging in a protocol, which may be good for conservation outcome, but will hinder personality or other forms of long term assessment. Furthermore, there may be unintended injury or death to individuals or non-target species if extremely aversive stimuli like simulated predation or chemical deterrents are used. Additionally, multiple stimuli are likely necessary to ensure desired behavioural modification in toutouwai, and how one would enact that in a

targeted training session or at a landscape scale is unclear. Therefore, it is necessary for those implementing anti-predator training of any kind to determine that the training has the desired effect on behaviour and determine the maintenance of those behaviours over ecologically relevant time scales and work on improving the protocols to enhance both these factors.

#### Assessing personality during anti-predator training

Through careful planning of a predator training protocol, it was possible to confirm personality in *toutouwai* in the most thorough and robust way for any native New Zealand species to date (Chapter 2). Previous research in *toutouwai* attempting to assess personality had assessed the repeatability of one behaviour in one task (Barnett et al., 2013; He et al., 2017), whereas, in this study, I assessed multiple behaviours across different tasks validating these behaviours through repeatability testing and factor analysis following the best practices in the field (Chapter 2; Carter et al., 2013; Dingemanse & Wright, 2020; Réale et al., 2007). In the process of quantifying personality, I provide evidence for Réale et al.'s (2007) assertion that the test being administered is what dictates the personality measured, as behaviours aligned to factors by test context, rather than aligning solely based on being the same behavioural measure. This raises questions about much of the work done in the field of personality research, as very often, personality is quantified by using a single test or even a single behaviour, rather than a multi-test/multi-behaviour validation method as has been suggested (Carter et al., 2013; Dingemanse & Wright, 2020) and used in the current study.

One of the most interesting findings of this study comes from the initial factor analysis that included all four personality tests. Although this analysis did not meet the rigorous statistical requirements that I set, it did appear to show that behaviours recorded during the novel object tests loaded almost evenly across FAC1 (boldness) and FAC2 (exploration). There are two potential explanations for this peculiar finding. The first and most likely is that due to the small sample size, there was limited power in the factor analysis and providing more data with the loadings would have been more interpretable (Budaev, 2010; Yong & Pearce, 2013). The second is that the novel object task measures something other than simply exploration, as has been suggested by Réale et al. (2007). Novel object tests may measure a different personality trait like boldness, or perhaps the interaction between exploration and boldness. The potential for novel object tests to be measuring boldness or a boldness-exploration interaction has merit at face value, as the responses of an individual to an object they have seen for the first time could reasonably be explained by both willingness to take risks alongside environmental curiosity. Indeed, novel object tests have been used to measure boldness in a

multitude of studies (Carter et al., 2013), despite Réale et al. (2007) explicitly describing not to and many studies find correlations between these two measures (Carter et al., 2013). It may be that in species like toutouwai novel object tasks elicit behavioural responses where there is an interaction between exploration and boldness, therefore being unable to measure neither. Moreover, this ambiguity in determining what a task is measuring may be more widespread, with evidence from experiments with hermit crabs (*Coenobita clypeatus*) also indicating that different measures can lead to different inferences (Watanabe et al., 2012). This finding alongside a recent survey of personality researchers finding there is no universal or coherent methodologies used across the field (Sánchez-Tójar et al., 2022), indicates that there are fundamental issues with personality research that may yet prohibit personality from being ready as a conservation tool.

The finding that personality can be quantified robustly in a small number of free-living animals with relatively simple tests that were part of another type of experiment is exciting. However, careful consideration of the tests used and methodology used to quantify personality is necessary for appropriate interpretation of any personality research, particularly in the field of conservation (Chapter 2). For example, one of the limitations of how I quantified personality is that it was done over a short time scale, which has been shown to influence repeatability estimates (Bell et al., 2009). Testing over the life span of individuals is likely necessary to capture the true personality of individuals and can overcome flaws in methodological design (Dingemanse & Wright, 2020). Behaviourists and conservationists alike should think where the opportunity to record behaviours multiple times and act to make those recordings in typical or manipulative management of their species. The information may not be immediately helpful but understanding how individuals respond and act across time and contexts could have significant implications for future management actions. I have shown that despite the high statistical thresholds for quantifying personality, implementing these methods can be done provided there is some thought on the methodological design from a personality perspective beforehand. I hope that high-quality personality quantification will become more integrated into conservation management to improve the field from its current state (Chapter 2) and eventually improve conservation outcomes. However, there needs to be unity of philosophy and methodology across personality researchers before a significant expenditure of resources is made in the conservation space.

Does personality influence anti-predator training uptake?

Exploration was the only personality trait that showed some relationship with

behavioural change after anti-predator training, specifically time spent with head down, despite accounting for much less of the variance in behaviour than boldness in the EFA. This was unexpected, as boldness should dictate the response to a threat (Réale et al., 2007). Intriguingly, time spent with head down did not contribute to the factor score for exploration, indicating that perhaps time spent with head down related to the post-training response to the cat model is more a by-product of the explorative qualities of an individual rather than as a risk-taking measure.

This raises some interesting questions as to the usefulness of head down as a perceived measure of vigilance. In this species, having the head down may not lead to an increase in predation risk as would be expected. Another possible explanation is that having their head down is how toutouwai explore their immediate environment, as they must put their head down to forage which involves clearing away leaf litter on the ground. What initially might be perceived as risky behaviour is more explorative behaviour, and they have other mechanisms for avoiding predation than being overly reliant on sight. Toutouwai responded to and became involved in 'mobbing' displays where a cohort of different species alarm call and harass predators like ruru (*Ninox novaeseelandiae*) (St Paul, 1977). It may be that there is an interspecies component to anti-predator behaviour in toutouwai as they use environmental cues in addition to individual vigilance behaviours. Furthermore, there may be physiological reasons why simply having a head-down posture in toutouwai does not meaningfully decrease vigilance, as toutouwai have eyes on the side of their head, meaning the field of view may not be greatly reduced during this act.

Despite previous findings that boldness is associated with aversion training (de Azevedo et al., 2017; Lopes et al., 2017), it is likely that the way personality is quantified has a significant impact on the results and relationships obtained. For example, research on aversion training in lizards has shown that shyer animals performed better, but they implemented a simplistic measure of boldness, a rank score based on one observation of behaviour (Ward-Fear et al., 2019, 2020). This technique is not uncommon, with many studies using single behaviours and/or tests sometimes without repeatability or validity testing to determine personality (Carter et al., 2013; Dingemanse & Wright, 2020). In conservation contexts where time and resources are limited, the feasibility of implementing in-depth, highly structured testing is low. However, when it comes to personality, high levels of methodological rigour are necessary at least once before establishing proxy ways of measuring personality (Carter et al., 2013). The work done by this study shows that it provided some forethought on

methodological frameworks for personality; it is relatively easy to meet the methodological rigour required to quantify personality to modern standards in an ideal study system. The ease of implementation may be more challenging in less ideal systems, or in situations where resources are more limited making the feasibility of such work more questionable. However, previous studies show that there is no guarantee that cross-species consistency in the relationship's personality traits will have to be ecological/physiological measures (Chapter 2). Without rigorous and exhaustive attempts to quantify personality, all researchers will accomplish is finding that some behaviour *a priori* determined to represent personality correlating/predicting another behaviour, not actually showing a legitimate relationship to personality. Ultimately, I find it challenging to interpret the results of this study in relation to other personality studies because so few of them meet modern standards and definitions as to what personality is (Chapter 2).

## Conclusion

I implemented an anti-predator training protocol in the wild intending to use the same protocol to quantify personality. Unfortunately, I did not elicit the desired response in behavioural change from the population after anti-predator training. However, I was able to quantify personality in the most robust way to date for any native New Zealand species. Ultimately, however, this personality information was not very informative in interpreting individual-level responses to anti-predator training. This study does examine the feasibility of incorporating animal personality into aversion type experimentation, finding it possible but resource-intensive. This study also demonstrates that anti-predator training in wild situations takes a great deal of time in both planning and implementation for the benefit of relatively few individuals. Furthermore, it appears that techniques will not be interchangeable between species because they are likely to depend on the ecology and behaviour of the target species, how they perceive predators, and their ability to learn. However, if planned well, future anti-predator protocols could improve behavioural outcomes by using more stimuli, conspecific interactions, and a more developed understanding of natural anti-predator behaviours in their focal species. Additionally, even if the protocol does not have the desired outcome, the data can be interpreted differently, i.e., through a personality framework. This information may not help interpret the outcome of the training as evidenced by the results of this study, but it could help validate proxy measures of personality or understanding of other aspects of the species' biology. Animal behaviour researchers applying their research to conservation should be looking to maximise the applications of their work for conservationists, mainly when that

research is reasonably intrusive or disturbing to conservation dependent species. Ultimately it appears that personality as a conservation tool has limited use and little value in its current iteration, and until there is more unity in the philosophy and methodology of personality research conservationists should be cautious of implementing resource-intensive protocols without sufficient groundwork that establishes usefulness in their species.

## Chapter 5: General discussion

This thesis aimed to synthesise how animal personality has been used in conservation and to test how personality can be a tool for conservationists. I will begin this discussion by summarising the main results from each chapter, and then discuss what is necessary for personality to be useful as a conservation tool. Finally, I will provide an example of how personality can be effectively integrated into conservation by outlining how conservation practitioners could incorporate personality measurement within future toutouwai management.

### Chapter Summaries

Chapter 2 provides the first systematic review of the integration of animal personality within conservation biology. The results of this review paint a worrying picture for the field, with approximately half of all papers not meeting basic research standards for the quantification of personality. This has implications for future meta-analyses of personality, with any such studies needing to carefully review the methodologies used in a paper before its inclusion in the analysis. Chapter 2 shows that when personality is quantified correctly, it has been applied to a broad range of conservation contexts, but not as broadly as previous reviews have asserted (Merrick & Koprowski, 2017). However, even for studies that do quantify personality correctly, there is relatively little conservation content. By evaluating and collating the best studies at the interface of personality and conservation, this chapter presents information to suggest that personality as a conservation tool is still in the early stages of development. This chapter also provides a resource for conservationists looking to incorporate personality using acceptable research methods (Dingemanse & Wright, 2020), hopefully improving future conservation outcomes and behavioural theory.

Chapter 3 investigated how personality can be quantified in actual conservation contexts using toutouwai in a mainland island reserve, an ideal system for personality integration. The results show that with few changes to current management protocols and a minor increase in resources (time), both single behaviour and multi-behaviour personality tests can be implemented. However, there was no relationship between personality and the ecologically important variable of reproductive output in this species. This chapter demonstrates that to establish personality as a conservation tool for a particular species there will need to be traditional personality research, combined with an investigation of how personality measures relate to ecological variables that conservationists care about. Without linking ecologically important variables to personality measures in the species of conservation concern, it is difficult to justify the extra resource expenditure.



Finally, Chapter 4 investigated how personality can be incorporated alongside conservation behaviour interventions. Using the toutouwai and a mainland island reserve system as a real-world context where in situ anti-predator training might occur, I developed and implemented the first in-situ anti-predator training protocol that simultaneously measures personality. Unfortunately, the anti-predator training was not very successful in eliciting anti-predator behaviour post-training, but I was able to quantify personality at the level suggested for current best practice (Carter et al., 2013; Dingemanse & Wright, 2020). Individual personality was somewhat helpful in interpreting the impact of the training protocol, with an individual's exploration score predicting a decrease in time spent with head down after training, head down being used as a measure of vigilance in other species (Bednekoff & Lima, 2005). Surprisingly individuals' boldness scores were unrelated to their behaviour post-training, despite literature suggesting there should be. The null results in this chapter were most probably due to an ineffectual anti-predator training protocol. Nonetheless, this chapter serves as proof of concept for integrating personality into future research using conservation behaviour tools.

Taken together, these chapters show that personality is increasingly being applied in many conservation contexts and that personality methodologies and in certain cases can feasibly be incorporated into current and future conservation management plans. However, this work also highlights that personality needs to be quantified correctly, that the requirements to measure personality correctly may limit the conservation contexts where personality can be incorporated into conservation, and that establishing ecological links with personality measures is necessary for personality to be a helpful tool for conservationists.

## Personality in conservation

Personality has been suggested as a tool that can be applied to almost all aspects of conservation biology, from captive breeding to climate change (Brooker et al., 2016; Merrick & Koprowski, 2017; Wolf & Weissing, 2012). However, the historical literature regarding personality is confused not only in terms of nomenclature but also in methodologies on how to measure personality (Beekman & Jordan, 2017; Jungwirth et al., 2017). Approaching the field of personality without understanding recent developments and consensus around terminology and methodological approaches, it could be easy for those looking at applying personality to be misguided and perform inadequate studies, an idea supported by my findings in Chapter 2. Furthermore, most of the studies that quantified personality appropriately had some form of a captive component to their personality quantification, and relatively few had significant

conservation-related content. Therefore I wanted to identify whether it is feasible for conservationists to implement personality measurement in conservation management and interventions in the wild (Chapters 3 & 4). The results of this thesis have made it clear that two essential requirements limit personality as a conservation tool. First, the system being studied needs to be amenable to appropriate methods for the quantification of personality. Second, the personality measures recorded can be used to address the conservation goals for the species, be it improved survival, reproduction or some other ecological measure. However, these requirements may be too onerous for many conservationists to meet on their own.

### Personality quantification

The first step to ensuring that appropriate methods can be used to measure personality is to identify where and how repeated measures of behaviour can be taken (Carter et al., 2013; Dingemanse & Wright, 2020; Réale et al., 2007). Once the opportunities for repeated measures testing have been established, the next step is to determine the types of personality tests that can be used with the animal. The types of personality tests available will probably determine the aspects of the animal's personality that can be measured as test type dictates what personality can be measured (Chapter 4, Carter et al., 2013). This is a potential barrier to generalisability in personality studies. A potential solution to this problem is to only refer to behaviours that are repeatable in a given test type, forgoing any generalisability in how we describe personality. The alternative is to come to a level of acceptance as to what personality traits can be measured under what testing conditions in some form of unified criteria. However, this solution can only be implemented after a field-wide acceptance of the philosophical and methodological underpinnings of what personality is, which does not currently exist (Sánchez-Tójar et al., 2022). For now, any meta-analysis of personality must analyse each study in its full detail and not rely on words like boldness or activity to be universally defined. Finally, for personality to be accurately measured, there needs to be appropriate statistical analysis. Each of these steps has limitations that determine how personality can be incorporated into any given conservation project.

### *Where can personality be quantified?*

If animals are kept in captivity for any amount of time, such as for a breeding program (Allard et al., 2019), transfer for translocation (Baker et al., 2016), or capture for banding/welfare check (May et al., 2016), this presents an opportunity to record behaviours multiple times. Most of the studies that have looked at personality in a conservation context have used captive measures at some point (Chapter 2). Captivity allows for control over diet,

environment, social interactions, and stimuli which in turn means that when measuring behaviour, there is an assurance that the individual is a motivated, active participant in the task and not distracted (Pritchard et al., 2016). However, there are many situations where wild contexts present an opportunity for repeated measures testing that conservationists can exploit. For example, this may include situations where there is a repetition of the same protocols such as checking on nests (Arroyo et al., 2017), doing welfare checks (Carbillet et al., 2019; May et al., 2016) or most commonly during population monitoring (Carrete et al., 2016; Hertel et al., 2019; Holtmann et al., 2017; Michelangeli et al., 2016; Schwarz et al., 2021; Spiegel et al., 2015; Wong et al., 2017).

#### *How can personality be quantified?*

Two approaches can be made here, single behaviour or multi-behaviour testing. Each method has strengths and weaknesses and varied applicability depending on the conservation context. (Carter et al., 2013; Réale et al., 2007). Single behaviour testing typically requires less video analysis, and thus more individuals may be able to have behaviour recorded. Nevertheless, single behaviour quantification requires some degree of *a priori* assumptions about what personality trait the behaviour is related to. Alternatively, single behaviour measures can be validated by assessing their relationship to more robust measures of personality. Multi-behaviour testing can account for some of the limitations of single-behaviour testing by validating behavioural measures against each other and investigating the relationship of behaviours to personality traits without requiring *a priori* assumptions. They are also typically used to validate single behaviour measures.

#### *What types of tests can be used?*

The type of tests available to conservationists will first be dependent upon the type of testing condition. For example, testing in captivity may be the only way to appropriately submit animals to the clearest multi-behaviour test of exploration of a novel environment task, outside of releasing individuals into an actual novel environment (Germano et al., 2017). There has been some use of popup enclosures used in measurements of the wild lemon shark (*Negaprion brevirostris*) and common voles (*Microtus arvalis*), but these enclosures still prohibitively restrict movement and do not allow for the subject to voluntarily disengage with the task (Finger et al., 2018; Kowalski et al., 2019). In that case, the only viable ways left for exploration can be measured in the wild are emergence, movement tracking, open field tests and novel object tests (Carter et al., 2013; Réale et al., 2007). There is a problem with at least two of these measures in that that it can be difficult to discern if an individual is taking a risk or exploring

during emergence and novel object tests. As shown by the latency to acquire a MW as a measure in chapter 3 and the ambiguous factor loading of behaviours from the novel object test in chapter 4, there can be ambiguity in interpreting what novel object tests are measuring. Moreover, in many cases, novel exploration and emergence tests are used interchangeably to measure boldness and exploration, despite recommendations not to do so (Carter et al., 2013; Réale et al., 2007). Therefore, the most precise ways to measure exploration appropriately and interpretably are probably limited to movement tracking, open field tests and novel environment tests, with limitations on measuring this personality trait in the wild.

Another personality trait that may be limited to measurement in captivity is sociability. In order to test sociability in the wild, there need to be natural occurrences of systems that have variable group sizes over time. This variation may be difficult to find, particularly in animals that school, shoal, flock, and roost together where presumably sociability will be highly selected. Of all the studies I reviewed in chapter 2, only five instances of sociability testing occurred, all of which manually manipulated group size and none of which were performed in wild conditions (Finger et al., 2018; Martin-Wintle et al., 2017; Michelangeli et al., 2016; Skinner & Miller, 2020; Williams et al., 2019). It is likely testing for sociability will require manipulating social groups through the addition and removal of individuals from a group which seems only be achievable by captive testing or limited to the study of socially limited species like toutouwai and other territorial species (Carter et al., 2013; Réale et al., 2007).

The types of tests available will be even more depending on the characteristics of the animals being studied. One limitation of wild testing is the need to identify individual animals reliably over time. Many animals can be marked for individual identification (Silvy et al., 2005), and advances in technologies like computer vision make photographic identification based on physical characteristics more feasible in the future (Vidal et al., 2021). Another limitation of wild testing is that the animal being studied will have to regularly visit fixed locations, be amenable to some degree of altered environment, and be observed during a personality test. The need for identification and observation is a limitation that could exclude many inherently skittish, dangerous, or hard to access animals like marine mammals.

An alternative way to record repeated measures where captivity or interactions with animals in the wild is not feasible is to use movement tracking through data recording devices (Germano et al., 2017; Hertel et al., 2019; Schwarz et al., 2021; Villegas-Ríos et al., 2017). However, this type of measurement does not capture the varied contexts that an individual could be experiencing from a personality perspective, so it usually requires advanced mapping

and geo-spatial analysis to record anything other than activity. For example, measuring boldness using movement tracking data requires knowledge of any risky environments that an animal must move through, such as bears encountering highways (Hertel et al., 2019). While movement tracking can be a helpful alternative, for many conservation projects, the technology might not be appropriate, such as with birds or insects with weight restrictions, or it may be prohibitively expensive (Thomas et al., 2011). Conservationists interested in personality in the wild may be limited to movement studies and animals that are able to be observed, regularly frequent the same places, and are not overly neophobic.

The way behaviours are recorded will also limit the types of personality tests that can be used. For example, Boldness is perhaps the easiest personality trait to measure from a single behaviour, provided a clear risk is imposed on the individual. Typically boldness measures are accomplished through capture events (May et al., 2016; Michelangeli et al., 2016; Ward-Fear et al., 2018) or disturbances (Carrete et al., 2016; Holtmann et al., 2017). For example, the boldness score measured in yellow-spotted monitor lizards (*Varanus panoptes*) was the degree of struggle during the capture of a risky event (Ward-Fear et al., 2018). However, single behaviour measures can have issues. For example, when there is ambiguity in the way the behaviour is recorded, it may lead to difficulty interpreting results (McCowan et al., 2015). The problem with the single behaviour measures used in Chapter 3 is that they relied on the individual making investigations. It is often difficult to determine how people or objects are perceived by the animal, making it hard to distinguish between risk-taking and exploration. This difficulty in distinction may explain why exploration and boldness are claimed to be measured even when the same type of task is being used across different studies and why boldness and exploration measures are often found to be correlated (Carter et al., 2013). Ideally, single behaviour measures should be validated by comparing scores to the results of more traditional personality tests to confirm what personality trait they are in fact measuring (Carter et al., 2013).

Multi-behaviour testing does not have a priori assumptions, so it can overcome or help interpret results from personality tests that are somewhat ambiguous, as was shown in Chapter 3 with the novel object test. A potentially prohibitive feature of multi-behaviours testing is the need for video recording and analysis due to the speed and co-occurrence of behaviours of interest in many personality tests (Allard et al., 2019; Finger et al., 2018; Hammond et al., 2021). For example, I spent approximately six months coding the videos of behaviours from the multi-behaviour tests included in this thesis, with relatively short videos taking hours to

extract data. In some cases, particularly in captivity, machine learning can be used to extract data more efficiently (Hammond et al., 2021), but this will not be the case for more wild oriented personality testing where boundary parameters and conditions are harder to standardise. The time needed to get data is not often considered when personality is suggested as a tool, but this is likely to be a massive barrier to its uptake in applied conservation contexts.

Moreover, even when multi-behaviour repeated measures tests are used, there can be subtle differences in task design that means they will sometimes work and other times fail. Take, for example, the multi-behaviour tray task used in Chapter 3 and the open-field task used in chapter 4 of this thesis. Both tasks measured the same behaviours, and yet the tray task did not show any behaviour to be repeatable, while in the open field task, behaviours were shown to be repeatable. This is despite both tasks meeting the definitions of open field tasks with little difference between the two. One explanation for this discrepancy is that the tray task presented in chapter 3 differed too much from the open-field task in Chapter 4, meaning the test context was not the same. The context of a test is therefore likely to be a primary driver of the personality traits present (Carter et al., 2013; Réale et al., 2007). The mechanism behind this may be the intensity of stimulation that an individual receives. If so, then in wild testing as was performed in this thesis, only tasks with a high intensity of stimulus will record personality traits. In my attempt to disguise the tray and mimic a real-world foraging situation, I may have reduced the novelty of the stimulus too much for an appropriate measure of exploration to be recorded. Another possible cause is that the open field task that measured exploration in chapter 4 had twice the number of sampling occurrences compared to the tray task used in chapter 3, creating two potential confounds. First, although designed to be limited in novelty, the tray task apparatus may have required some habituation before accurate measures of exploration could be recorded. Secondly, more recording events may have aided in capturing the repeatability of behaviour and personality in the tray task.

#### *How to statistically quantify personality?*

The statistics of personality have not been emphasised as a feature in reviews suggesting personality as a conservation tool (Merrick & Koprowski, 2017) and has often not been executed well in this literature (Chapter 2), but it is a fundamental component of personality (Carter et al., 2013; Dingemanse & Wright, 2020). Personality studies should use intra-class correlation coefficients (ICC) to obtain repeatability estimates of behaviours. In addition, for validation and multi-behaviour testing, rather than using a PCA to approximate or validate several behaviours, using an Exploratory Factor Analysis (EFA) approach is more

appropriate (Budaev, 2010; Nakagawa & Schielzeth, 2010; Stoffel et al., 2019). Not only are ICC and EFA approach perhaps the best way to quantify personality, but they will also help with later meta-analysis of results (Dingemanse & Wright, 2020). While these are best practice suggestions, several other approaches may be valid (Dingemanse & Wright, 2020); however, most of the best papers in the field at least use the Nakagawa & Schielzeth, (2010) approach to repeatability estimation (Chapter 2).

### The usefulness of personality for conservation

The second requirement for personality to be useful for conservation is that personality measures should help conservationists make decisions to meet the conservation goals of the species being studied. Therefore, for personality measures to be useful, they should be linked to ecological variables that conservationists care about, like survival or reproduction. However, while assumptions of the types of relationships between personality traits and critical ecological variables can be made (Merrick & Koprowski, 2017), they do not appear to be universal in conservation settings. There were several examples in the studies reviewed in Chapter 2 where personality traits had differing relationships to ecologically important variables. For example, boldness had no relation to age in studies of San Joaquin kit fox (*Vulpes macrotis mutica*) and cheetahs (*Acinonyx jubatus*) but was positively related to age in dunnocks (*Prunella modularis*) (Bremner-Harrison et al., 2018; Holtmann et al., 2017; Wielebnowski, 1999). Furthermore, boldness was not related to survival in desert tortoises (*Gopherus agassizii*) or Blanding's turtles (*Emydoidea blandingii*), yet was positively related to survival in European mink (*Mustela lutreola*) and burrowing bettongs (*Bettongia lesueur*), and negatively related to survival in swift fox (*Vulpes velox*), pheasants (*Phasianus colchicus*), Spotted hyenas (*Crocuta Crocuta*), Yellow-spotted Monitors (*Varanus panoptes*) and brushtail possums (*Trichosurus vulpecula*) (Allard et al., 2019; Bremner-Harrison et al., 2004; Germano et al., 2017; Haage, Maran, et al., 2017; Madden & Whiteside, 2014; May et al., 2016; J. W. Turner et al., 2020; Ward-Fear et al., 2019, 2020; West et al., 2019). Similar variation in the nature of ecological links to personality measures was apparent in exploration, with it being positively related to survival in desert tortoises (*Gopherus agassizii*) but negatively related to survival in Blanding's turtles (*Emydoidea blandingii*). Furthermore, the relationship between exploration and detectability varied, with a positive relationship in Bahamas mosquitofish (*Gambusia hubbsi*) and a negative relationship in Blanding's turtles (*Emydoidea blandingii*) (Allard et al., 2019; Germano et al., 2017; Heinen-Kay et al., 2016). Each conservation context is unique, so relying on assumptions based on previous literature on how personality should

relate to ecological variables may not be the best path forward for conservationists. Indeed, this was likely to be a key issue with the way I approached the application of personality in toutouwai conservation. I expected previous findings would likely be present in this system, and as a result, I did not take thorough ecological measures across a range of contexts. Moreover, I was working with a system ideal for the investigation of personality in a wild context, something that will be harder to find elsewhere. The null results reported in Chapters 3 and 4 highlight a need for more traditional personality investigations to take place prior to implementing personality as a tool. Determining the ecological links of personality measures have been suggested as a requirement for future studies that are to be submitted to *Ethology* and related journals (Dingemanse & Wright, 2020). Increasing investigation into the possible ecological links will mean that personality measures are more valuable to conservationists and allow behaviourists to test assumptions to better understand personality from an evolutionary perspective, particularly because personality appears to be heritable (Dingemanse & Wright, 2020).

There may be space for incorporating personality prior to the establishment of ecological links with personality measures in some cases. If conservationists can bear the burden of early adoption of personality measurement, we can address a common criticism of personality, namely that behavioural repeatability is often estimated over time spans that are too short (Bell et al., 2009; Carter et al., 2013). While this thesis is also guilty of measuring behaviour over short time spans, it does serve as a proof-of-concept to demonstrate that personality can readily be measured over the lifespan of toutouwai as part of regular monitoring procedures. Many conservation systems provide an ideal context for the long term measurement of behavioural data. Provided that adaptations to conservation protocols can be made that facilitate repeated behavioural measurement, conservation contexts provide an exciting opportunity to record and analyse the effects of personality over more ecologically valid periods. Simultaneously, important ecological variables could also be recorded as part of a conservation management plan, allowing for future investigations of the ecological function of the personality measures. This could be as simple as recording the time of arrival when entering an individual's territory or the time to return to the nest during the breeding season. Overtime including records of repeated behaviour observed under conservation management could provide an extremely useful dataset to establish quick behavioural measures that indicate something ecologically important that conservation managers would want to know. Ultimately, the decision as to whether to implement this type of data collection programme long term will



be at the discretion of conservation managers, as their resources will be limited.

In summary, personality should only be applied to systems that can cope with some degree of additional investment in time and resources because these are already primary drivers of conservation failures (Catalano et al., 2019). Whether or not to incorporate personality into a conservation context is a decision that can only be made by the conservation managers involved in the preservation of that species. However, this decision will need to be predicated on whether or not the personality measures will assist conservation management, something that can only be determined through experimental work within the species of concern. To overcome this problem, both conservationists and personality researchers must work collaboratively to develop tools that have the best chance of being useful in improving conservation goals. Not every personality test or personality trait is measurable in every conservation dependent species, so behaviourists and conservationists need to collaboratively identify what is feasible, what is measurable and what information will be valuable to the conservation of the species. Through this collaboration, decisions can be made on when, where and how personality measures can be made in a way that maximises the quality of personality measurement and the value to conservationists

### Incorporating personality into future toutouwai conservation

I have argued that personality can be incorporated into conservation prior to establishing ecological function if there is a negligible increase in resources, and opportunities for appropriate personality measurement can be made. To demonstrate this concept, I will describe how personality could be incorporated into the future conservation of toutouwai.

Toutouwai fair better than many other endemic avifaunae in Aotearoa-New Zealand, but still rely heavily on conservation interventions to exist at substantial population sizes (Armstrong et al., 2000; Collen et al., 2014; Robertson et al., 2013). The territoriality, habituation to human presence and ability to colour ID band individuals makes them an ideal candidate for repeated measures of individual behaviour (Collen et al., 2014). Current best practices for toutouwai translocation consider population diversity, emphasising even sex ratios and including different ages (Collen et al., 2014). However, the importance of behavioural diversity is not mentioned in the translocation protocols, despite capture techniques having the potential to select for personality types (Biro, 2013; Hammond et al., 2021; Roche et al., 2016; van de Pol, 2012). The most important selective event for toutouwai is during the pre-conditioning and capture phases of the translocation procedure. The translocation protocol describes pre-conditioning as training toutouwai to take Mealworms

(hereafter MW; *Tenebrio molitor*) as a food source and associate it with a noise (clapping) or a clear patch of forest floor (Collen et al., 2014). Eventually, individuals can be trained to take MW from near people and alongside a trap, habituating them to the presence of unfamiliar or potentially risky objects. If this process is done under time constraints, as many conservation endeavours are, individuals that are bolder or more explorative may make it through to the capture process, while shyer or less explorative individuals are excluded for taking too long. The behavioural selection of individuals could have consequences for both the source and founder populations if personality is an integral part of the ecology of toutouwai, as has been shown in other passerine species (Abbey-Lee et al., 2016; Araya-Ajoy & Dingemanse, 2017; Jablonszky et al., 2017, 2018; Klueen et al., 2014). Current protocols describe monitoring during the breeding season as one of the best ways to identify the sex of adult toutouwai and the post-breeding season (March-May) as a good time for translocation (Collen et al., 2014). Monitoring the population through the breeding season (September – February) helps select candidates for translocation based on their reproductive history, and post-translocation monitoring is suggested as an essential feature of translocations to ensure an understanding of why translocations succeed or fail (Collen et al., 2014).

During a toutouwai translocation project, alterations to the selection process should be made to test if the current translocation protocols are selected for certain personality types. The first alteration would be a requirement that a random selection of individuals in the source population goes through pre-conditioning and capture processes regardless of speed to habituate and capture. The processes of pre-conditioning, habituation, and trapping toutouwai then serve as opportunities to take repeated measures of behaviour. A single behaviour measure like latency to approach or latency to acquire a MW will not increase resource expenditure significantly as it only requires a stopwatch and a notebook to record, but it will require validation with known personality tests at some stage. Once habituated, prior to capturing, multi-behaviour open field/novel object and threat stimuli tasks could be given to measure exploration and boldness. Once captured, physiological measures can be taken such as tarsus and wing length, age estimation, and sex. Individuals will then be placed in a container for transport; once in the container, the behaviours of how the individual moves can be used as a novel environment test to measure exploration. Alternatively, novel object and threat stimuli tests could be performed during this short period of captivity. At the release site, the movements post-release can also serve as a novel environment test in a different context. After release, open field/novel object and threat stimuli tests could be repeated. During post-release

monitoring, measures of survival, reproduction, and territory size can be recorded as important ecological variables. The measures taken during the capture process can be validated by investigating their relationship to the better contextualised open field/novel object and threat stimuli personality tests. Analysing the behavioural measures together, it could then be determined if the current selection process for translocation is selecting individuals of a particular personality type and if personality traits are related to physiological aspects like size, age or sex, alongside ecological variables like reproduction and survival post-release. Moreover, suppose personality tests were performed during both pre and post translocation. In that case, this could serve as an interesting case to see if the experience of translocation impacts individual behaviour. The extent to which personality tests are included in the translocation and post-release monitoring of toutouwai will ultimately be up to the project managers. However, this thesis has demonstrated that both open field and threat stimuli tests are feasible in toutouwai.

### Concluding remarks

I believe personality has a place in conservation, but perhaps in not as many contexts as has been previously suggested. The motivation to incorporate personality should be to improve or work toward a conservation goal, not just to do it because it can be done. Unless there is an apparent reason to incorporate personality based on findings of ecological validity in the species, or the project can accommodate increasing the time and resources required to measure personality appropriately, there needs to be careful consideration of whether or not to incorporate personality into a conservation management practice. Ultimately I do not see conservationists adopting personality as a tool, but rather personality researchers collaborating with conservationists to use conservation systems as laboratories for investigating personality. Conservationists can then use the outcomes of these investigations into personality in conservation systems, but it will take time to realise the usefulness of personality measures.

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## Appendices

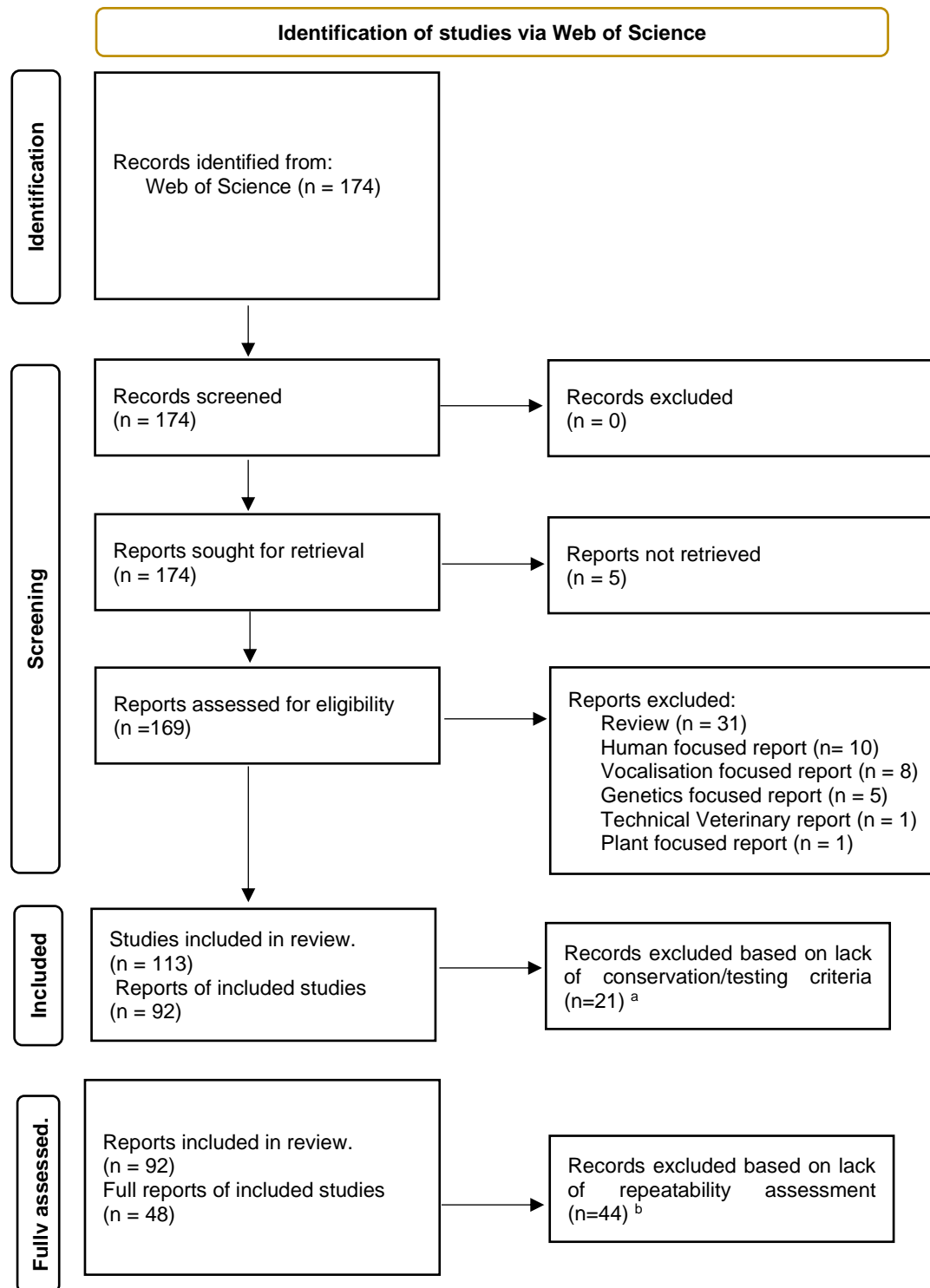
Appendix S1. List of personality tests from Réale et al (2007) to better define tests.

Personality test	Definition
Activity	A subject is equipped with monitoring equipment. e.g. radio, acoustic, PIT tags). Time spent being active recorded.
Emergence	A modified version of the open-field test if a subject is emerging into a novel environment. Typically, latencies to emerge from a shelter or resume normal behaviour are recorded.
Flight initiation distance	A subject is approached by a human experimenter or stimulus at constant velocity. The animals' flight initiation distance is recorded
Foraging	A subject is observed foraging or given a patch to forage. Percent time spent foraging and movement typically measured.
Mirror image stimulus	A subject is presented with mirror. Aggressive display or contact are typically measured.
Movement tracking	A subject is observed and/or outfitted with tracking equipment. Tracking of movement through space is typically measured. Often performed in conjunction with another test.
Novel environment	A modified version of the open-field test; a subject is introduced into an unfamiliar environment, the environment may or may not include novel stimuli, or familiar stimuli arranged in a novel manner. Movements, location, and interaction with stimuli typically measured.
Novel object	A subject is presented with a novel object. Latency to approach the object close to a food source and/or percent time spent in contact with the object typically measured.
Open-field	A subject is introduced into an arena, usually novel. Can be 'forced' if the subject is given no choice to enter or 'free' if it is allowed to enter at will. Movements and location in the arena are typically measured.
Predator presentation	A subject is presented with a real or model predator. Typically measures avoidance or inspection of the predator.
Predator stimulus	A subject is presented with something approximating a predatory action e.g., predator scent, predator sound. Startle response near a food patch and latency to return to the food source are typically measured.
Proximity to conspecific	A subject's tendency to approach a conspecific in an adjacent compartment. Latency and time spent in proximity typically measured.
Resistance to handlers	Holding subject in hand (often during banding/tagging), where latency to move and/or number of movements are measured.
Response to threat stimuli	A subject is presented with a threatening stimulus e.g., human chase is performed on subjects. Typically, latency to enter a trap or probability of capture are measured.
Separation	A subject is removed from a social group. Reaction to separation from a group/latency to re-join a group typically measured.
Social interactions, dyadic encounter	A subject is introduced to a group/pair. Reaction to the presence of a conspecific, latency of attack, solicitation of interactions typically measured
Tonic immobility	Forcing a subject to a state of tonic immobility (typically fish), where latency to move is measured.
Trappability	Capture of subject where tendency to fight, attack or bite is usually measured.

Appendix S2. List of conservation contexts and corresponding definitions as described in Griffiths & Dos Santos, 2012.

Conservation context	Definition
Community based conservation	Projects that incorporate improvement to the lives of local people while conserving areas through the creation of national parks or wildlife refuges.
Community ecology	Species interactions, invasive species, succession, competition, predation, and diversity work.
Economics	Production, distribution, consumption of goods, all financial aspects of wildlife and conservation.
Habitat change	Habitat loss fragmentation, pollution, disturbance, succession, climate change.
Habitat management	Human based interventions to enhance conservation.
Population biology	The study of biological populations of organisms, including population declines, trends, factors influencing population size, population dynamics, reintroduction of species, rehabilitation of species, relocation and population genetics.
Protected areas	Studies in which parks and reserves and their associated fauna and flora are the main focus.
Species conservation	Phylogenetic and taxonomic related work, single and multiple species case studies.
Sustainable resource use	Sustainable and unsustainable utilization of wildlife.
Wildlife disease	Wildlife disease in general, including genetic problems.
Wildlife law & policy	Common law, treaties, conventions, regulations and policies which seek to protect the natural environment which may be affected, impacted or endangered by human activities. Additional factors dealing with environmental safety standards.
Wildlife trade	The sale (legal or illegal) of animals and plants and their products.
Conservation education	Promoting public education and awareness in relation to the conservation.

### Appendix S3. PRISMA flow diagram for systematic review



<sup>a</sup>These reports had missing information therefore they were excluded from further analysis.

<sup>b</sup>These records did not show evidence of repeatability estimation, therefore they were excluded from reporting on repeatability methodology, personality traits, ecological/physiological traits, relationship, validity estimation, and conservation ranking.

*Modified From:* Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 2021;372:n71. doi: 10.1136/bmj.n71

For more information, visit: <http://www.prisma-statement.org/>

Appendix S4. Datasheet summarising information on reports assessed by systematic review. Datasheet can be accessed by following the link.

<https://drive.google.com/drive/folders/1LU4wbeWNXlv3hNMMTcZwSUqQAly0S9Uq?usp=sharing>



Appendix S5. Reference list of all studies captured during the systematic review

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Appendix S4. Reports identified as attempting to assess repeatability of behaviour captured during systematic review of studies incorporating personality and conservation

Source <sup>a</sup>	# <sup>b</sup>	Country	Species	Conservation context	Personality trait(s)	Repeatability method
(Allard et al., 2019)	1	USA	Blanding's turtles <i>Emydoidea blandingii</i>	Population biology	exploration	Intraclass Correlation Coefficient
(Andersson et al., 2014)	2	Sweden	domestic rabbit <i>Oryctolagus cuniculus domesticus</i>	Sustainable resource use	exploration, activity	Formulaic
(Arroyo et al., 2017)	3	France	Montagu's harrier <i>Circus pygargus</i>	Habitat change	boldness	Mixed effects model
(L. Baker et al., 2016)	4	USA	kangaroo rats <i>Dipodomys stephensi</i>	Population biology	exploration	Correlation
(Bastille-Rousseau & Wittemyer, 2019)	5	Kenya	African elephant <i>Loxodonta africana</i>	Habitat use	activity	permutation regression
(Bremner-Harrison et al., 2004)	6	USA	swift fox <i>Vulpes velox</i>	Population biology	boldness	Correlation
(Bremner-Harrison et al., 2018)	7	USA	San Joaquin kit fox <i>Vulpes macrotis mutica</i>	Population Biology	boldness	Kendall's coefficient of concordance
(Carbillet et al., 2019)	8	France	wild roe deer <i>Capreolus capreolus</i>	Habitat change	boldness	Mixed effects model
(Carlson & Langkilde, 2013)	9	USA	American Bullfrog <i>Lithobates catesbeianus</i>	Community ecology	activity, boldness, exploration	Intraclass Correlation Coefficient
(Carrete et al., 2016)	10	Argentina	burrowing owls <i>Athene cunicularia</i>	Habitat change	boldness	Mixed effects model
(Carrete & Tella, 2010)	11	Argentina	burrowing owl <i>Athene cunicularia</i>	Habitat change	boldness	Mixed effects model
(Castanheira et al., 2016)	12	Portugal	gilthead seabream <i>Sparus aurata</i>	Sustainable resource use	boldness	Correlation
(Ellenberg et al., 2015)	13	New Zealand	Fiordland crested penguins <i>Eudyptes pachyrhynchus</i>	Population biology	boldness	Correlation
(Finger et al., 2018)	14	USA	lemon sharks	Sustainable resource	sociability	Correlation, linear Modelling

(Geffroy et al., 2015)	15	France	<i>Negaprion brevirostris</i> European eel	use Population biology	activity	Mixed effects model, Bayesian modelling
(Germano et al., 2017)	16	USA	<i>Anguilla anguilla</i> desert tortoises	Population biology	exploration	Correlation
(Haage, Maran, et al., 2017)	17	Estonia	<i>Gopherus agassizii</i> European mink	Population biology	boldness	Formulaic
(Hammond et al., 2021)	18	USA	<i>Mustela lutreola</i> Mountain yellow-legged frog	Population biology	activity, exploration	Intraclass Correlation Coefficient
(Heinen-Kay et al., 2016)	19	Bahamas	<i>Rana muscosa</i> Bahamas mosquitofish	Habitat change	exploration	ANOVA
(Hertel et al., 2019)	20	Sweden	<i>Gambusia hubbsi</i> European brown bear	Habitat use	activity, exploration	Bayesian Modelling
(Holtmann et al., 2017)	21	New Zealand	<i>Ursus arctos</i> dunnocks	Habitat change	boldness	Intraclass Correlation Coefficient
(Kowalski et al., 2019)	22	Germany	<i>Prunella modularis</i> Common Voles	Population biology	exploration	Mixed effects model
(Dutra et al., 2016)	23	Brazil	<i>Microtus arvalis</i> Saffron finches	Population biology	boldness	ANOVA
(Madden & Whiteside, 2014)	24	UK	<i>Sicalis flaveola</i> phesants	Sustainable resource use	boldness	Mixed effects model
(Maes et al., 2013)	25	Belgium	<i>Phasianus colchicus</i> Natterjack toads	Habitat use	activity	Intraclass Correlation Coefficient
(Martin-Wintle et al., 2017)	26	China	<i>Bufo calamita</i> giant panda	Species conservation	aggression, activity, boldness, sociability	Intraclass Correlation Coefficient
(May et al., 2016)	27	Australia	<i>Ailuropoda melanoleuca</i> brush-tail possums	Population biology	Boldness	Correlation
(Mettke-Hofmann et al., 2020)	28	Germany	<i>Trichosurus vulpecula</i> Gouldian finch	Habitat use	Exploration	Mixed effects model
			<i>Erythrura gouldiae</i>			

(Michelangeli et al., 2016)	29	Australia	delicate skink <i>Lampropholis delicata</i>	Community ecology	activity, exploration, sociability, boldness	Correlation Intraclass Correlation Coefficient
(Nogueira et al., 2017)	30	Brazil	collared peccary <i>Pecari tajacu</i>	Habitat change	exploration	Correlation
(Nogueira et al., 2021)	31	Brazil	Paca <i>Cuniculus paca</i>	Sustainable resource use	activity	Correlation
(Diaz Pauli et al., 2019)	32	Norway	Medaka <i>Oryzias latipes</i>	Habitat change	boldness	Mixed effects model
(Schwarz et al., 2021)	33	Ecuador	Galápagos sea lions <i>Zalophus wollebaeki</i>	Habitat change	activity	Cluster modelling
(Silva et al., 2014)	34	Norway	Nile tilapia <i>Oreochromis niloticus</i>	Sustainable resource use	activity	Correlation
(Skinner & Miller, 2020)	35	Canada	Eastern garter snakes <i>Thamnophis sirtalis sirtalis</i>	Population biology	boldness, sociability	Mixed effects model
(Spiegel et al., 2015)	36	Australia	sleepy lizards <i>Tiliqua rugosa</i>	Habitat use	aggression, boldness	Mixed effects model
(Tetzlaff et al., 2018)	37	USA	eastern box turtles <i>Terrapene carolina</i>	Habitat use	exploration	Mixed effects model
(J. W. Turner et al., 2020)	38	Kenya	Spotted hyenas <i>Crocuta crocuta</i>	Habitat change	boldness	Mixed effects model
(Végvári et al., 2011)	39	Finland Hungary	common crane <i>Grus grus</i>	Habitat use	boldness	Mixed effects model
(Villegas-Ríos et al., 2017)	40	Norway	Atlantic Cod <i>Gadus morhua</i>	Sustainable resource use	activity, boldness	Bayesian modelling
(Ward-Fear et al., 2019)	41	Australia	Yellow-spotted Monitors <i>Varanus panoptes</i>	Community ecology	boldness	Mixed effects model
(Ward-Fear et al., 2020)	42	Australia	yellow-spotted monitors <i>Varanus panoptes</i>	Community ecology	boldness	ANOVA
(Webber & Willis, 2020)	43	Canada	little brownbats	Wildlife disease	activity	Correlation

(Wengström et al., 2016)	44	Sweden	<i>Myotis lucifugus</i> Brown trout <i>salmo trutta</i>	Wildlife disease	activity	Bayesian modelling Correlation
(West et al., 2019)	45	Australia	burrowing bettongs <i>Bettongia lesueur</i>	Population biology	boldness	Intraclass Correlation Coefficient, Mixed effects model
(Wielebnowski, 1999)	46	USA	cheetahs <i>Acinonyx jubatus</i>	Species conservation	boldness	Correlation
(Williams et al., 2019)	47	UK Ireland	African elephant <i>Loxodonta africana</i> Asian elephant <i>Elphas maximus</i>	Species conservation	sociability	Intraclass Correlation Coefficient
(Wong et al., 2017)	48	Australia	wide-band anemonefish <i>Amphiprion latezonatus</i>	Population biology	Boldness, aggression	Mixed effects model

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<sup>a</sup>The reports that assessed repeatability organised alphabetically.

<sup>b</sup> These numbers are only used to indicate corresponding notations in Appendices S8 & S9

Appendix S7. Table of results from Fishers' row-wise exact test. Testing category, Fisher's row wise estimate, Simulated P value (P (sim), 95% Confidence Interval Low & High (95% CIL, 95% CIH), and adjusted P value (P (adj) reported.

Testing category	Fishers' row wise estimate	P (sim)	95% CIL	95% CIH	P (adj)
1999	0	1	0	42.54617	1
2004	0	1	0	42.54617	1
2006	Inf	0.226	0.205804	Inf	1
2010	0	1	0	42.54617	1
2011	1.09196	1	0.013619	87.54205	1
2012	Inf	0.0486	0.742314	Inf	0.68
2013	1.094153	1	0.076182	15.71544	1
2014	1.096449	1	0.138929	8.65494	1
2015	0.352485	0.618	0.006502	4.58461	1
2016	0	0.00596	0	0.57919	0.0894
2017	1.657349	0.44	0.534995	5.353734	1
2018	2.346676	0.302	0.46368	15.47682	1
2019	0.32083	0.124	0.052067	1.409568	1
2020	2.042692	0.272	0.600685	7.577494	1
2021	0.538395	1	0.008869	10.69011	1
Amphibian	0.716871	1	0.057252	6.582497	1
Bird	1.616356	0.456	0.545668	4.949898	1
Fish	0.687021	0.58	0.182337	2.406984	1
Invertebrate	Inf	0.105	0.457699	Inf	0.56
Mammal	1.158124	0.833	0.465625	2.889014	1
Reptile	0.241473	0.0934	0.023642	1.31202	0.56
Community ecology	1.404978	0.732	0.28033	7.605318	1
Habitat change	0.490923	0.267	0.119999	1.755672	1
Habitat use	0.92562	1	0.234167	3.543099	1
Population Biology	1.38024	0.515	0.536965	3.583689	1
Protected areas	Inf	0.478	0.027972	Inf	1
Species conservation	2.346676	0.302	0.46368	15.47682	1
Sustainable resource use	0.432374	0.321	0.067492	2.057717	1
Wildlife disease	0.538395	1	0.008869	10.69011	1
Activity	1.068888	1	0.086389	9.687084	1
Emergence Test	4.980189	0.158	0.387259	267.5795	1
Flight initiation distance	0.788646	1	0.121818	3.907817	1
Foraging test	1.210924	1	0.169869	7.50373	1
Mirror image stimulus	0.390195	0.648	0.007723	4.095659	1
Movement tracking	1.138374	0.796	0.340558	3.603395	1
Novel environment test	0.331455	0.104	0.057439	1.299882	1
Open-field test	0.784049	0.766	0.163277	3.131045	1
Predator presentation test	0.516302	0.71	0.049041	3.042091	1
Predator stimulus test	0.957761	1	0.142146	5.186943	1
Resistance to handlers	Inf	0.146	0.302442	Inf	1
Response to threat stimuli	4.69013	0.0169	1.254237	21.80314	0.237
Social interactions	0.687904	0.765	0.146119	2.644983	1
Trappability	0.667644	0.74	0.106205	3.10616	1

Appendix S8. Examples of personality tests used in studies that incorporate personality and conservation captured by systematic review, sorted by testing condition and conservation context. Superscript citation numbers refer to Appendix S6.

Conservation context	Testing condition	Tests
Community ecology	Wild	novel environment test <sup>41</sup> novel object test <sup>41</sup> social interactions <sup>41</sup>
	Captive	flight initiation distance <sup>42</sup> foraging test <sup>9</sup> mirror image stimulus <sup>9</sup> movement tracking <sup>29</sup> open field test <sup>9</sup> predator presentation test <sup>9</sup> response to threat stimuli <sup>41</sup> .
Habitat change	Wild	activity <sup>11,3</sup> mirror image stimulus <sup>8</sup> movement tracking <sup>10,3</sup> novel environment test <sup>8,21</sup> novel object test <sup>8,38</sup> open field test <sup>11,21</sup> predator presentation test <sup>38</sup> response to threat stimuli <sup>33</sup> trappability <sup>19</sup>
	Captive	novel environment test <sup>30</sup> novel object test <sup>30</sup> predator presentation test <sup>30</sup> trappability <sup>32</sup>
Habitat use	Wild	emergence test <sup>20</sup> foraging test <sup>20</sup> movement tracking <sup>20</sup> novel environment test <sup>39,20,5,36</sup> novel object test <sup>36</sup> open field test <sup>20</sup> predator presentation test <sup>20</sup> predator stimulus test <sup>36</sup> social interactions <sup>20,36</sup>
	Captive	flight initiation distance <sup>21</sup> novel environment test <sup>20</sup> novel object test <sup>19,20</sup> predator stimulus test <sup>21</sup>
Population biology	Wild	flight initiation distance <sup>18</sup> novel object test <sup>13,45</sup> predator stimulus test <sup>18,45</sup> social interactions <sup>7,45</sup> trappability <sup>13,48</sup>
	Captive	flight initiation distance <sup>17,18</sup> foraging test <sup>17</sup> human survey <sup>15</sup> mirror image stimulus <sup>15,1</sup> movement tracking <sup>23,4</sup> novel environment test <sup>17,23</sup> novel object test <sup>22</sup> predator presentation test <sup>17</sup> predator stimulus test <sup>18,1</sup> resistance to handlers <sup>16</sup> response to threat stimuli <sup>17</sup> social interactions <sup>6,22</sup> trappability <sup>16</sup>
Species conservation	Wild	NA
	Captive	open field test <sup>46,26</sup> movement tracking <sup>47</sup>
Sustainable resource use	Wild	flight initiation distance <sup>40</sup> response to threat stimuli <sup>40</sup>
	Captive	activity <sup>34</sup> foraging test <sup>24</sup> movement tracking <sup>30</sup> novel object test <sup>34,24</sup> open field test <sup>12</sup> predator presentation test <sup>24</sup> social interactions <sup>12,34</sup> trappability <sup>14,2</sup>
Wildlife disease	Wild	NA
	Captive	movement tracking <sup>43</sup> , novel object test <sup>44</sup>

Appendix S9. Examples of the relationships found between personality and other traits in studies that incorporate personality and conservation captured by systematic review. Superscript citation numbers refer to Appendix S6. N = No relationship found, Y(+) = A positive relationship between the personality trait and ecological/physiological trait, Y(-) = A negative relationship between the personality trait and the ecological/physiological trait. Y (Other) = a complex relationship between personality trait and ecological/physiological trait.

Personality trait(s)	Ecological Physiological traits	N	Y (+)	Y (-)	Y (Other)
Activity	Growth	age <sup>33,46</sup> body condition <sup>33</sup> mass <sup>33</sup> rearing condition <sup>46</sup>			
	Health	faecal glucocorticoid metabolites <sup>31</sup>	parasitic infection <sup>44</sup>	serotonergic activity in the hypothalamus <sup>32</sup>	
	Reproduction	breeding status <sup>46</sup> sex <sup>46</sup>	breeding success (when pairs are dissimilar) <sup>26</sup>		sex (males more active) <sup>2</sup>
	Survival				
	Other Behaviour	habitat selection <sup>20</sup> trapping method <sup>29</sup> detectability <sup>18</sup>	movement speed <sup>25</sup> social association <sup>43</sup> roost emergence <sup>43</sup> abnormal behaviour <sup>31</sup> detectability <sup>18</sup>		habitat use (higher in low resistance habitats) <sup>25</sup> difference between populations <sup>40</sup>
Aggression	Growth	age <sup>46</sup> rearing condition <sup>46</sup>	size rank <sup>48</sup>		
	Health	baseline faecal cortisol concentration <sup>4</sup>			
	Reproduction	breeding status <sup>46</sup> sex <sup>46</sup>	breeding success (when male more aggressive than female) <sup>26</sup>		
	Survival	survival <sup>1</sup>			
	Other Behaviour	detectability <sup>1</sup>	group size <sup>48</sup>		space use (quadratic response) <sup>36</sup>



Boldness	Growth	age <sup>7,47,46</sup>	body size <sup>24</sup>	size <sup>16</sup>	age <sup>21</sup>	body mass	body size <sup>32,</sup>	age (juveniles more) <sup>6</sup>
		rearing origin <sup>47</sup>	method <sup>46</sup>	body weight <sup>35</sup>			food <sup>40</sup>	availability <sup>32</sup>
	Health	baseline faecal cortisol concentration <sup>4</sup>					neutrophil:lymphocyte ratio <sup>8</sup>	
	Reproduction	sex <sup>6,7,11,23,24,38,47</sup>	family <sup>6</sup>	breeding success <sup>26</sup>			nest failure <sup>3</sup>	within familial groups <sup>7</sup>
		relatedness <sup>47</sup>					to return to nest <sup>13</sup>	heritability <sup>10</sup>
								ex (males bolder) <sup>16,35,46</sup>
								breeding status (breeders bolder) <sup>46</sup>
	Survival	survival <sup>16,1</sup>	predator	survival <sup>17,45</sup>			survival <sup>6, 24, 38,41,42,27</sup>	novel
		recognition <sup>23</sup>	refugia				prey	
		use <sup>6,16</sup>					avoidance <sup>41</sup>	
	Other Behaviour	trapping	method <sup>29</sup>	distance	moved <sup>6,45</sup>		detectability, group	space use (quadratic response) <sup>36</sup>
		detectability <sup>1,18</sup>	territory	disturbance			size <sup>48</sup>	social
		location <sup>11</sup>	dispersal <sup>16</sup>	tolerance <sup>38,21</sup>	habitat		interactions <sup>47</sup>	different
		social rank <sup>38</sup>		choice <sup>39</sup>			group size <sup>48</sup>	habitat preference <sup>1</sup>
								social context <sup>12</sup>
								aggregation patterns <sup>35</sup>

Exploration	Growth	size <sup>16</sup> , age <sup>47</sup>					
	Health			plasma glucocorticoid concentrations <sup>30</sup>	baseline faecal cortisol concentration <sup>4</sup>		
	Reproduction	sex <sup>16</sup> relatedness <sup>47</sup>				sex (males more) <sup>2,47</sup> sex (females less) <sup>19</sup> heritable <sup>19</sup>	
	Survival			survival <sup>16</sup> use <sup>16</sup>	refugia survival <sup>1</sup> predation levels <sup>19</sup>	survival (positive one year, negative the other) <sup>17</sup>	
	Other Behaviour	habitat trapping detectability <sup>1,18</sup> movement <sup>22</sup> context <sup>28</sup> association <sup>43</sup> social interactions <sup>47</sup>	selection <sup>20</sup> method <sup>29</sup> social social dispersal <sup>16</sup>	detectability <sup>18</sup> movement distance <sup>1</sup> home range size <sup>1</sup> movement speed <sup>25</sup> basking likelihood <sup>1</sup>	detectability <sup>1</sup> trapping method <sup>29</sup>	habitat preference <sup>1</sup> head colour (black headed slower) <sup>28</sup>	
Sociability	Growth					age <sup>47</sup>	
	Health						
	Reproduction	relatedness <sup>47</sup>		breeding success (when male lower than female) <sup>26</sup>			
	Survival						
	Other Behaviour	trapping method <sup>29</sup> composition <sup>14</sup> association <sup>43</sup>	group social	roost social interactions <sup>47</sup>	emergence <sup>43</sup> boldness <sup>35</sup>	aggregation patterns <sup>35</sup> association network <sup>35</sup>	