USE OF PERSONALITY TO IMPROVE REINTRODUCTION SUCCESS: THE EFFECTS OF BEHAVIOURAL VARIATION WITHIN RELEASE GROUPS

TIM D. STRATTON

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Abstract

The study of personality (consistent individual differences in behaviour) is a growing area in behavioural ecology. The majority of studies have investigated the proximate or ultimate causes of these individual differences. However, there is growing interest in their practical applications, particularly to conservation. Previous studies have shown that personality scores can affect individual behaviour response after release into a novel environment. Experimental and theoretical discussions have since suggested that varying the composition of personality types within a release group may therefore affect the success of a translocation. This study investigates practical aspects of applying personality research to translocation projects using a non-endangered model species, the wood mouse (*Apodemus sylvaticus*). Chapter Two begins by confirming that wood mice have consistent personality traits using a simple personality testing procedure, carried out in the field to avoid potential biases from transporting animals to captivity. Chapter Three assesses some potential biases and confounds that may be faced from trapping and testing animals in the wild, identifying variations in trapping probability and microhabitat use between personality types. Chapter Four looks at changes in personality composition caused by long term captive breeding and the potential impacts this may have of translocation projects are discussed. In Chapter Five an experimental translocation is carried out to investigate the effect personality composition has on both individual and group success, by focussing on the key short term effects of dispersal and mortality. Overall, this study demonstrates that personality traits affect aspects of habitat use, dispersal and risk taking in the wood mouse and provides a number of recommendations for future studies and translocation projects. It is also the first study to provide empirical evidence that personality composition can affect the result of a translocation and recommends that individuals with a mix of personality types should be released.

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1 Chapter One: Background

This chapter begins by discussing common problems affecting translocation success and goes on to suggest that personality research may provide the tools to tackle some of these problems. It then defines what personality is, some common personality traits measured and how they are studied. Included here is a discussion of some of the factors that need to be considered to accurately measure personality scores, including a discussion of behavioural plasticity. This goes on to discuss some of the higher order behavioural constructs and potential additional correlates with physiology and life history that may be included. The chapter concludes with a brief discussion of the models that have been developed to explain the existence of personality traits both proximately and ultimately. Finally the aims of this project are stated and how they will be achieved.

1.1 Conservation Translocations

Translocation is currently used as an overarching term encompassing both the intentional and unintentional movement of animals. The International Union for conservation of Nature (IUCN) defines translocation as “(i) reinforcement and reintroduction within a species’ indigenous range, and (ii) conservation introductions, comprising assisted colonisation and ecological replacement, outside indigenous range” (IUCN/SSC, 2013). This study focuses on conservation translocations defined as “the intentional movement and release of a living organism where the primary objective is a conservation benefit” (IUCN/SSC, 2013). The aim of conservation translocations is to successfully establish a self-sustaining founder population at a release site. This is achieved either by releasing animals into an existing population to enhance its viability (reinforcement) or by releasing individuals to an area which the species previously occupied but has since disappeared (reintroduction; IUCN/SSC, 2013). Individual project success is often measured through the assessment of population size at a pre-defined period after release, often specifying a desired number or percentage of animals surviving and breeding within the release area. Many studies also note whether the released animals are displaying appropriate behaviours, such as activity patterns, social behaviours and breeding patterns (IUCN/SSC, 2013).

Animal translocations have been used as a tool for conservation for over 100 years, with possibly the first true reintroduction being 15 American bison (*Bison bison)* into a reserve in Oklahoma in 1907 (Kleiman*,* 1989). Costs of translocation projects are often very high, ranging into hundreds of thousands of dollars (Snyder *et al.,* 1996). Despite high financial outlay, when recorded, the success rate of translocation projects has historically been very low (Kleiman*,* 1989) and a review by Wolf *et al.* (1996) showed no improvement in success between 1989 and 1996. Recent reports on translocation success from 2008-2013 found only 45% of translocations were reported as either successful or highly successful in this time period (Soorae (ed.), 2008, 2010, 2011, 2013). In response to this poor success, combined with large resource usage, the field of reintroduction biology has emerged, with the focus on reviewing why translocations have failed in the past and improving success in the future (Armstrong and Seddon, 2008).

1.1.1 Problems with Translocation

A series of review papers have attempted to identify what factors contribute to the success or failure of translocations. Although management of factors such as high release habitat quality, multiple releases (even when releasing the same total number) and having a rapidly expanding source population (Griffith *et al.,* 1989) have been found to be important to a successful release, behaviour of the animals also consistently has a large impact. Reviews show that translocations are more likely to succeed when utilising wild caught animals than when releasing those bred in captivity (Griffith *et al.,* 1989). Evidence suggests this difference in success may be due to behavioural differences between wild and captive populations (Jule, Leaver and Lea, 2008). For example, Jule, Leaver and Lea (2008) identified that within previous carnivore reintroductions captive bred individuals suffered from a number of behavioural problems that led to decreased post release success: tameness towards humans, lack of social influence from conspecifics and lack of foraging or hunting skills.

However, it is not just behavioural deficiencies that affect translocation success, but also how individuals respond to their new habitat. Commonly cited causes of failure in translocation studies have been high post release dispersal (Mihoub *et al.,* 2011) and low survival rates (Armstrong and Seddon, 2008) shortly after release. Both of these factors effectively reduce the size of the introduced founder population and therefore the probability of successful breeding and establishment. The majority of mortality of introduced populations happens shortly after release when animals are exploring novel locations and potentially encountering unfamiliar conspecifics, competing heterospecifics and predators (Stamps and Swaisgood, 2007; Stamps, 2007). An individual's probability of survival during this period has been linked to the animal's behavioural response to these factors (Kleiman, 1989). Translocated animals also often display excessive dispersal after release, travelling further than would normally be expected in the wild (Stamps and Swaisgood, 2007). These long distance movements expose individuals to novel habitats and predators (Linklater and Swaisgood, 2008) and may divert time and energy away from activities required for survival, such as finding or creating shelter (Shier, 2006). Excessive dispersal also causes animals to move away from release habitat which has been selected to optimize the released individual's probability of survival.

Translocation projects aim to select individuals with the greatest chance of surviving and breeding in the wild with the least amount of pre-release preparation required (Kleiman, 1996; Woodroffe and Ginsberg, 1999). One potential avenue to improve the success of translocations is through measuring and manipulating individual behavioural responses. A number of recent studies have suggested that individual variation in behaviour may play a major role in the success of conservation translocations (Bremner-Harrison, Prodohl and Elwood, 2004; Pinter-Wollman, 2009; Pinter-Wollman, Isbell and Hart, 2009; Mathews *et al.,* 2005). By understanding how individual animals behave and respond to stimuli involved in an introduction it may be possible to adjust release strategies to improve success. Maximising the probability of individual success should reduce the number of individuals required to form a successful founder population and reduce the high levels of mortality often associated with translocations (Linnell *et al.,* 1997). Individual behavioural differences are commonly referred to as personalities and potentially provide the tools to tackle behavioural problems relating to translocation failure. This may avoid the need for extensive pre-release training, post-release management or intensive selective breeding employed in many translocations, or when necessary may aid to inform these processes to maximise their efficacy.

1.2 Personality

1.2.1 Defining Animal Personality

In the field of behavioural ecology there has been a recent upsurge of interest in individual behavioural variation in animals (van Oers, Klunder and Drent, 2005). Historically, individual variation has been relatively ignored, considered as noise around a ‘golden’ adaptive mean (Wilson *et al.,* 1993), often accompanied by the assumption that behaviour is infinitely variable or plastic. Traditional behavioural models such as the hawk-dove game assume that animals can instantly switch behaviour depending on which provides the greatest fitness benefits (Smith and Price, 1973). These types of models also imply that all individuals within a population are identical and will always select the most effective strategy for the situation. In contrast to this, personalities (also known as temperament or behavioural types; Reale *et al.,* 2007) are defined as consistent individual behaviour across time (and sometimes across contexts), suggesting a limit to behavioural flexibility.

The various terminology used to refer to this phenomenon may have led to the initial slow growth of the field. Although the term personality has become widely used there is, as yet, no single universally accepted term for consistent individual behavioural variation. At the 1991 Ethological conference it was decided that temperament had less anthropomorphic connotations than personality, however this has not been universally accepted as traditionally temperament has been used to describe innate behaviour from birth (Mather and Anderson, 1993). Gosling and Vazire (2002) advocate the use of the term personality by using the same criteria as for human personalities. They give evidence that animal personalities “(a) show strong levels of inter-observer agreement, (b) show evidence of validity in terms of predicting behaviours and real-world outcomes, and (c) do not merely reflect the implicit theories of observers projected onto animals." These are the same criteria as those which were used to justify human personalities when a similar debate raged in the psychological literature in the seventies and eighties (Kenrick and Funder, 1988). This study adopts the term 'personality', as despite its anthropomorphic connotations it provides an unambiguous term within the realm of animal behaviour.

Between studies there are variations in the definition of what determines a personality trait (Reale *et al.,* 2007). Two main definitions have emerged: first, a broad scale definition of a personality trait as any behaviour which differs between individuals but is consistent across time or contexts; and second, a more narrow definition of a personality trait as consistent differences in a narrow range of behaviours in a specific context. These two definitions have been discussed elsewhere as context-specific and domain-general expression of personality traits (Coleman and Wilson, 1998). Domain general traits are displayed at a similar level across a range of contexts and imply a limited flexibility of behaviour between contexts (Sih, Bell and Johnson, 2004). For example, more aggressive individuals are expected to be aggressive in mating, predator and conspecific interactions. Context-specific traits imply that an individual displays a different level of response based on the context and that individuals may display different responses in different situations (Coleman and Wilson, 1998). For example, an individual which is consistently aggressive in mating contexts may display a different level of aggression in territorial interactions.

An important component of both of these definitions of personality traits is repeatability; individuals should consistently show the same behavioural score across time. In practice this is often reduced to the animals showing the same rank order of behaviour relative to the population, allowing for population wide fluctuations in behaviour e.g. between seasons the most aggressive will still be the most aggressive, even when population mean aggression has increased due to the breeding season (Bell, 2007). However, discussion of the timescale of this consistency is often neglected. Different studies have calculated behavioural scores interpreted as reflecting personality traits which individuals consistently show over hours, days or their entire lifetimes (Sih, Kats and Maurer, 2003) and this may change their ecological and evolutionary significance. A meta-analysis by Bell, Hankison and Laskowski (2009) showed that across studies repeatabilities of individual behavioural scores were generally higher when measurements were repeated over shorter time periods.

1.2.2 Personality Dimensions

Reale *et al.* (2007) suggest that there are 5 major dimensions of personality that have been studied to date; shyness/boldness, exploration/avoidance, activity, sociability and aggressiveness. The definition and the measurement of these traits can greatly differ between studies, provoking caution when interpreting different studies from the literature (Gosling, 2001). However, Reale *et al.* (2007) acknowledge that this is an initial attempt to provide structure to the field and is open to improvement.

1.2.2.1 Boldness

Perhaps the most studied personality trait has been that of boldness. Boldness has been described as a fundamental aspect of human behavioural variation and this may also be the case in animals (Wilson *et al.,* 1994). Boldness is usually defined as the propensity to take risks but has been measured in a number of different ways (Reale *et al.,* 2007). Generally a bold animal is defined as more likely to approach novel objects (Bremner-Harrison, Prodohl and Elwood, 2004) and take risks (Reale *et al.,* 2007) and also often incorporates “the propensity to move through and explore unfamiliar space” (Fraser *et al.,* 2001). Previous studies have found that bold individuals use habitat more widely, potentially allowing them to evaluate potential mates, gain knowledge about the environment and increase their foraging ability (Boon, Reale and Boutin, 2008). However there are trade-offs to this behaviour, such as an increased risk of predation (de Azevedo and Young, 2006), and the potential to lose cached food resources or their offspring while out exploring (Boon, Reale and Boutin, 2008).

1.2.2.2 Exploration/Activity

Although exploration and activity are defined as separate traits by Reale *et al.* (2007) their distinction is less evident in the literature. Exploration is usually defined as the propensity to investigate a novel environment; however activity, which refers to the general level of activity of an animal, is regularly tested in a novel environment, blurring its interpretation. A number of suggestions have been given to tease apart the influences of activity and exploration, such as only measuring activity in a non-risky and non-novel environment (Renner, 1990; Reale *et al.,* 2007) and the use of hole-board tests to measure exploration (Martin and Reale, 2008), where the subject has to put its head into a hole rather than move around an arena to explore. However, in the literature the terms are often interchangeable and their specific interpretation must be examined on a case by case basis.

1.2.2.3 Sociability

Many species have been noted to have more and less social individuals. For example Pruitt, Riechert and Jones (2008) found that there were 2 morphs of the comb-footed spider (*Enoplognatha ovata*), a social and non-social morph; females either defended their own nest or cooperated and shared a nest with other females. In other species the distribution of sociability may be more continuous and definitions of what defines a social individual are likely to be largely species specific, but generally refer to individuals which are happy to remain in more densely populated areas. Sociability often interacts with aggressiveness (below) if less social individuals become aggressive when population densities rise (Myers and Krebs, 1971). Sociability has been measured in a number of ways including setting up dyadic encounters between individuals (Schoepf and Schradin, 2012) or presenting individuals with a mirror to provoke social responses (Boon, Reale and Boutin, 2008).

1.2.2.4 Aggression

Aggression, defined as an animal’s antagonistic response to a conspecific, has been a commonly studied trait as it has been frequently studied outside of the personality literature. Aggressiveness is usually displayed towards conspecifics in dominance (Verbeek, Boon and Drent, 1996) or mating situations (Sih and Watters, 2005). Benus *et al.* (1989) showed in a shock-avoidance study that in a stressful situation aggressive house mice (*Mus* *musculus*) were likely to employ a fight or flight response, whereas non-aggressive mice were more conservative and withdrawn. Aggression is frequently linked with sociability as mentioned above, but is also often positively related to boldness (Verbeek, Boon and Drent, 1996; Koolhaas *et al.,* 1999).

1.2.3 Applying personality research to conservation

Behavioural ecologists believe that personalities are important because they have the potential to significantly affect proximate ecological processes, such as niche expansion, dispersal and social organisation (Reale *et al.,* 2007). There is also extensive evidence that there are links between personality traits and factors important to fitness such as reproductive rate and survival (Dingemanse and Reale, 2005). To date, personalities have been identified in a wide range of taxa (Bell, Hankison and Laskowski, 2009), however the majority of research has focussed on the proximate and ultimate causes for personality rather than the potential applications of this research. Conservation science is constantly seeking ways to improve translocation success and is currently beginning to adopt an individual approach to survival and welfare (McDougall *et al.,* 2006). Studies have therefore suggested that taking into account personality may be as important as other factors such as age, sex, genetics and health when selecting individuals for release (Watters and Meehan, 2007) and has the potential to reduce individual mortality and therefore the numbers required to release to produce a self-sustaining population (Kleiman, 1989).

Variation in personality has been shown to affect dispersal, survival and reproduction, factors which strongly affect the probability of producing a self-sustaining founder population in the wild (McDougall *et al.,* 2006). In a meta-analysis of previous personality studies Smith and Blumstein (2008) looked at the effect boldness, exploration and aggression had on reproduction and survival. They found that boldness scores consistently show a positive correlation with reproductive success but negatively correlated with survival across a range of species. Similarly they found that exploration scores were positively associated with survival, and aggression was positively correlated with reproductive success.

Watters, Lema and Nevitt (2003) have suggested that personality could be practically utilised to improve translocation success by testing behaviour in captivity and using this to tailor which individuals are placed in release groups. Bremner-Harrison, Prodohl and Elwood (2004) investigated this by looking at dispersal and survival rates in the swift fox (*Vulpes velox*) during a reintroduction in the US. Using a series of simple novel object tests the study identified a consistent personality trait of boldness in captive swift foxes being prepared for release. A bold animal was defined as one which would approach novel objects faster and closer than shy individuals (Bremner-Harrison, Prodohl and Elwood, 2004). The foxes were fitted with radio-collars for post-release monitoring; radiotracking data combined with boldness scores was then used to assess the effect personality type had on release success. The study found that in the six months after release, bold swift foxes dispersed further and explored more than shyer individuals but also had a higher probability of mortality (Bremner-Harrison, Prodohl and Elwood, 2004). This research highlights that personality traits have the potential to impact translocations by affecting two factors important to release success in the period immediately after release; dispersal and survival.

1.2.3.1 Survival

Translocated populations often show high rates of mortality shortly after release, with reports of 85% mortality in mule deer (*Odocoileus hemionus*) reintroductions (McCullough *et al.,* 1997) and even as high as 97% for grey squirrels (Sciurus carolinensis) in the US (Adams, Hadidian and Flyger, 2004). This high mortality in translocations has often been attributed to high predation rates or stress-induced mortality (Teixeira *et al.,* 2007). With this, there is an ethical debate over whether animals should be released if they have a high probability of dying within days of release (Cayford and Percival, 1992). This emphasises the need to develop new release methods other than just releasing large numbers of individuals and hoping some will survive.

Personality traits have been linked to risk taking and subsequent high levels of predation on a number of occasions. The meta-analysis by Smith and Blumstein (2008) showed that boldness is consistently linked to higher reproductive success but a short lifespan, particularly in wild fish, demonstrating an obvious trade-off to this behaviour (Sih, Bell and Johnson, 2004). A number of studies of boldness have been carried out on fish, using predator inspection behaviour (where one or more fish leaves a shoal to approach a predator) as a measure of boldness. These studies have shown that bold fish, which are more likely to inspect predators and enter traps (Wilson and Godin, 2009), generally gain greater breeding and foraging success (Wilson *et al.,* 1993), but also put themselves at risk in the presence of predators, in some cases through fighting conspecifics and drawing the attention of predators (Brick and Jakobsson, 2002). These studies suggest that bolder individuals may do well in low risk environments by outcompeting shyer individuals but may suffer fitness costs in riskier environments through injury, parasitism or enhanced mortality risks (Sih, Kats and Maurer, 2003; Kortet, Hedrick and Vainikka, 2010).

However, patterns of survival are likely to rely on complex interactions between personality and the environment (McDougall *et al.,* 2006). In some species or situations, lower levels of activity and boldness can result in higher mortality rates, such as in captive reared voles (*Microtus rossiaemeridionalis)* where being sedentary increased odour levels providing cues for predators (Banks, Norrdahl and Korpimaki, 2002). Whereas in other situations higher boldness and activity can potentially expose individuals to higher rates of predation and other negative effects (van Oers *et al.,* 2004; Woodroffe and Ginsberg, 1999). In different reintroduction studies survival rates have been either positively (Sinn *et al.,* 2014) or negatively (Bremner-Harrison, Prodohl and Elwood, 2004) related to boldness.

In a comprehensive study of survival in great tits (*Parus major*) over a number of years, Dingemanse and Reale (2005) showed that survival rates for individuals with different personality types changed over time based on environmental factors. When there was low competition for food less exploratory females had higher rates of survival, whereas when there was high competition for food more exploratory females had higher survival. Then in the following spring if there were high recruitment rates more exploratory males had higher survival rates, but in years with low recruitment rates less exploratory males had greater survival. The study suggested these results were because more exploratory individuals performed better when competing for a resource (e.g. females competing for food, or males competing for mates), but did less well when competition was not as strong.

Cause and effect of behaviour can be unclear as some studies have found that individual's adjust their personality in response to future survival probabilities. Nicolaus *et al. (*2012) found that individuals with decreased survival probability increased their risk taking and therefore level of boldness, presumably to increase their fitness in the short term. However, Cole and Quinn (2014) found that shyer individuals seemed more focussed on their long term fitness benefits as they prioritised their own survival over reproductive investment more than bold individuals, by taking longer to return to incubating their eggs after being presented with a novel object. Results like these leads to complication in interpreting behaviour seen in the field and promotes caution in leaping to broad conclusions before understanding the different factors which may be affecting behaviour.

Stress has been defined as 'the biological response elicited when an individual perceives a threat to its homeostasis' (Moberg, 1999), the source of this stress is referred to as the stressor. The adverse effects of stress are caused when the cost of responding to the stressor is large enough that it requires diverting resources from normal biological function. Stress can be a serious cause of mortality in translocation programmes and can come from many sources, including human-induced environmental disturbance, capture, veterinary procedures, transport, adaptation to a novel environment and tracking (i.e. the effect of radio collars Teixeira *et al.,* 2007). Personality can affect the way in which individuals respond to this stress (Koolhaas *et al.,* 1999). For example, Fucikova *et al. (*2009) found that bolder and more exploratory great tits showed a greater stress response to handling than less exploratory individuals. To survive in a novel environment, released animals need to be behaviourally competent (Mathews *et al.,* 2005), however stress can impair cognitive function and decision making (Mendl, 1999). This effect can last for a significant time after the event; a study showed that exposing tree shrews (*Tupaia belangeri)* to a stressor affected their memory for up to ten weeks without being reinforced (Ohl and Fuchs, 1998). Therefore, understanding individual responses to specific stressors could help to identify which individuals suffer less from the negative effects of stress or to particular forms of stressor. This data could then be applied to reduce the negative impacts of stress in a translocation.

1.2.3.2 Dispersal

Dispersal has been described as a key life history trait (Gaines and McClenaghan, 1980) and has previously been linked to individual traits such as size, weight (O'Riain, Jarvis and Faulkes, 1996; Holekamp, 1984), age, condition (Gaines and McClenaghan, 1980) or previous experience (Krackow, 2003). In a review, Cote *et al.* (2010) identified that dispersal is also often related to the personality traits of boldness, sociability or aggressiveness. In nature dispersal tendency may be correlated with personality traits which are more likely to succeed when entering a new environment (Sih *et al.,* 2004). However due to the artificial nature of a translocation program, this selection often needs to be made by the researchers prior to release. Animals tend to naturally disperse as juveniles; leading many previous reintroduction studies to utilise juveniles in their release group selection (Sarrazin and Legendre, 2000).

In studies of invasion biology, colonising individuals are often found to have different personality traits than more sedentary individuals. Studies have found similar patterns; in mole rats (*Heterocephalus glaber*) dispersing individuals measured post dispersal had higher rates of locomotory and feeding activities (O'Riain, Jarvis and Faulkes, 1996), common lizard (*Zootoca vivipara*) dispersers were more active 8-10 months after dispersal (Meylan *et al.,* 2009) and male house mice (*Mus musculus*) dispersal latency decreased with increasing exploratory activity before dispersal (Krackow, 2003). Duckworth and Badyaev (2007b) investigated an invasive bluebird (*Sialia mexicana*) in North America. They found that it was the highly aggressive males that dispersed, but although the trait for aggression was highly heritable it was quickly lost from the population once settled in a new area. Aggressive males did well in aggressive encounters but showed reduced reproductive investment, causing a substantial reproductive cost. This suggests that dispersing types may have an advantage when colonising a new environment but there may be fitness costs in other situations.

However, even in stable populations dispersal has been consistently positively linked to aggression (Duckworth and Badyaev, 2007b), boldness (Short and Petren, 2008), activity (O'Riain, Jarvis and Faulkes, 1996) and exploration (Dingemanse *et al.,* 2003). Dingemanse *et al,* (2003) found that natal dispersal tendency was related to both individual exploration score but also parental exploration score. Dispersal has also been negatively correlated to sociability (Cote and Clobert, 2007), a pattern predicted by Bekoff (1977), who suggested that individuals who socialise with others should be less likely to disperse. For example, Blumstein, Wey and Tang (2009) found that dispersal in yellow bellied marmots (*Marmota flaviventris*) was negatively related to the number of affiliative interactions they carried out. However, the effect of sociability on dispersal may be modified by the local environment. In some situations the effect may be density dependant; Cote and Clobert (2007) found that less social common lizards were only more likely to disperse when population density was high. In other situations dispersal may be related to predation levels; Cote *et al.* (2013) found that with no predation less social mosquitofish (*Gambusia affinis*) dispersed, however when predators were present dispersers were as social as non-dispersing individuals (Cote *et al.,* 2013).

Despite general trends, these patterns are not consistent in all cases. For example, in some studies dispersing individuals have been shown to have lower rates of activity/exploration (Myers and Krebs, 1971). A potential explanation for this is presented by Cote *et al.* (2010), who describe three phases of dispersal; leaving the natal site, travelling between sites and settling in a new site, and suggest that the personality type required for each of these phases can be quite different. Leaving a natal patch is likely to be most common in individuals forced out through some kind of competition (Brandt, 1992). High population densities may cause less social animals to disperse, or aggressiveness and increased interference competition may cause less aggressive and dominant individuals to disperse (Sih and Bell, 2008). To be willing to travel between patches individuals then need to be relatively bold and exploratory for initial exploration of novel environments, foods and conspecifics. Finally, when entering a new site individuals may need to be more aggressive, to compete for territory and displace existing competitors (Duckworth and Badyaev, 2007a), or more social to settle in places with higher population densities (Sih and Bell, 2008). Exactly which subset of the population successfully disperses will therefore depend on which of these factors is the main driving force of the population and this may differ between species and populations and over time.

1.2.3.3 Habitat Use

There is a strong interplay between behaviour and the environment. Personality can affect habitat use to a greater extent than just affecting the probability of dispersal, particularly in a novel environment such as in a translocation program. Fraser *et al.* (2001) found that boldness measured in the laboratory accurately predicted the distance moved by fish released back into their native stream. Similarly, a study of swift fox movement after release found that bolder foxes moved around more (greater inter-fix distance while radio tracking) than shyer foxes when released into a novel environment (Bremner-Harrison, Prodohl and Elwood, 2004).

Studies have suggested that proactive (more active/bold) individuals may have more exploratory foraging routines, causing them to range further (Wilson and McLaughlin, 2007). This was found in a series of studies of great tits which found that individuals generally fall into one of two categories: fast explorers, who explore a novel environment quickly but superficially; and slow explorers, who explore a novel environment more slowly but more thoroughly. van Overveld and Matthysen (2010) found that when food supplies were removed then fast-exploring great tits were more likely to change their foraging habits by searching for food in different patches further from the original site.

A number of studies have suggested that bolder individuals may also be more willing to forage in the open (Wilson *et al.,* 1994) or in unfamiliar environment (Fraser *et al.,* 2001). However, despite a large number of studies suggesting that bold individuals may be more willing to expose themselves to predators or enter risky environments; few have shown this in the field. One of the few studies supporting this is by Boon, Reale and Boutin (2008), who found that bolder squirrels tended to occupy a wider range of habitats, including those with potentially higher numbers of predators. Intriguingly they also found that both proactive (active/bold) and reactive (less active/shy) individuals move further from their nests than intermediate individuals. Pearish, Hostert and Bell (2013) also found that more exploratory fish were more likely to be found in more open areas of a stream. Despite data on microhabitat use being limited it seems plausible that personality types would affect when and where individuals were found. This may be particularly evident when discussing boldness as risk taking (see below), as some environments and habitats provide a higher risk/reward ratio than others.

1.2.4 Selecting Release Groups

Analysing the effect group composition has on the probability of population establishment has been identified as one of the key questions for reintroduction biology (Armstrong and Seddon, 2008). Given that boldness in particular is often positively related to both dispersal and mortality some studies have suggested that release groups should just include individuals with a low level of boldness, as these individuals would be more likely to stay at the release site and less likely to die (McDougall *et al.,* 2006). Along these lines Stockwell, Hendry and Kinnison (2003) recommend small initial releases to identify which individuals are most likely to survive and then subsequently only releasing individuals of that type. However, this may be short sighted as it takes a variety of individuals and behavioural strategies to create a sustainable population (Stamps and Swaisgood, 2007). A number of studies have suggested that the fitness of different personality types may be dependent on the current environment (Sih and Watters, 2005; Dingemanse *et al.,* 2004). Personality traits have been repeatedly shown to have trade-offs; in a variable environment a personality type that is advantageous in one situation may, due to a relative inflexibility of behaviour, cause an animal to act inappropriately in another situation (Sih, Kats and Maurer, 2003). Therefore some personality types may benefit under one condition, whereas others benefit under another (Stamps, 2007; Wolf *et al.,* 2007).

Therefore, Watters and Meehan (2007) suggest that by creating release groups with animals displaying a range of personality types managers may ‘hedge their bets’ against environmental uncertainty, making release populations more resilient to environmental change (Watters, Lema and Nevitt, 2003). This may be why personality types are maintained in the wild, as in a changing and unpredictable environment no one personality type ultimately has a selective advantage (Dingemanse *et al.,* 2007). Michelena *et al.* (2010) developed a model of individual distribution and social attraction through observation of homogenous bold and shy groups of sheep (*Ovis aries*) that supports this suggestion. Their model showed that the presence of both bold and shy individuals produces behavioural flexibility at the population level allowing them to better optimize the exploitation of environmental resources. Producing variation in behaviour may be an adaptive strategy as Bremner-Harrison and Cypher (2011) found that even in areas where the adult population was biased towards lower levels of boldness foxes still produced litters containing a variety of personality types, suggesting producing this variation may have a selective advantage.

However, the effect individuals have on one another also needs to be taken into account. Group social composition is an important part of an individual’s environment and can affect fitness (Sih and Watters, 2005). Social context can affect physiology and neuroendocrinology, which subsequently affects behaviour (Sih and Bell, 2008). Sometimes individuals in a group tend to conformity, with each individual being more likely to perform the behaviours of its nearest neighbours (Efferson *et al.,* 2008). This is particularly useful for species which gain a benefit such as anti-predation from being in a group, where often it is the unusual or different individuals who becomes targeted (Webster and Ward, 2011). Alternatively, the fitness of different personality types may be frequency dependent as in classic game theory (e.g. the hawk-dove game; Smith and Price, 1973; Sih and Watters, 2005), as it may allow individuals to exploit different niches within an environment (Stamps and Groothuis, 2010). In this case individuals may intentionally change their behaviour to alternative tactics to increase fitness (Sih and Bell, 2008). In some cases individuals may intentionally move to groups with complimentary personality types to improve their own fitness (Sih and Bell, 2008). For example, Dyer *et al.* (2009) found that shy fish tended to follow bold fish and fed more when in mixed groups, although the benefit to the bold individuals was unclear.

Social selection theory (Wolf *et al.,* 1998) suggests that a group's mean trait value needs to be taken into account when assessing the relationship between a trait and fitness at the individual level. This was demonstrated to be true for personality traits by Sih and Watters (2005) who showed that in an experimental study individuals in groups of all aggressive water striders (*Aquarius remigis*) mated considerably less than individuals in mixed groups. These groups had a higher probability of containing hyper aggressive individuals that drove away females, drastically reducing the reproductive success of the group. Cote *et al.* (2010) found that the density of particular personality types can affect individual behaviour, as mosquitofish (*Gambusia affinis*) were more likely to disperse from a population containing a high number of asocial/bold individuals, regardless of their own personality type.

A model by Fogarty, Cote and Sih (2011) looked at the success of groups of individuals with different combinations of personalities in colonizing an environment. Their model suggested that the inherent trade-offs in different personality types, particularly those relating to density-dependent dispersal and sociability, can be overcome by introducing a mix of personality types. This mix produces faster colonization and higher population densities in the established population. Asocial individuals spread quickly to new patches and breed quickly but have inherently lower densities, whereas social individuals breed and spread more slowly but prefer higher densities. Fogarty, Cote and Sih (2011) suggest that this model may be applied to any density-dependent trait related to dispersal, for example more aggressive western bluebirds (*Sialia Mexicana*) are more likely to disperse when densities are high, therefore these individuals are the first individuals to colonize new environments (Duckworth and Badyaev, 2007a).

The interactions between these different forces may be complex and there is limited research on the effect of behavioural group composition on survival (Webster and Ward, 2011), particularly in the unique situation of a translocation where animals are forcibly released into a novel environment. Therefore the effectiveness of behavioural measures in predicting ecologically relevant factors at both the individual and group level needs to be tested in real world environments on wild populations (Archard and Braithwaite, 2010). Further to this, with enough understanding of the trade-offs involved, release strategies could be tailored based on the personality composition of the source population and the habitat pressures in the environment in which they are to be released. For example, there may be some benefit to introducing individuals with different personality types at different stages of a translocation program, e.g. in areas with high predation biasing release placement towards shyer individuals with higher chance of survival initially and releasing bolder individuals later (Bremner-Harrison *et al.,* 2013). Release placement within a release site could also be adjusted based on personality type; if bolder individuals move around more they will expose themselves to greater risks of predation but have greater access to food and mates (Bremner Harrison *et al.,* 2013) and so placing them in areas where they are unlikely to encounter risks but are more likely to exploit novel resources could be advantageous.

1.3 Measuring Personality

Personality traits have generally been tested and scored in two distinct ways (Carlstead *et al.,* 1999; Carlstead, Mellen and Kleiman, 1999): (i) behavioural rating - creating behavioural profiles subjectively by those who know the individual animals; and (ii) behavioural coding - taking objective measures of individual behaviours in a naturalistic environment or by using standardised tests (Carlstead, Mellen and Kleiman, 1999). Both ways attempt to create a behavioural score which accurately reflects underlying personality types.

Using the rating method, observers, usually zoo keepers, owners or others that know the animal well are provided with a questionnaire asking for ratings of each individual for a series of traits or descriptions. These traits are then verified by assessing their repeatability between multiple observers and those repeatable traits are then used to create one or more composite scores defining personality dimensions (see below). Researchers who regularly use these methods are working to create standardised questionnaires for individual species or groups of species which produce consistent results (e.g. Weiss *et al.,* 2009). A key study by Carlstead, Mellen and Kleiman (1999) used ratings to analyse behavioural profiles of rhinoceroses (*Diceros bicornis*) across different zoos. Using this method they discovered that an individual's personality is affected by its inherited tendencies, its experience, and its present and past surroundings and identified 3 main personality dimensions which they defined as approach/aggression/boldness, avoidance/escape/anxiety and sociability/curiosity/exploration.

Coding can be subdivided into two distinct methods; (i) coding animals in a natural setting (sometimes referred to as ethological coding; Carlstead, Mellen and Kleiman, 1999), and can be used to target specific behaviours e.g. during eating or grooming. (ii) Coding during a standardised experimental protocol, a common example is where the animal is placed in a novel arena or presented with a novel object, and its response in this situation is recorded. This type of coding tends to be focussed towards measuring certain personality traits provoked by the experimental situation. The ethogram for the coding method can either be comprehensive then reduced down to a limited number of traits, or alternatively success has been found in a number of studies using direct simple measure of a limited number of behavioural responses. For example Hansen (1996) showed that quite simple experimental tests can be used quickly and consistently to assess personality in mink (*Neovison vison*). To select individuals to breed to create bold and fearful lines of individuals they used simple tests involving extending a stick towards mink in their cage and then scoring the mink's response on a simple scale. This gave consistent results, resulting in two lines of animals with highly different behaviours.

Each of these different methods has its criticisms; behavioural profiles can be subjective in their interpretation, rely on a detailed knowledge of the species in question and require keepers or handlers who have significant experience with the individuals being studied (Highfill *et al.,* 2010). A review of this method by Highfill *et al.* (2010) also noted that ratings can be unreliable if the response of individual animals is different to different raters e.g. if one is associated with feeding and the other with veterinary procedures. On the other hand, experimental tests usually involve placing animals in situations detached from their natural conditions, causing difficultly in interpreting the animals responses to the situation (Reale *et al.,* 2007). For this reason, Reale *et al.* (2007) recommend testing the ecological and biological validity of behaviours shown in these kinds of standardised tests when possible. For example, when looking at the results of a behavioural test of aggressive reactions to a mirror, it may be beneficial to see if this correlates with aggressive behaviours towards conspecifics in the wild. A number of studies have therefore recommended using a combination of different methods to ensure the validity of traits measurement (Highfill *et al.,* 2010).

The ideal approach to measure a particular personality trait depends largely on the species, the situation and the aims of the project in question. Behavioural ratings have become common in zoo, companion animal and some farm studies, where animals can regularly be observed and people who know the animals well are available. Watters and Powell (2012) advocate the use of behavioural ratings by experts or long term collection of behavioural codings for zoo animals as it is completely non-invasive, reducing the required manipulation and potential confounding factors. On the other hand, behavioural coding in a standardised experimental setting is more common in studies of animals in the wild or a laboratory because it can be performed rapidly in an objective manner. Behavioural ratings may not be feasible or appropriate in many studies when large sample sizes are needed and researchers cannot observe individual animals for long periods of time in their natural environment.

1.3.1 Experimental tests for behaviour

When using the experimental method of coding behaviour a wide variety of tests can be used even when studying the same trait. The test used largely relies on the personality trait of interest and the species in question. Boldness in particular has been tested in a wide variety of different ways, often because the behaviours which the experimenter perceives to represent boldness differ between species and studies. Some tests are specifically designed to test what the experimenter presumes would be bold behaviour, whereas others use correlation analyses on a number of measures to produce a measure of boldness *post hoc* (see below). A selection of measures used to indicate boldness can be seen in Table 1.1.

Table 1.1. A selection of studies utilising different methods as a measure of boldness

Author/s	**Species**	**Indicator of boldness**
Reale *et al.* (2007)	Great tit (*Parus major*)	Latency to return to a feeding source after a mild startle
Carere and van Oers (2004)	Great tit (*Parus major*)	Latency to approach and shortest distance from a novel object
Bremner-Harrison and Cypher (2011)	San Joaquin kit fox (*Vulpes macrotis mutica*)	Reaction to trapping and handling
Michelena *et al.* (2010)	Sheep (*Ovis aries*)	How much of a novel arena was explored and how many novel objects were approached
Oosten, Magnhagen and Hemelrijk (2010)	Perch (*Perca fluviatilis*)	Duration of time spent near a predator and latency to feed in the predator's presence
Carter, Goldizen and Tromp (2010)	Namibian rock agama (*Agama planiceps*)	How close a human could approach before the subject fled
Fuxjager *et al.* (2010)	White-footed mouse, (*Peromyscus leucopus*)	High urination spread

However, there is some debate over whether the behaviours measured in these different tests all represent the same personality trait. For example Fox *et al.* (2009) measured mountain chickadee (*Poecile gambeli*) behaviour in two common tests which can be used to assess boldness, a novel object test and an open field test (discussed in detail later) and found they were not correlated. Similarly Coleman and Wilson (1998) found no link between responses to a threatening stimulus and a novel food. This suggests that sometimes tests do not measure the behaviours assumed. One test can also potentially measure multiple traits simultaneously, making interpretation complex (Reale *et al.,* 2007). When principal component or factor analytic techniques are applied, studies frequently find multiple axes of behaviour measured in the same test (see below for a description of these methods). Carter *et al.* (2013) suggest a few ways to improve the methodology of personality studies on this front. First, using more than one test to measure each trait to verify what personality trait is being measured (convergent validity), although this can also be achieved by finding valid correlates in wild behaviour. Second, by ensuring the behavioural score does not correlate with tests assumed to measure different personality traits (discriminant validity). By using controls and ecological correlates it is possible to verify if the behaviours seen in individual tests relate to the trait of interest. For example, do more ‘exploratory’ individuals in an open field test explore more in the wild? It is particularly important to think about the species or taxon being tested, as a test for one species may not be appropriate for another (Weiss and Adams, 2008). For example, some animals may avoid open habitat due to a perceived predation risk (Simonetti, 1989), whereas others will avoid enclosed areas for the same reason (Whittingham *et al.,* 2004), which may change the experimenters interpretation in some behavioural tests.

1.3.2 Behavioural Tests

The following experimental tests are quick and easy to perform, have been previously well used and the conditions in the test are highly repeatable. There is also the scope to carry out these tests in the field using portable equipment preventing some of the problems caused by taking animals into captivity.

1.3.2.1 Open field Test

A common standardised test for personality has been the Open Field Test, first used in the biomedical literature to look at rodent behaviour (reviewed in Archer, 1973). The test involves placing the study animal into a novel arena (which often has the floor divided by a grid pattern) and observing its behaviour. The actual measures used and interpretation of them can differ substantially between studies, but common measures include activity, being the number of gridlines crossed (Budaev, 1997), and more recently boldness, measured as the willingness to enter the centre of the arena where there is least cover (Montiglio *et al.,* 2010). Previous research suggests individual differences are often more stable and predictable in mildly stressful situations, particularly those that may be brought on by the novel environment of the open field test (Budaev, 1997).

The design of the arena used in open field tests varies substantially between studies in both size and shape, so Eilam (2003) tested what effect changing arena size had on behaviour and results of the test. The study found that changing the size changed the patterns of behaviour displayed, but these changes were consistent between individuals. In larger arenas mice made longer but more infrequent trips across the arena, whereas in smaller arenas they made frequent short trips. From this Eilam (2003) support the use of different sized open fields, as although it may change the values measured it should not affect the underlying behaviour.

However, there is some debate around what personality traits the open field test actually measures. The original open field test was designed to measure ‘emotionality’, a combination of fear and anxiety (Walsh and Cummins, 1976). This was regularly measured by looking at the amount of urine and faeces left during the test as an indicator of sympathetic activation of the nervous system. More recently studies generally refer to behaviour in the open field as activity, exploration or boldness. A large difference in this interpretation comes from the methods used. Some studies force the individual into the open field by placing it in the centre of the arena, whereas others allow it to enter of its own accord. Similarly some studies provide a shelter for the animal whereas others do not (Carter *et al.,* 2013). Budaev (1997) suggests that open field behaviours can be broadly divided into two categories: approach behaviour (activity/curiosity/sensation/seeking/ sociability) and fear avoidance (emotionality/shyness/autonomic responsiveness). The exact methods used may emphasise one set of behaviours over the other, so each study should consider the techniques used and the species before defining the personality traits measured.

1.3.2.2 Novel Object Test

Another common behavioural test, particularly in rodents, is the novel object test. Novel object tests are regularly used as a measure of boldness e.g. (Bremner-Harrison, Prodohl and Elwood, 2004; Wilson and Godin, 2000; Frost *et al.,* 2007), although Reale *et al.* (2007) class them as a measure of exploration. Novel object tests involve introducing the subject to an unfamiliar object, then measuring the subject's response to the object e.g. latency to approach. Some studies have used variants of the novel object test to suit their aims or study species, such as introducing a novel food (Groothuis and Trillmich, 2011; Groothuis and Carere, 2005; Groothuis and Carere, 2005) or smell (Rodriguez-Prieto, Martin and Fernandez-Juricic, 2010); however, the methodology is essentially the same. Different types of stimuli can also potentially be used to provoke a different set of behaviours for example Bremner-Harrison and Cypher (2011) looked at kit foxes response to both a positive (novel food) and negative object (simulated predator). These behaviours were independent as they found that the response to a novel food differed between populations but not the response to predators.

Studies suggest a novel object test represents a balance between neophilia and the avoidance of risk associated with the unknown (Richard *et al.,* 2008). However, it has also been suggested that novel objects can cause increased levels of physiological stress, therefore behaviour exhibited during these tests may represent a response to stressors in general (Herborn *et al.,* 2010). Some evidence was provided for this interpretation by Groothuis and Carere (2005) who showed a strong link between a stress response to handling and behaviour in a novel object test.

An inevitable problem with novel object tests for studying personality is that the novelty of the object will wear off over repeated exposures as the subject habituates (Reale *et al.,* 2007). This can be overcome by introducing the animal to a new object each time (Verbeek, Drent and Wiepkema, 1994) or by statistically including a measure of habituation in analyses (Reale *et al.,* 2007).

1.3.3 Testing animals in Captivity

A large number of studies on personality have been carried out on captive individuals, which have often been captive-bred for multiple generations (Archard and Braithwaite, 2010) and many of these studies have been performed in artificial laboratory environments. Only using captive animals for studies of personality has numerous limitations. Firstly, trapping animals to bring them into captivity can cause biases if the most bold or active are more likely to enter traps (Wilson *et al.,* 1993; Boon, Reale and Boutin, 2008), giving a false impression of the distribution of personalities in wild populations. Secondly, the stress of capture and captivity can affect behaviour, particularly when individuals respond differently to stress (Kock *et al.,* 1990). To combat this many studies recommend that animals should be left to acclimate to captivity before testing, but how long this period should be is unclear and may differ markedly between species (Archard and Braithwaite, 2010). However, if habituation rates differ between individuals as suggested by a number of studies (Dingemanse *et al.,* 2012; Dingemanse *et al.,* 2010) this can cause additional bias, creating problems translating the results to wild individuals. Thirdly, time in captivity may erode (Butler and Dufty, 2007) or remove (Wilson *et al.,* 1993) individual differences. Wilson *et al. (*1993) demonstrated that even just taking animals into a laboratory can reduce behavioural differences between individuals, suggesting that sometimes it may not be beneficial to allow animals to habituate to captivity before testing. Fourthly, behaviour measured in a stable laboratory environment may not give a true indication of behaviour, if the interaction between environment and behaviour is important to provoking behavioural differences (Dingemanse *et al.,* 2004). For this reason Niemelae and Dingemanse (2014) argue that behavioural tests in a lab will usually give a false impression of behaviour if the test conditions fall outside of the animals' normal range of experience under which the behaviour developed.

To understand personality traits and how they vary over time and across environments, studies of captive populations can cause serious misinterpretation if not paired with studies of wild populations, providing knowledge of the natural habits and habitats of the study species (Lambrechts *et al.,* 1999). Although some argue that as long as behaviour measured in captivity is related to behaviour in the wild it can be ecologically valid (Herborn *et al.,* 2010). However, this interaction between environment and behaviour, particularly valuable for studies of conservation, is best understood through studies carried out on wild populations (McDougall *et al.,* 2006). To support this, a number of recent reviews have advocated developing behavioural tests that can be carried out in a natural setting (Groothuis and Trillmich, 2011). Recent studies have achieved this by either observing behaviour in the wild and using this to create personality scores (Carter *et al.,* 2012), or through developing portable tests that can be applied without removing the animals from the field (Martin and Reale, 2008). For example, Bremner-Harrison and Cypher (2011) successfully developed a series of handling and novel object tests that could be carried out on free ranging kit foxes in the wild.

However, studying animals in the wild can be difficult. Logistically it can be more difficult to find and observe subjects in the field. Environmental variables can have a strong effect on behaviour and therefore need to be taken into account. There is the possibility of observer effects due to the animals not being habituated to manipulations by humans. Studies of wild animals also need to find some way to mark individual animals so they can be tracked, which can be time consuming and stressful for the animal (Teixeira *et al.,* 2007). Even when these hurdles are overcome and studies are carried out in the wild it is important to understand the species ecology and what effect this may have on behaviour. To combat any potential bias, measures need to be taken of the numerous factors that may affect behaviour during testing and these must be controlled for when analysing behavioural scores.

1.3.4 Creating Personality Scores

How variables measured in behavioural tests have been used to create behavioural scores differs between studies. The simplest method is to measure a variable which the experimenter believes to give an accurate representation of the personality trait in question. For example, many of the studies of fish use simple measures of predator inspection behaviour as an indication of boldness (e.g. Wilson and Godin, 2009). This method has its benefits in its simplicity and its lack of requiring interpretation. However, it relies on an acute understanding of the response of the animal to the stimuli provided in the test used.

A more complex behavioural score can be obtained by measuring a range of variables believed to relate to the personality trait in question and creating a composite score. For example, Bremner-Harrison, Prodohl and Elwood (2004) measured a large number of behaviours in the swift fox, then scored them as either indicators of boldness (+2) or caution (+1) and summed scores to give an overall boldness score. This method may provide a greater level of validity if individual measures co-vary then it can be assumed they are measuring the same underlying trait.

Many recent studies of personality have used Principal Component Analysis to create a composite behavioural score from data collected from standardised personality tests (Boon, Reale and Boutin, 2008). These analyses take a number of variables measured in a behavioural test and analyse correlations between them before combining the variables into aggregate Principal Components. The benefit of this technique is that it removes some of the subjectivity of deciding which behavioural variables represent which personalit trait and therefore should be used to form the composite score. Factor Analysis is a functionally similar technique, but makes the additional assumption that there is an unobserved latent construct causing the measured behaviours to be correlated (Budaev, 2010). This makes it computationally more intensive, but ideal for the analysis of personality data where the assumption is there is an underlying personality trait causing the observed behavioural profiles (Trillmich and Hudson, 2011). The factors calculated accurately describe the variation in behaviour between individuals and can be interpreted as reflecting different personality dimensions.

To increase the statistical power of these analyses Bell, Hankison and Laskowski (2009) suggest that measuring more individuals on fewer occasions, rather than a few individuals regularly, gives more powerful and reliable results. Studies using these methods have found similar patterns of behavioural traits across different species (Gosling and John, 1999). However, interpretation of factors is still relatively subjective as it still relies on the researcher's interpretation and description of the behaviour incorporating all of the variables contributing to each factor. Because of this subjectivity, the behavioural measures incorporated to create the factors should be investigated before drawing comparisons between studies.

Some studies of personality (particularly those carried out in captivity) have defined personalities as discrete behavioural types often with two alternative phenotypes, rather than occurring along a continuum e.g. fast/slow, bold/shy, proactive/reactive (Koolhaas *et al.,* 1999; Groothuis and Carere, 2005; Drent, Oers and Noordwijk, 2003). Methodologically some studies have used simple tests to which the animals provide a binary response (e.g. Hansen, 1996). Although this is usually implemented when studies need quick and simple responses, it potentially loses a lot of fine scale data about personality traits. Alternatively studies have, after recording data, divided animals into 'bold' or 'shy' categories for further tests for ease of analysis (e.g. Carere and van Oers, 2004). This again loses a lot of information about individual behaviour, particularly as it negates the potential for non-linear correlates with personality (e.g. Boon, Reale and Boutin, 2008). Finally, some studies have identified multiple peaks in the frequency of different personality scores, suggested to be created through disruptive selection (Bergeron *et al.,* 2013), which in some studies have been interpreted as alternate strategies (Verbeek, Drent and Wiepkema, 1994). This implies a very different interpretation to that usually applied to personality traits. This interpretation is similar to a classical view of ecology, such as in the hawk-dove game, and implies there are a limited number of alternative optimal strategies, which is quite different from the personality literature's discussion of how continuous rather than discrete variation in behaviour may be adaptively maintained. Using powerful statistical techniques such as mixed effects modelling it should be possible to analyse most personality data as a continuum without losing any fine scale data, and this is the method championed in many reviews of personality (e.g. Dingemanse *et al.,* 2007).

1.3.5 Behavioural Plasticity

Behavioural plasticity describes the ability of animals to adjust their behaviour to different situations or environments. Optimality theory would suggest that all individuals should be infinitely plastic, allowing individuals to select from a wide range of behaviour to suit the situation. However, personality studies have shown that this is not the case and that often behavioural consistency is prevalent and flexibility is limited (Sih, Bell and Johnson, 2004). There are two possible reasons why natural selection may favour limited plasticity, because it provides limited benefits, or has high costs. Limited benefits may be through; (i) unreliable information – information may be unavailable on which is the best current phenotype, (ii) time lag – it takes time to change phenotype and during this time the environment may have changed again, (iii) developmental range limit – there is always going to be a limit to the range of phenotypes possible, (iv) epiphenotype problems - traits may be less effective when switched during an individual's lifetime than when incorporated into development. Alternatively, plasticity may have high costs and in some species those costs may outweigh the negatives of behaving sub-optimally in some situations through inflexible behaviours (Sih, Bell and Johnson, 2004). These costs may come in a variety of forms including; (i) maintaining sensory equipment to identify the optimum state and regulation of that state, (ii) costs to produce the new phenotype, (iii) information acquisition costs e.g. exploration to identify the best phenotype for the current environment, (iv) developmental instability – plasticity may be linked with poor development leading to asymmetry and other problems causing reduced fitness, (v) Genetic costs – little is known about the genetics of plasticity but it could be linked to other genes with negative consequences (DeWitt, Sih and Wilson, 1998).

Behavioural plasticity is of particular interest to personality research as it affects estimates of personality traits. The mean value of a trait may not provide the full picture of behavioural variation, as a number of studies have noted variation in the ability of individuals to adapt behaviourally to different situations (Watters and Meehan, 2007). Dingemanse *et al.* (2010) have therefore recommended combining the theory of personality with behavioural plasticity as behavioural reaction norms. They suggest that flexibility of behaviour is a trait as much as personality itself and may be an adaptive trait suited to the animal's environment. The level of plasticity of an individual can be measured via the individual by environment interaction, essentially how much an individual's behaviour changes when tested in different environments. The plasticity of a trait could theoretically evolve separately from the level of a trait, for example in less stable environments it might be expected that animals are more flexible in their behaviour even if the mean value is the same. However, a number of studies have also noted that at least in some species behavioural plasticity is linked to personality, with more extreme behavioural types being less plastic than intermediate behavioural types (Sih and Bell, 2008; Coppens, de Boer and Koolhaas, 2010). For example, highly aggressive mice adjust their behaviour between social and non-social situations less than less aggressive mice (Benus *et al.,* 1990).

To fully understand behavioural variation studies need to simultaneously consider both personality and plasticity of individuals. Random regression, a mixed effect modelling approach, allows the representation of different individuals' behaviour as a line, with the intercept corresponding to the individual's personality, and the slope as the individual's behavioural plasticity over an environmental gradient (Dingemanse *et al.,* 2010). This allows the description of both an individual's average level of behaviour but also how much its behaviour changes over an environmental gradient (Dingemanse *et al.,* 2010). Behaviour can then be partitioned into within-individual and between-individual variance. Even when plasticity is not the focus of interest, not taking account of potential plasticity of behavioural traits will reduce the power of analysis and potentially skew results.

1.4 Behavioural Syndromes

Personalities may have coevolved along with a series of other behaviours (Sih, Bell and Johnson, 2004), physiological traits (Careau *et al.,* 2008) and life history traits (Stamps, 2007; Wolf *et al.,* 2007; Biro and Stamps, 2008; Reale *et al.,* 2010). In a number of studies looking at personality it has been noted that independent behaviours in different situations seem to be correlated. Sih *et al.* (2004) have termed this phenomenon a behavioural syndrome, with each individual within the population showing a behavioural type within this syndrome. The notion of behavioural syndromes implies even more restricted behaviour than that of personality as it suggests that individuals are limited in their plasticity of behaviour between situations which may cause trade-offs; for example, in an aggressive syndrome individuals would show varying levels of aggression across situations, more aggressive individuals may do well in competitive situations, but this behaviour would carry over and the individual may be unsuitably aggressive in mating situation (Sih and Watters, 2005). These trade-offs in behaviour may therefore have significant consequences for individual fitness (Stamps, 2007, Wolf *et al.,* 2007).

Despite causing trade-offs, behavioural syndromes may still be adaptive. Although the carryover of behaviour between different situations causes individuals' behaviour to diverge from the optimum (Bell, 2007) and appear to show behaviour that is suboptimal when viewed in isolation, this behaviour may still be significantly beneficial in other situations. For example, (Johnson and Sih, 2005) examined the puzzling behaviour of precopulatory sexual cannibalism in spiders, which clearly reduces fitness. Their study showed that individual female spiders differed in their tendency for cannibalism and that this was linked to their voracity towards prey as juveniles. High voracity resulted in faster growth and increased fecundity, benefits which potentially outweigh the costs of occasionally eating a male before mating. Studies such as this suggest that the benefits of syndromes may therefore still outweigh the costs (Johnson and Sih, 2005).

A series of studies on sticklebacks also support the notion that behavioural syndromes can be adaptive. Studies have shown that aggression, activity and exploration are only correlated in populations where predation is high (Dingemanse *et al.,* 2007). Bell and Sih (2007) demonstrated that this link could be artificially generated by exposing fish to high levels of predation. The authors suggest this represents adaptation to levels of predation in the environment as the fish are demonstrating alternative strategies to cope with predation - sedentary and solitary or a more high risk active, aggressive strategy. These different strategies then require a suite of correlated behaviours to be carried out effectively (Dingemanse *et al.,* 2007).

Alternatively, behavioural syndromes may not be adaptive at all; behaviours across situations may be genetically or physiologically coupled. Genes for related behaviours in different situations may be linked, causing individuals and populations to show correlations between certain behaviours. Physiologically, certain hormones or organ sizes may cause an individual to be generally more aggressive or active in all situations and these mechanisms may be difficult to decouple (Sih, Bell and Johnson, 2004) unless there is strong selective pressure.

The line between behavioural syndromes and domain-general personality (a personality trait displayed across a range of circumstances) is not entirely clear and in many cases may come down to differences in terminology and interpretation. When behaviour displayed in multiple tests is correlated this can either be considered as multiple traits linked in a behavioural syndrome, or a single trait expressed across multiple contexts (the jingle - jangle fallacy; Carter *et al.,* 2013). In many cases, making this distinction may not be particularly helpful with the limited data available. However, because of these potential correlation in behaviours Sih *et al.* (2004) encourage studying suites of behaviour that may be correlated together to avoid missing the overall picture. A number of different higher order patterns of behaviour have been observed which could be interpreted as behavioural syndromes and these are outlined below.

1.4.1 Pace of Life

The Pace of Life Syndrome hypothesis (POLS) was developed independently of the personality literature, but has recently shown some direct relationships to it. The hypothesis suggests that different ecological conditions will promote different life history strategies which will cause closely related species (or individuals) to differ in a series of physiological attributes. This difference in life history and traits can affect a whole range of attributes and has its roots in the theory of r-selected and K-selected life history strategies (Pianka, 1970). The POLS is usually linked to stable physiological traits, often using measurements of metabolic rate as a basis (Careau *et al.,* 2008). Individuals with a high metabolism generally have high growth, a short lifespan and more precocious reproduction than individuals with a lower metabolism (Reale *et al.,* 2010). More recently, however, studies have been linking the pace of life hypothesis with behavioural as well as physiological traits (Reale *et al.,* 2010) and a number of papers have explored the link between personality and metabolic rate. Careau *et al.* (2008) suggest two alternate models of how personality may be affected by metabolic rate. The performance model suggests individuals with high metabolic rate will have higher levels of energetic throughput and so will show high levels of activity and aggressiveness. Alternatively, the allocation model suggests that because of their high metabolic rate these individuals will have less energy to spare and so will have lower levels of activity or aggressiveness. Support for these two models seems to be mixed. For example, Adriaenssens and Johnsson (2011), looking at wild trout (*Salmo trutta)*, found that less exploratory individuals grew faster than bolder individuals and Carere and van Oers, (2004) found that shy great tits had a faster breathing rate and higher body temperature than bold individuals when handled, giving support to the allocation model. Alternatively, Careau *et al.,* (2009) found that more bold and aggressive muroid rodents (family *Muroidea*) had a higher metabolism supporting the performance model.

1.4.2 Fast/Slow exploration

The POLS has many parallels with the idea of a fast-slow exploratory behavioural continuum identified in a long term study looking at personality in great tits (Koolhaas *et al.,* 1999). In these studies of great tits, birds have been classified as either fast or slow explorers. Fast explorers are bolder, approach novel objects quicker and explore more quickly, however they explore more superficially and are more prone to routine. Slow explorers are shyer, but more thorough in their exploration and more flexible to environmental change. Studies have shown that exploration score is relatively consistent across an individual lifetime but that birds become gradually faster explorers over time (Koolhaas *et al.,* 1999). Captive breeding studies have also shown that these traits are heritable (Drent, Oers and Noordwijk, 2003). Drent, Oers and Noordwijk (2003) identified a series of traits that were correlated with fast individuals including; making rapid decision, manipulating stressful events, being insensitive to external stimuli, being more routine, aggressive and bold, having high levels of testosterone and high reactivity of the sympathetic nervous system.

Patterns of fast/slow exploration and its effect on life history have been observed in studies of other species. For example Careau *et al.* (2009) found a similar pattern in muroid rodents, identifying fast individuals who explore more superficially, reproduce early and are more bold and aggressive. They also identified that faster individuals also had a higher basal metabolic rate, linking into the pace of life hypothesis.

1.4.3 Coping Styles

A further parallel can be drawn between the POLS, fast-slow life history and the literature on coping styles developed in rodents. Coping styles refer to an animal's response to a stressful situation, often focussing on hormonal and other physical effects. Individuals are defined as either proactive or reactive copers (Koolhaas *et al.,* 1999). Proactive individuals actively manipulate situations that cause stress by avoidance or aggression, whereas reactive individuals adjust to stressful situations by immobility and passiveness (Careau *et al.,* 2008). Proactive individuals are usually more active, explorative, aggressive and bold (Koolhaas *et al.,* 1999; Groothuis and Trillmich, 2011) and tend to act on previous experience, which allows them to respond quickly but with the risk of inaccurate responses (Coppens, de Boer and Koolhaas, 2010).

Coppens, de Boer and Koolhaas (2010) carried out a review of the coping style literature, attempting to identify an underlying mechanism behind variation in response to stress. They suggest that patterns of coping styles are consistent with those predicted by the pace of life hypothesis identified in birds (Verbeek, Drent and Wiepkema, 1994) and the shy/bold axis in fish (Wilson *et al.,* 1994). Studies have shown that similar to the predictions of the POLS hypothesis, proactive individuals generally have higher resting metabolic rates (Huntingford *et al.,* 2010) and are also more aggressive but routine, similar to a fast life history, whereas reactive individuals display behaviour similar to a slow life history, are less aggressive and better at coping with change (Koolhaas *et al.,* 1999). Careau *et al.* (2008) suggest that whether an animal freezes or struggles when it is trapped is an effective measure of coping styles.

1.5 Maintenance of Personality Traits

Personality differences are often assumed to be adaptive due to their prevalence in a large number of studied populations. However, there is much debate about the proximate and ultimate mechanisms maintaining these individual differences. A number of studies have shown that personality traits are, at least in part, heritable (van Oers *et al.,* 2005). However, there is evidence that individual behaviour can also be strongly affected by rearing environment and maternal affects (Trillmich and Hudson, 2011). This potentially complex interplay of genes and environment has led to a number of models attempting to explain the adaptive significance of personalities and why they are maintained within populations.

Dingemanse and Wolf (2010) compiled a detailed review of the different theories put forward for the evolution and maintenance of these differences. They divide these models into three categories: models based on differences in state; models based on feedback between state and behaviour; and models not based on state.

1.5.1 Differences in stable states

A number of models of animal personalities revolve around differences in stable states (Wolf and Weissing, 2010). These are features of an individual that do not change over time, from the obvious such as sex, or castes in insects (Wolf and Weissing, 2010), to the less obvious such as organ size (Biro and Stamps, 2008) or basal metabolic rate (Careau *et al.,* 2008). A large number of different physiological traits have been suggested to be the underlying cause of personality traits, including growth rates (Stamps, 2007), hormones (Ketterson and Nolan, 1999) and metabolic rate (Careau *et al.,* 2008). Stamps (2003) suggests that individuals have a reaction norm of possible personality types based on these fixed phenotypic traits, but that being raised in different environments causes them to select a personality type from within this range, which then becomes fixed. The author suggests this can be their physical or social environment, and parental effects can have a particularly strong influence on behavioural development.

1.5.2 Differences in variable states

Some models of personality traits have linked them to individual states that can differ over time, such as energy reserves or factors related to experience or learning. The problem with suggesting that these types of attributes cause differences in personality is in how changeable traits cause stable behaviours, an important feature of personality traits. Many of these models therefore either explicitly or implicitly include feedback mechanisms to explain this consistency (Dingemanse and Wolf, 2010).

Feedback can be due to learning and experience, such as more experienced individuals either becoming more (Mettke-Hofmann *et al.,* 2006) or less neophobic (Sih *et al.,* 2004). Alternatively this feedback can come from current assets; individuals with low assets are more likely to take risks to gain resources, whereas those with high resources will take fewer risks (Luttbeg and Sih, 2010). These resources can include potential future reproduction (Wolf *et al.,* 2007). Some models suggest that boldness and other related behaviours are an honest signal and pursuit deterrent to predators (Oren, 1991). In this case individuals with high energy reserves will act more boldly in the face of predators, but this may in turn reduce their energy reserves (Lopez *et al.,* 2005).

1.5.3 Models not based on state differences

Finally Dingemanse and Wolf (2010) discuss models that aren't based on state differences. These include the suggestion that personality traits are frequency-dependent (Wilson *et al.* (1994). This theory suggests that bold and shy individuals are exploiting different niches, leading to shy and bold specialists. However, when more individuals use one tactic it becomes overexploited and reduces fitness and so the alternative tactic carries greater rewards. This may lead to the development of more responsive individuals, who are more behaviourally plastic and can change their tactic to suit the situation, and less plastic individuals who specialize in one tactic.

A variation on this model suggests that individuals may maintain different personalities through social niche specialisation (Bergmueller and Taborsky, 2010). It suggests that within-species competition encourages individuals to create their own niche, reducing conflicts with other individuals and reducing the costs involved with regularly switching behaviour. In simple terms, individuals are pushed away from the optimum behaviour by competition.

1.6 Project Aims

Seddon, Armstrong and Maloney (2007) have criticised the reintroduction literature for relying on *post hoc* analyses of factors affecting project success, suggesting that more direct research needs to be done on ways to improve reintroductions. They encourage the use of the hypothetical-deductive method, with future studies utilising modelling techniques and identifying research questions *a priori* to produce practical data which can be applied to future studies. Watters and Meehan (2007) have recommended that the next step in improving the application of personality research to conservation is for studies to follow animals after release into the wild to determine their survival and success and to relate this to ecological contexts. This has been done in a few studies working with endangered species (Bremner-Harrison *et al.,* 2013). However, due to utilising protected species, the studies were limited in sample size and in the amount of manipulation possible with the release populations. Watters and Meehan (2007) also recommend forming different groups of animals, consisting of different frequencies of behavioural phenotypes, to observe how this affects post release behaviour and survival, a recommendation that has been echoed in the recent review of translocation case studies from the IUCN (Soorae (ed.), 2013). By determining how individuals are likely to respond to environmental variation it may be possible to plan accordingly, optimise release strategies and provide pre-release training where necessary to improve release success (Bremner-Harrison *et al.,* 2013). Understanding these different factors should allow the adaptation of release strategy to suit the release individuals and available habitat.

This study aims to develop previous work carried out by Bremner-Harrison *et al.* (2013) using a non-endangered species to investigate factors affecting personality in further detail and carry out manipulations of release strategies not possible in a reintroduction programme with an endangered species. This study therefore explores the applications of personality research to improve translocation practices using the wood mouse (*Apodemus sylvaticus*) as a model for other mammalian species. Wood mice are used as a model as they are common in the UK and can be easily trapped and tested in the wild. Many personality testing methods were originally developed for use with mice and so are robust and provide an interesting comparison with mice maintained in a laboratory environment (Archer, 1973). Extensive research has been carried out on their ecology aiding in interpretation of results (e.g. Malo *et al*., 2013). Studies of mice and other small mammals to date have also shown similar patterns of personality traits and fitness consequences to other species studies (Gosling, 2001; Smith and Blumstein, 2008).

The first step was to confirm that mice have consistent repeatable behavioural traits (personalities) by developing a test that can be carried out on wild mice in the field. As discussed earlier, testing animals in the field reduces many of the stresses and confounds caused by transporting and testing the animals in captivity. Data collected here are used to accurately model personality and the plasticity of these traits and to establish how they change due to habituation and whether traits are consistent between populations. Using these data provides the opportunity of investigating a number of the questions currently being broached in the personality literature; these include investigating the plasticity of behaviour both within and between populations and how this relates to individual personality traits and fitness. During this first stage, additional data was also collected including; physiological data on the mice tested, habitat data on the locations trapped and environmental data on the conditions during trapping and testing. These data provide an indication of which variables are affecting behavioural scores during the tests but also when and where mice with different personality traits are likely to be trapped. These data are used to examine what biases can arise from trapping animals for personality studies and to attempt to avoid these biases in later parts of the study.

To explore what effect long term captivity has on the personality traits measured, data were also collected from a population of mice in captivity. This provided data on what factors define an individual’s personality during ontogeny and enable a calculation of the amount of heritable variation in personality traits in the wood mouse. These data are also used to examine how personality changes over multiple generations in captivity and how this may relate to captive bred populations due for release.

Finally, to examine the effect personality has on the behaviour of mice at each step of the translocation process, a simulated reintroduction was carried out, particularly focusing on the response of individuals to being released into a novel habitat. This study investigates how individuals differ in their initial response to release, through habitat use, dispersal and survival. A key focus at this stage is on how group composition affects behaviour as this is currently an important point in conservation research. Bringing animals into captivity as part of this study also allows direct investigation into how personality is affected by captivity in the short term and what affect this may have on estimated personality traits and release strategy.

Using the data collected during this study a number of recommendations are drawn up regarding the measurement, handling and application of personality traits at each stage of the translocation process.

2 Chapter Two: Assessing the behaviour of wood mouse at three levels of variance; within individual, between individual and between population

2.1 Introduction

Within a species, behavioural variation can occur at multiple levels; within-individual (behavioural plasticity), between-individuals (personality) or between populations (population mean personality and plasticity; Dingemanse *et al.,* 2010). Understanding variation across these hierarchical levels is necessary to fully understand the drivers of personality; however few studies have previously done this (but see Dingemanse *et al.,* 2012). The maintenance of both behavioural plasticity and consistent personality in many populations suggests there are evolutionary or developmental trade-offs between these two traits. For example maintaining the mechanisms required to be behaviourally plastic may be costly, but being highly consistent runs the risk of behaving mal-adaptively in some situations (Briffa, Rundle and Fryer, 2008). The resulting balance of these trade-offs may vary between locations and populations based on local selection pressures (Komers, 1997). Studying multiple wild populations allows investigation into how population mean personality and level of plasticity may differ in a potentially adaptive way to local conditions (an approach suggested by Dingemanse and Reale, 2005), as well as providing an important validation of findings through study replication not often found in personality studies. Previous studies have identified how mean personality may differ adaptively between populations in response to local conditions (Martin and Reale, 2008) and that correlations between traits can also differ (Dingemanse *et al.,* 2007; Bell and Sih, 2007; Bell and Stamps, 2004). Using similar techniques it should be possible to also identify if levels of behavioural plasticity differ between populations. These factors can be simultaneously addressed using random regression models, which represent each individual as a line, with the intercept describing the individuals behaviour in an average environment (I), and the slope describing how that behaviour changes over an environmental gradient (IxE) and can also incorporate the population mean change in behaviour over the environmental gradient (E; Nussey, Wilson and Brommer, 2007).

Exploration and activity behaviours are often measured by observing an animal’s response to a novel environment, typically an empty arena in an open field test. Similarly, novel object tests are often used to measure neophilia or boldness (response to risk) by scoring an animal’s response to an object not found in their natural environment (Carere and van Oers, 2004). However, in accordance with the definition of personality, repeated tests are needed to confirm the consistency of behaviour, which can lead to habituation to the stimuli used in these tests and a gradual change in the behaviours recorded. This can be partially overcome by varying the environment or novel object between tests (Mettke-Hofmann *et al.,* 2006), however this potentially produces problems by introducing unknown or difficult to measure variables such as reactions to different aspects of the objects introduced (e.g. object complexity; Mettke-Hofmann *et al.,* 2006, shape or texture; Heinrich, 1995), or habituation to novelty itself (Reale *et al.,* 2007). These features of an object can affect how quickly it is approached and how long it is explored for (Mettke-Hofmann *et al.,* 2006). Unfortunately, responses to these variables may also differ between individuals potentially confounding the measurement of personality traits. An alternative approach is to use the same experimental apparatus between tests but statistically account for habituation within random regression models, thus removing the confounding effect and providing an estimate of individual rates of habituation (Dingemanse *et al.,* 2010).

Habituation measured in this way can be used as a measure of behavioural plasticity, as the change in perception of novelty can be considered an environmental gradient (Rankin *et al.,* 2009). Habituation to low levels of risk can provide a fitness advantage (Rodriguez-Prieto, Martin and Fernandez-Juricic, 2010), therefore the direction and strength of the change in behavioural response over this gradient (slope) can be an important aspect of an individual’s behavioural profile (Ensminger and Westneat, 2012). Habituation affects a number of aspects of the behavioural ecology of wild animals including their ability to adjust to changes in their environment (Martin and Reale, 2008) or to human presence (Walker, Boersma and Wingfield, 2006). This pattern of habituation can differ between individuals within a population (Ellenberg, Mattern and Seddon, 2009) and may itself be a heritable trait under selection (Dingemanse *et al.,* 2010). Unfortunately, statistical methods for measuring behavioural plasticity often have limited power to reject the null hypotheses (Martin *et al.,* 2011) and previous studies investigating between-individual differences in habituation have been inconclusive (Martin and Reale, 2008). By studying multiple populations it may be possible to observe differences in habituation at the population level not evident at the individual level. In addition, taking account of habituation is an important aspect of testing the repeatability of personality traits that is regularly overlooked. If habituation is not considered, it can potentially skew repeatability estimates and the calculation of personality traits (Dingemanse *et al.,* 2010), which may falsely suggest the existence of personality traits when there are none (Westneat *et al.,* 2011).

Mice are commonly used to study personality in lab studies. Tests such as the novel object test and open field test were originally developed for use with mice and rats (Hall, 1941). However, there is a lack of studies examining if the findings from lab-reared mice also apply to their wild counterparts. In this study three separate wild populations of the wood mouse (*Apodemus sylvaticus*) are used to ascertain the presence of, and quantify, personality and behavioural plasticity. Previous studies have shown that wood mice have high levels of inter-individual variation in behaviour (Gurnell, 1975), which is consistent over time (Lodewijckx, 1984a) and may affect daily activity patterns in the wild (Halle, 1988). This makes them an excellent mammalian model to investigate personality and plasticity in more depth. Studying wild populations of animals has been suggested to be vital to fully understanding personality (Archard and Braithwaite, 2010), but the stress of taking animals into captivity from the wild for testing produces major concerns about how this affects behaviour and whether traits measured in captivity relate to natural behaviours in the field (Niemelae and Dingemanse, 2014). This study seeks to find a middle ground between laboratory and field assessment, as observing many mammals in the wild is logistically difficult. Data here were collected using artificial testing apparatus but located at the trapping site. Behavioural data were therefore collected from mice *in situ* at the trapping site within a few hours of capture. Mice were tested from three separate populations to examine the consistency of personality traits, habituation rates and behavioural correlations between traits.

The first aim of this study was to calculate the repeatability of individual behaviour, tested *in situ* in the field, to confirm the existence of personality traits in wood mice. The second was to calculate individual levels of behavioural plasticity through habituation to the testing environment. The third aim was to examine if there were population differences in mean personality and behavioural plasticity between the three sites studied.

2.2 Methods

The wood mouse (*Apodemus sylvaticus)* is a small woodland rodent commonly found in the UK. Wood mice are nocturnal, active throughout the year (they do not hibernate) and territorial during the breeding season (Spring/Summer), but are known to share nests in winter (Harris and Yalden, 2008). Wood mice make an excellent model species as they are very common in the UK, are well studied and easily trapped in large numbers. Additionally much of the research on personality to date has been on rodent species, particularly for the medical literature (Kazlauckas *et al.,* 2005), making study techniques very reliable and behavioural tests robust (Archer, 1973).

Mice were trapped at three sites in the UK; Sherwood Forest National Nature Reserve (53˚ 12’ 31.9”N, 01˚ 04’ 04.8”E), Brackenhurst campus of Nottingham Trent University (53˚ 03’ 35.2”N, 0˚ 59’ 40.8”E) and the Silwood Park campus of Imperial College London (51˚ 24’ 50.4”N, -0˚ 38’ 43.5”E; see Appendix for a map of locations). The three sites have different levels of anthropogenic disturbance which could potentially affect behaviour; Brackenhurst Campus is an active agricultural university estate with high levels of disturbance through dog walkers, students, hedge trimming and other agricultural activity; Sherwood Forest is a protected predominantly oak and birch woodland but still suffers some disturbance through land management, grazing cattle and dog walkers; and the site at Silwood Park is an enclosed research site in a mixed deciduous woodland with limited access and only low levels of disturbance through ongoing research activities.

2.2.1 Trapping and Marking

Mice were trapped at periods throughout the year between May, 2012 and August, 2013 (See Table 2.1 for details) using standard small mammal trapping techniques (Gurnell and Flowerdew, 2006). Traps were set in the evening, within a few hours of sunset, and checked again within a few hours of sunrise. Traps were left closed during the day. Upon capture, mice were weighed to the nearest half gram, sexed and reproductive status was recorded (the presence of descended testes was recorded in males and pregnancy, visible nipples or perforate vagina, were recorded in females). Mice were classified as adults, subadults, and juveniles according to weight (adults: 18 g or over; subadults: 14–17.99 g; and juveniles: 7–13.99 g; Malo *et al.,* 2013) although traps were set to avoid trapping individuals under 10g. During handling a subjective restlessness score was taken ranging from 1 – moved little/docile to 4 – very active/agitated. Season and ambient temperature during testing were recorded, as both have been shown to affect behaviour (e.g. Gracceva *et al.,* 2014; Biro and Dingemanse, 2009a). Some methodology differed at Silwood due to ongoing research at the site (Malo *et al.,* 2013), as outlined below. These differences may potentially cause differences in the subset of the population trapped but should not change the behavioural response of the mice to the testing apparatus. In total 650 captures were made of 312 mice (Brackenhust – 136, Sherwood – 103, Silwood Park – 73). Protocols for trapping, handling and behavioural testing of mice were approved by the Nottingham Trent University Animal Ethics Committee (Ref: ARE56).

Table 2.1. Number of trapping sessions (number of trapping nights) for each location for each season.

	Brackenhurst	**Sherwood**	**Silwood**
Spring 2012	0(0)	0(0)	9(9)
Summer 2012	4(16)	6(24)	6(6)
Autumn 2012	2(8)	1(4)	0(0)
Winter 2012/2013	2(8)	2(8)	4(4)
Spring 2013	1(4)	1(4)	0(0)
Summer 2013	0(0)	2(8)	0(0)
Total	9(36)	11(44)	19(19)

2.2.1.1 Brackenhurst and Sherwood

Longworth traps (aluminium, 13.8 cm x 6.4 cm x 8.4 cm) were used and baited with rolled oats and a piece of carrot and contained hay bedding. Grids of 25 traps set at ten meter intervals covering ¼ hectare each were placed at varying locations within the site and set for 4 consecutive nights per session. Traps were covered with moss and leaf litter to provide insulation and disguise the trap, leaving the entrance clear. Traps were collected early next morning and mice extracted. Whilst still in the handling bag, mice were fur clipped for individual identification (only removing the top layer to reduce loss of insulation). Mice were behaviourally tested between 0600 and 1200 hours.

2.2.1.2 Silwood

Sherman traps (16.5 x 5.1 x 6.4 cm) were used and baited with peanuts and a slice of apple and contained non-absorbent cotton wool bedding. Traps were placed in trap shelters (providing protection from predators and adverse weather) at a subset of fixed grid locations in 10 x 10m quadrats throughout the site for a single night. The same locations were used repeatedly at Silwood which may lead mice to become familiar with traps and trap locations affecting the probability of being trapped. Mice were marked by PIT (Passive Integrated Transponder) tags used as part of an ongoing project (Home Office Project licence no. 7007314). PIT tags were implanted subcutaneously in the interscapular area using a syringe whilst manually restraining the mouse (Francis Scientific Instruments, Cambridge, 1.41x9mm, glass, 0.035g, <0.4% body weight). All mice were PIT tagged during previous trapping sessions before being recaptured for behavioural testing. As mice were tested over a longer period at Silwood (between 0600 and 1800), they were kept at thermoneutrality before testing (Malo *et al.,* 2013; Godsall, Coulson and Malo, 2014), which may have affected behaviour, this was taken into consideration when interpreting results.

2.2.2 Behavioural Tests

Two behavioural tests were used, first the open field test to measure activity and exploration behaviours in a novel environment, followed by a novel object test to measure neophobia and fearfulness in response to an unfamiliar object (Reale *et al.,* 2007). The variables recorded were selected to provide a general picture of the behaviours carried out during the tests with particular focus on their response to the novel environment in the open field test and the novel object in the novel object test. Most of the behaviours recorded in the open field test were designed to measure activity and exploration behaviours, but in addition entering the centre of an open field has sometimes been considered a bold behaviour (e.g. Dahlbom *et al.,* 2011) and time grooming may represent mild stress or anxiety in a novel environment (Moyaho and Valencia, 2002; Komorowska and Pisula, 2003). Behaviours recorded in the novel object test were designed to measure the animals' response to the introduction of the novel object, with the addition of *time frozen* as this was a common response to inserting the object and represents a fear/antipredator response (Eilam, 2005).

To avoid potential confounds when measuring repeatability the same arena and object were used in subsequent trials, however this inherently reduces the novelty of the arena and object over time. To control for this effect, habituation was accounted for statistically, providing at the same time a reliable measure of behavioural plasticity (Dingemanse *et al.,* 2010; see below). In addition, by not changing the apparatus between tests this study aims to reduce potential confounding factors such as mice habituating to novelty in general (Reale *et al.,* 2007) or the presence of between individual differences in response to aspects of the objects introduced (colour, shape etc), which may be difficult to measure and interpret.

2.2.2.1 Testing Procedure

Captured mice were transferred to the testing apparatus, which consisted of a blue plastic crate measuring 50 x 33 x 30cm with a Perspex lid. A tripod with camera (Canon, Legria FS306 E, Japan) recorded mouse behaviour in the arena (Figure 2.1) and an umbrella was fixed above the camera to prevent glare on the Perspex lid. The bottom of the crate was divided into 15 squares measuring approximately 10x10cm, which were used to quantify exploratory movements (Figure 2.1). Before each set of tests, the arena and the novel object were cleaned using 70% ethanol and allowed to dry, to remove any scent cues remaining in the arena from previous mice. Each trial subject was placed at random into one of the corners of the arena. After a 5 minute open field test, the novel object (consisting of 2 stacked duplo bricks) was placed into the area where 4 of the squares intersect in one corner of the arena, then left for a further 5 minutes. After both tests were complete the subject was returned to its point of capture and number of faecal boli and urinations in the arena were counted.

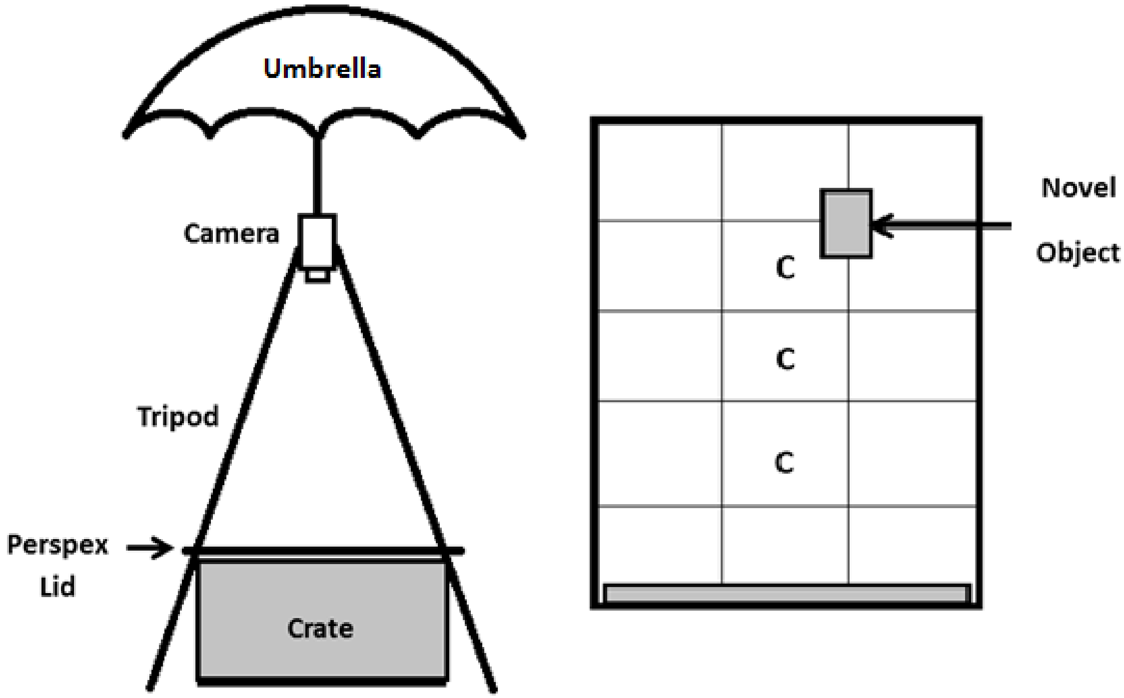


Figure 2.1. Equipment set up from side view (left) and top down view (right). Centre squares depicted with 'C'.

2.2.3 Scoring Behaviours

Behaviours were scored using JWatcher event recording software (Version 1.0; Stankowich, 2008). All videos from Sherwood and Brackenhurst were scored by the same observer, whereas videos from Silwood Park were scored by the first observer plus an additional observer. Inter-observer reliability scores were found to be significantly positively correlated using Spearmans rank correlation coefficient for each behavioural measure (Spearman rank correlation, X+SE: $r_s = 0.89+0.13$, N = 9, all $p < 0.05$ except for time frozen - $p=0.086$). When carried out on final factor scores both were significantly correlated between observers (Spearman rank correlation: *activity*; $r_s = 0.87$, N = 9, $p < 0.01$, *boldness*; $r_s = 0.87$, N = 9, $p < 0.01$, see below for factor calculations). The ethogram used to score the behaviours and a description of the variables is shown in Table 2.2, a separate ethogram was used for the novel object test and the open field test. Scoring for each test began once the lid was replaced.

Table 2.2. Ethogram used to score behaviours during behavioural testing, all durations and frequencies were recorded in milliseconds

Variable	Variable Type	Description
Open field Test		
Enter Centre Square	Frequency	Number of times mouse's head and shoulders entered a centre square
No. Lines Crossed	Frequency	Total number of lines crossed by mouse's head and shoulders
Time in Centre	Duration	Total time spent in centre squares
Latency to Enter Centre	Latency	Time before the mouse first entered a centre square
Time Grooming	Duration	Total time spent grooming
No. Rears	Frequency	Number of times the mouse reared up on hind legs
No. Jumps	Frequency	Number of times the mouse jumped leaving the ground
Novel object test		
Latency to Approach	Latency	Delay to first moving within one body length of novel object
Latency to Touch	Latency	Delay to first touch the object
Time Frozen	Duration	Time spent completely stationary
Time Near	Duration	Time spent within one body length of object
Time Touching	Duration	Time spent in contact with object
No. Approaches	Frequency	Number of times the mouse came within one body length of object
No. Touches	Frequency	Number of times mouse touched object

2.2.4 Data Analysis

2.2.4.1 Creating factor scores

The measured behavioural variables were reduced to a smaller number of factors using factor analysis, conducted separately for the open field and the novel object tests. Factor analysis is used to measure unobservable latent constructs that account for correlations between variables (Budaev, 2010), and to summarize the information of several behavioural variables into a single factor. This essentially produces one or more behavioural scores for each individual in each test, which can be subjectively named based on the behavioural variables contributing to each factor as representing a personality trait.

Untransformed variables were used for the factor analysis (Timm, 2002). Factor analysis (via Principle Axis Factoring) was used followed by Promax rotation on the correlation matrix. Promax rotation is an oblique rotation method allowing multiple factors created from a single test to be correlated, which was used as it may allow higher order behavioural constructs (behavioural syndromes) to be identified.

Bartlett's sphericity test and the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy were used to confirm that the correlation matrix was appropriate to carry out factor analysis (Budaev, 2010). In all cases, Bartlett's test was highly significant ($p<0.001$) and KMO exceeded 0.7 (OF – 0.8, NO – 0.79) suggesting that the correlation matrix was sufficient. The number of factors to extract was selected using a combination of the Minimum Average Partial analysis (Velicer, 1976) and a subjective observation of scree plots. The regression method was used to calculate factor scores.

Individuals were represented a variable number of times in these analyses depending on the number of repeated tests carried out, which violates the assumption of independent observations required for Factor analysis. Following the procedure of Dingemanse *et al,* (2007) to confirm the validity of factors, the analyses were rerun using only the result from the first test for each individual and compared to the initial analysis. This produced highly similar factors (Spearmans rank correlation: open field; $r_s = 0.99$, $N = 304$, $P < 0.0001$; novel object; $r_s = 0.99$, $N = 289$, $P < 0.0001$), allowing confidence in the results (see also Adriaenssens and Johnsson, 2011).

2.2.4.2 Modelling personality and behavioural plasticity

To calculate individual levels of personality and plasticity restricted maximum likelihood general linear mixed modelling (R; library nlme) with a Gaussian error distribution was used. Two sets of models were created to identify factors affecting the behavioural scores independently, the first using *activity* (the first factor from the open field test) as the dependant variable and the second using *boldness* (the first factor from the novel object test).

Random regression allows the partitioning of variance into within-individual variation and between-individual variation by retaining the same fixed effect structure but varying the random effects included and comparing the models to identify which best fits the data. Including mouse identity as a random intercept allowed the identification of between individual differences in behaviour (personality). Including trial number as a random slope within mouse identity allowed the calculation of individual plasticity over repeated testing (habituation).

Initially, the following fixed effects were added to the model: *sex, age* (adult, sub-adult, juvenile), *population* (Brackenhurst, Silwood or Sherwood) was included to observe if mean personality score differed between populations, *test number* to test if there was an overall habituation effect to repeated testing, and the two-way interaction to test if habituation rates differed between populations. The following variables were also included to control for potential confounding effects; *season* (divided into early breeding season; March-June, late breeding season; July-October, non-breeding season; November-February), *time* (minutes from 6AM), *interval* (days since last tested, log transformed) and *temperature during the trial* (˚C). *Observer* and an *observer by test number* interaction were also included as a covariate to control for potential variations in testing methods.

While keeping all the fixed effects in the model, the random effects were varied to produce the best model (models compared using likelihood ratios following Zuur (2009). Initially, individual ID was added as a random factor, if this was significant, trial number was included as a repeated measure within individual ID (random slope/regression model Dingemanse *et al.,* 2010). Once random effect structures were selected, significance of fixed effects was calculated using Type III sums of squares. Stepwise backwards elimination of non-significant fixed effects (P>0.05) was used as a model selection criteria.

To meet the assumptions of linear modelling, heterogeneity in the residual spread was corrected for by adjusting the variance structure to achieve the best fitting model (Zuur, 2009). Residual plots were used to ascertain that normality assumptions were met and both activity and boldness scores were square-root transformed to improve fit. All individuals were included in the analysis, even those that had only been tested once as this has been shown to increase the power of analyses (Martin *et al.,* 2011).

Adjusted repeatability of personality scores (r; the intraclass correlation coefficient) was calculated from the final restricted models as the ratio of the between-individual variance over the sum of the between- and within-individual variance (Nakagawa and Schielzeth, 2010).

Both of the above sets of models (for activity and boldness) were repeated using only data from each location separately, to allow a more detailed investigation into the factors affecting personality at each location. In this case the full model with all fixed effects was used to allow comparison between populations.

To identify if boldness and activity were correlated in a behavioural syndrome, first Best Linear Unbiased Predictors (BLUPs) of the random intercepts were calculated from the final restricted models for each trait. BLUPs essentially provide an estimate of an individual's overall personality score, taking into account the behavioural scores from each individual test and all of the variables retained in the model. Spearman's Rank correlation coefficients were then ran between boldness and activity BLUPs with all the data combined and then separately for each location to see if these correlations were consistent.

2.2.4.3 Timescale of Repeatability

To investigate over how long a period individual personality remained consistent, the above final restricted models were repeated iteratively only including individuals tested over longer periods. For each iteration only the first and last test of individuals with a minimum interval number of days were included, increasing the number of days by one each step. The significance of individual personality at each of these steps was tested by comparing models with and without ID as a random effect and the repeatability estimate at each step was calculated as above. This was repeated until individual ID became non-significant; the last significant step is then reported.

2.2.4.4 Additional Correlates with personality

Due to the ambiguity surrounding the interpretation of behaviours displayed in an open field or novel object test and to provide some validity of the personality traits created, a series of correlations were carried out between factors expected to relate to the personality traits measured.

Many classical studies in laboratory mice used amount of urination and/or number of faecal boli in an open field test as a measure of personality (Hall, 1941). Both scores were interpreted as a measure of 'emotionality' a form of fear or anxiety (Walsh and Cummins, 1976) in which case it may be expected to be negatively correlated with boldness. However, urine spread has also been linked with dominance in lab mice (Drickamer, 2001), which is frequently positively correlated with boldness. To explore if these measures were related to the behavioural scores used here a series of Spearmans Rank correlations were calculated between; urinations and faecal boli and activity and boldness BLUPs. Due to Bonferroni corrections for multiple comparisons analyses were only considered significant if $P<0.0125$.

Handling score has been used as a measure of docility (Reale *et al.,* 2000), boldness (Bremner-Harrison and Cypher, 2011) and linked to a fast exploratory syndrome (Fucikova *et al.,* 2009). Therefore it may be expected that handling would be positively related to either activity or boldness BLUP. To investigate if handling scores were related to behavioural scores recorded here a series of Spearman's rank correlations were ran between handling scores and activity and boldness BLUP. Again, due to Bonferroni corrections for multiple comparisons, correlations were considered significant if $P<0.025$

All statistical analyses were performed using R 3.0.0 (Ihaka and Gentleman, 1996).

2.3 Results

Overall 613 open field tests and 580 novel object tests were carried out on 304 individual mice (Table 2.3). Mice were recaptured and retested between 1 and 9 times (*X*±SE = 2.01±1.4 tests) with inter-trial intervals of between 2 days and 3 months (*X*±SE = 3.49±13.09 days).

Table 2.3. Summary of trapping data and personality scores used for analysis at the three trapping sites. Data given in counts or Mean ± SD.

	Sherwood	**Brackenhurst**	**Silwood Park**
no. mice	102	128	72
male/female	63/39	59/69	33/39
adult/sub-adult/juvenile	67/23/7	59/46/23	47/15/9
no. open field tests	1.85±1.49	1.71±1.13	2.77±1.45
days between tests	7.09±19.68	4.57±14.37	9.05±19.2
activity BLUP	1.39±0.12	1.41±0.12	1.4±0.13
bold BLUP	1.19±0.1	1.2±0.09	1.19±0.12

2.3.1 Calculating test scores

Only one component was retained from each factor analysis (Table 2.4). The factor retained from the open field test explained 45% of the total variance, with number of lines crossed, number of centre squares entered and number of rears loading positively. The factor was interpreted as a measure of activity and exploration behaviour, and is further referred to as activity (Table 2.4).The factor obtained from the novel object test explained 64% of the variance in behaviour. On this factor, number of touches and approaches to the novel object loaded positively and time spent frozen loaded negatively, and is further referred to as boldness, as it incorporates aspects of neophilia and fearlessness (Table 2.4).

Table 2.4. Factor loadings for results from open field and novel object test factor analyses, variables loading stronger than 0.5 in bold (Open Field, N=613; Novel Object, N=580)

Open Field Test	**Factor 1 (activity)**	**Novel Object Test**	**Factor 2 (boldness)**
Lines crossed	**0.96**	Latency to touch	**-0.9**
Enter middle squares	**0.83**	Number of touches	**0.88**
Rears	**0.8**	Latency to approach	**-0.84**
Latency to enter centre	**-0.58**	Number of approaches	**0.81**
Time grooming	-0.46	Time frozen	**-0.79**
Jumps	0.45	Time spent touching	**0.77**
Time in centre	0.36	Time spent near	**0.54**
Eigenvector	3.15	Eigenvector	4.46
Variance Explained	45%	Variance Explained	64%

2.3.2 Individual personality traits

Individuals were consistent in their behaviour over repeated tests for both activity and boldness ($p < 0.0001$) with adjusted repeatability's of 0.42±0.04 for activity and 0.27±0.04 for boldness, which is around the mean value for all traits measured in species previously tested (0.35; Bell, Hankison and Laskowski, 2009). This result provides evidence that wood mice have consistent individual personalities (Table 2.5).

This repeatability was significant across all three sites as shown by the significant effect of individual ID in all models conducted, except boldness at Brackenhurst which was verging on significance (Table 2.6 & 2.7). However, there was some variation in repeatability estimates between sites. Repeatability was notably lower for activity at Sherwood (0.19±0.09) and for boldness at Brackenhurst (0.14±0.1) than at other sites, which may indicate higher intra-individual variability in these traits at these sites (Stamps, Briffa and Biro, 2012).

Activity and boldness BLUPs were positively correlated in a potential behavioural syndrome (Spearman rank correlation: $r_s = 0.507$, $N = 289$, $p < 0.0001$). The correlation is also significant independently at the three sites (Spearman rank correlation: Brackenhurst; $r_s = 0.445$, $N = 116$, $p < 0.0001$, Sherwood; $r_s = 0.537$, $N = 100$, $p < 0.0001$, Silwood; $r_s = 0.541$, $N = 73$, $p < 0.001$).

2.3.3 Between individual variation in plasticity

The inclusion of test number as a random slope did not improve the fit of the full activity or boldness model, there is therefore no evidence to suggest that individual mice show individual differences in plasticity through habituation rates (Table 2.5). Overall mice reduced their activity over repeated tests suggesting habituation to the testing environment (GLMM: activity; β= -0.08±0.01, $F_{1,302} = 138.23$, $p < 0.0001$; Figure 2). Levels of both personality scores differed between seasons (GLMM: activity, $F_{2,302} = 23.26$, $p < 0.0001$; boldness, $F_{2,284} = 7.72$, $p < 0.001$), activity and boldness scores were both significantly higher during the late breeding season than at other times of year ($p < 0.0001$). Males were also more active than females ($F_{1,302} = 4.28$, $p < 0.05$). There was no significant effect of age, time, temperature or time between tests on behavioural scores.

Table 2.5. Results of model comparisons showing significance of random effects in linear mixed models of activity and boldness, models included mice from all three sites and contained all fixed effects.

Model			**Likelihood Ratio Test**			
	Random Factors	**Log L.**	**Test**	**LRT**	**df**	***p*-Value**
activity						
a	None	-81.98				
b	Intercept	-59.6	a vs. b	44.76	1	**<0.0001**
c	Intercept*Slope	-59.2	b vs. c	0.8	2	0.52
boldness						
a	None	-152.35				
b	Intercept	-131.6	a vs. b	41.51	1	**<0.0001**
c	Intercept*Slope	-130.02	b vs. c	3.15	2	0.14

2.3.4 Timescale of repeatability

Activity was still repeatable when only including individuals tested up to 27 days apart (L. Ratio = 3.74, $p < 0.05$, N=46 observations, 23 mice), with an adjusted repeatability of 0.23±0.17. Boldness was repeatable when only including individuals tested up to, 19 days apart (L. Ratio = 2.88, $p < 0.05$, N=71 observations, 36 mice) with an adjusted repeatability of 0.18±0.14. This provides a minimum bounding for the timescale of repeatability of personality traits in wood mice.

2.3.5 Between population differences in plasticity

The models containing all three sites showed no evidence for differences in plasticity between the three sites (*location* by *test number* interaction) for activity or boldness. However, there were some differences between sites in the factors attributing to personality scores. Differences in the significance of *time*, *season* and *interval* were seen between sites, but were likely due to the differences in sampling regime. Activity showed a significant decrease over *test number* at both Brackenhurst and Silwood but not at Sherwood, alternatively boldness showed a significant increase over *test number* at Sherwood and Brackenhurst but not at Silwood. *Age* and *sex* also had a significant effect on boldness at Silwood but not at the other two sites (Table 2.6, Table 2.7, Figure 2.2).

Table 2.6. Results of linear mixed models for activity individually for each location with model comparisons of full models using Likelihood Ratio (LR) tests to calculate significance of random effects

activity	**Sherwood**				**Brackenhurst**				**Silwood**			
	Coefficient	**DF**	**F-value**	**p-value**	**Coefficient**	**DF**	**F-value**	**p-value**	**Coefficient**	**DF**	**F-value**	**p-value**
(Intercept)	1.34±0.12	1,95	124.31	**<.0001**	0.32±0.4	1,124	7.54	**<0.01**	1.47±0.07	1,120	692.87	**<.0001**
Season		2,78	1.32	0.27		2,124	4.05	**<0.05**		1,120	1.65	0.2
Time	-0.19±0.22	1,78	0.74	0.39	-1.98±0.94	1,85	4.47	**<0.05**	0.44±0.22	1,120	3.99	**<0.05**
Test number	0.008±0.02	1,78	0.19	0.66	-0.16±0.06	1,85	8.76	**<0.01**	-0.09±0.02	1,120	33.37	**<.0001**
Interval	-0.14±0.06	1,78	4.73	**<0.05**	0.11±0.19	1,85	0.36	0.55	-0.08±0.03	1,120	5.27	**<0.05**
Sex		1,95	0.02	0.88		1,85	1.18	0.28		1,70	1.12	0.29
Age		2,78	0.76	0.47		2,85	1.26	0.29		2,120	2.72	0.07
Temperature	0.01±0.01	1,78	2.58	0.11	0.003±0.02	1,85	0.05	0.83	-0.01±0.004	1,120	13.88	**<0.001**
ID	LR	1	4.41	**<0.05**	LR	1	13.65	**<0.0001**	LR	1	24.47	**<0.0001**
ID* Test.no	LR	2	2.75	0.17	LR	2	0.93	0.48	LR	2	<0.001	0.99
Repeatability	0.19±0.09				0.38±0.07				0.43±0.05			

Table 2.7. Results of linear mixed model for boldness individually for each location with model comparisons of full models using Likelihood Ratio (LR) tests to calculate significance of random effects

boldness	**Sherwood**				**Brackenhurst**				**Silwood**			
	Coefficient	**DF**	**F-value**	**p-value**	**Coefficient**	**DF**	**F-value**	**p-value**	**Coefficient**	**DF**	**F-value**	**p-value**
(Intercept)	1.14±0.13	1,93	159.47	**<0.0001**	0.07±0.43	1,112	0.56	0.45	1.16±0.07	1,120	428.04	**<0.0001**
Season		2,71	1.19	0.31		2,112	0.1	0.9		1,120	1.05	0.31
Time	-0.27±0.23	1,71	1.3	0.26	-2.88±1.21	1,75	5.72	**<0.05**	-0.02±0.24	1,120	<0.01	0.94
Test Number	0.07±0.02	1,71	12.64	**<0.001**	0.2±0.08	1,75	6.33	**<0.05**	-0.02±0.02	1,120	0.9	0.34
Interval	-0.12±0.07	1,71	3.24	0.08	0.16±0.29	1,75	0.29	0.59	-0.03±0.04	1,120	0.57	0.45
Sex		1,93	0.22	0.64		1,75	0.55	0.46		1,70	5.62	**<0.05**
Age		2,71	1.79	0.17		2,75	0.38	0.69		2,120	8.85	**<0.001**
Temperature	0.001±0.01	1,71	0.03	0.1	0.009±0.02	1,75	0.23	0.63	-0.001±0.004	1,120	0.08	0.78
ID	LR	1.00	15.84	**<0.0001**	LR	1.00	2.53	0.06	LR	1.00	19.21	**<0.0001**
ID* Test.no	LR	2.00	3.74	0.10	LR	2.00	0.29	0.73	LR	2.00	0.43	0.67
Repeatability	0.47±0.07				0.14±0.1				0.32±0.06			

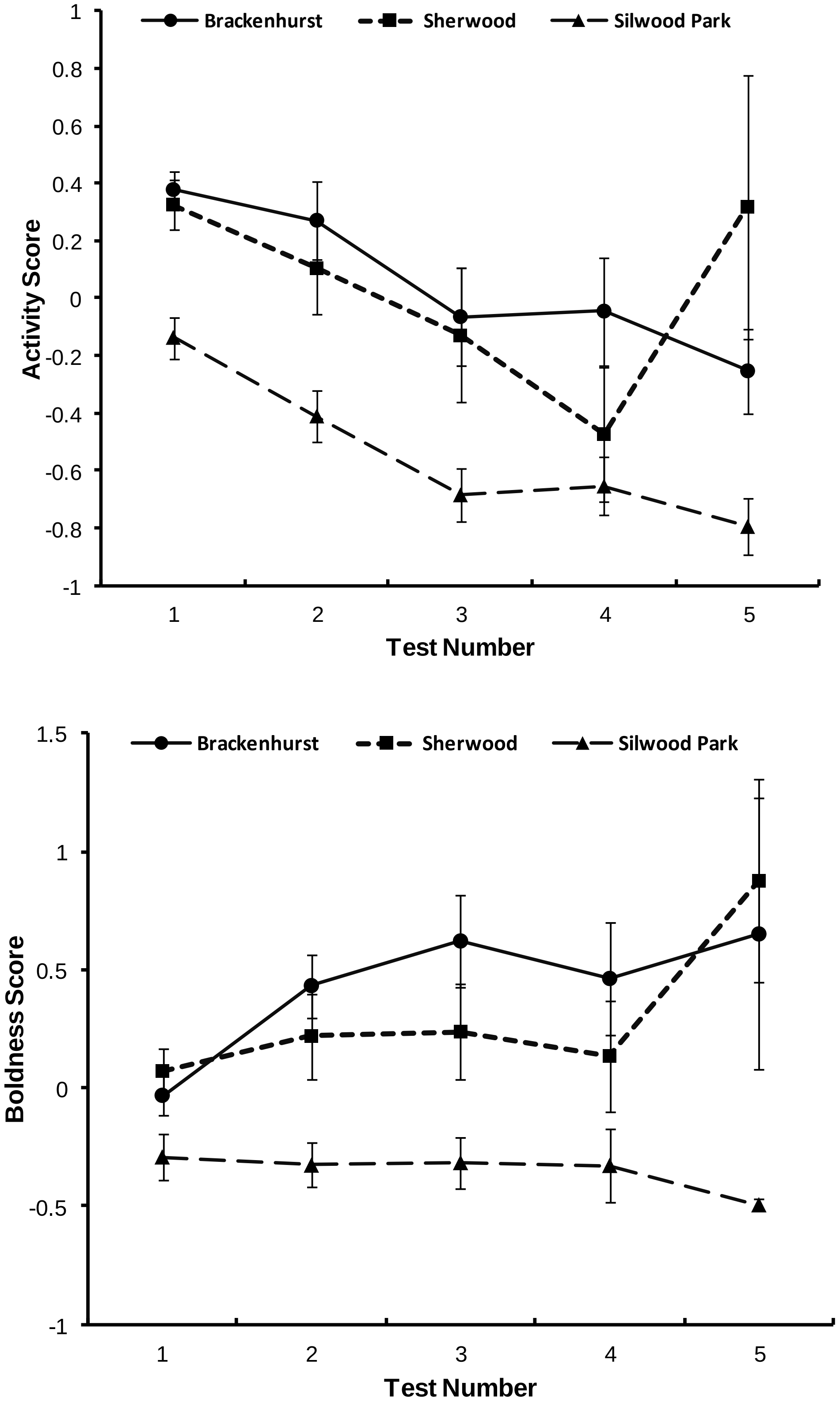


Figure 2.2. Mean personality score (± SE) over repeated tests for activity (top) and boldness (bottom) for the first five tests of each mouse for each population; scores corrected for season and observer.

2.3.6 Additional Correlates

Boldness was positively related to urinations ($r_s = 0.29$, N = 9, $p < 0.001$) and number of faecal boli ($r_s = 0.14$, N = 9, $p < 0.005$). Activity was also positively related to urination ($r_s = 0.34$, N = 9, $p < 0.001$) but not number of faecal boli.

Handling scores were significantly positively correlated with activity scores ($r_s = 0.29$, N = 612, $p < 0.0001$) and more weakly with boldness ($r_s = 0.11$, N = 578, $p < 0.01$).

2.4 Discussion

This study has quantified variation in behaviour at the within-individual, between-individual and between-population levels, allowing the comprehensive assessment of the presence and extent of personality and behavioural plasticity in the wood mouse. It has confirmed that wood mice show consistent behaviour in both the novel object and open field tests, representing activity and boldness personality traits. These two traits were correlated suggesting they may be part of a higher order behavioural syndrome, consistent with the proactive-reactive axis. Finally some differences in behavioural patterns were identified between the populations studied, which may indicate adaptation to local conditions.

Both boldness and activity scores were consistent within individuals over repeated tests and these traits varied significantly between individuals, meeting the requirements to be considered personality traits. The consistency across the three populations in the repeatability of traits points to the generalise-ability of these personality traits in wood mice. Boldness was repeatable for at least nineteen days and activity twenty seven days but potentially much longer. Twenty seven days represents a significant proportion of the lifespan of a wood mouse, which is usually little over a year (Harris and Yalden, 2008).

The aim of this study was not necessarily to identify or label specific traits, but to utilise replicable and portable tests to observe if behaviour was repeatable in the wood mouse in the wild, which has been successfully achieved. The equipment used here involved a simple replicable test that could be easily transported to the field with the aim of observing behaviour in wood mice shortly after capture, to avoid problems caused by the stress of transporting animals to captivity for testing. Thus, the behaviours recorded represent more accurately the individuals' response to the testing apparatus rather than excessive handling and manipulation. Despite being measured in an artificial arena, the variation in behaviour through different seasons is comparable to that seen in studies of wood mice in the wild, which show that mice are less active during the winter non breeding season (Montgomery, 1978; Lodewijckx, 1984b); providing some ecological validation that the traits scored here are representative of wild behaviours (Reale *et al.,* 2007). The increase in both activity and boldness in the later breeding season is likely to reflect the increased competition, particularly between males, at this time and the increased tendency for mice to disperse in autumn. Reduced levels of activity during the winter non-breeding season may also be explained by energetic constraints (Lodewijckx, 1984b). Unfortunately, few of the mice were caught over multiple seasons, so the individual plasticity of this change in behaviour could not be assessed.

The scores measured in this study were labelled 'Activity' and 'Boldness', but as stated previously there is some ambiguity over the interpretation of behaviour measured in these kinds of standardized tests (Reale *et al.,* 2007). Activity incorporated the number of lines crossed in the open field, a common measure of activity, as well as jumping and rearing in the arena, behaviours that could be interpreted as escape oriented. It also incorporated the tendency to move into the centre of the arena, which may reflect either high activity causing individuals to cross into the centre more often, or potential higher boldness as suggested in some previous studies if the mouse is intentionally moving into a 'high risk' area (e.g. Dahlbom *et al.,* 2011). Rodents generally avoid the centre of an open arena, which has been linked to a higher predatory risk and a lack of shelter (Eilam, 2003). However, due to the small size of the arena used in this study, this explanation seems unlikely as the centre of the arena would not represent much more of a threat than the outside edge. Activity was also negatively related to time spent grooming. Longer bouts of grooming demonstrate lower levels of stress in rodents (Komorowska and Pisula, 2003), which may indicate that more active individuals were more stressed in this study as their grooming bouts were shorter and more interrupted.

The boldness factor incorporated both the number of approaches but also time spent near the novel object so is likely not just a feature of increased activity causing chance approaches, as the object was placed in one corner of the arena. The score in the novel object test was negatively related to time spent frozen after the novel object was placed into the arena. The disturbance caused by the experimenter placing an object into the arena sometimes caused the mouse to freeze, an antipredator fear response in mice used with the aim of avoiding detection by a predator (Eilam, 2005). Taken together these behaviours are interpreted as boldness as they represent risk taking in response to novelty and a lack of fearfulness in response to potential predation.

Activity and boldness were positively correlated at all three sites suggesting these traits may be part of a higher order behavioural character (Araya-Ajoy and Dingemanse, 2014) or behavioural syndrome (Sih, Bell and Johnson, 2004). Unlike previous studies of sticklebacks (Dingemanse *et al.,* 2007; Bell and Sih, 2007; Bell and Stamps, 2004) the direction and strength of this correlation was similar between populations despite potential differences in environmental factors (e.g. predation, disturbance), suggesting that this correlation is constrained, actively maintained or selectively neutral in this species (Bell, 2005). The activity and boldness traits may have been correlated if they both represent aspects of exploration, of a novel object and novel arena respectively (Araya-Ajoy and Dingemanse, 2014). Alternatively as the nature of the tests used here involved forcibly placing the animals into the arena, responses to both tests may in part represent fear or anxiety in response to the test situation (Carter *et al.,* 2013). In rodents, coping styles have been used to describe how individuals respond to a stressful situation and are usually defined along the proactive-reactive axis. In stressful environments, individuals with a proactive coping style attempt to affect their surroundings by moving or manipulating them whereas reactive individuals freeze or hide (Koolhaas *et al.,* 1999). Whether an animal investigates novelty is a balance between approach and avoidance, a conflict between information seeking and harm avoidance (Tanaś and Pisula, 2011). Both a novel object test and novel environment test may be considered approach/avoidance trials (Herborn *et al.,* 2010). The behavioural data collected here may therefore suggest that the mice are displaying a gradient from a proactive to reactive response, with individuals scoring high in both boldness and activity being more proactive, and those scoring low being more reactive. Freezing, which was negatively related to boldness, is an indicator of a reactive coping style (Carere, Caramaschi and Fawcett, 2010). Conversely, high activity, manipulating objects and a strong reaction to handling which were positively related to activity and boldness, indicate a proactive coping style (Koolhaas *et al.,* 1999).

However, there is growing caution in the literature in interpreting correlations between scores measured in tests such as these as either the same behaviour measured in multiple situations or different behaviours correlated in a behavioural syndrome (e.g. the ‘jingle-jangle’ fallacy, Carter *et al.,* 2013). Trillmich and Hudson (2011) suggest drawing a distinction between underlying personality traits and the ‘behavioural profiles’ measured calculated from testing procedures. Identifying correlates with other behaviours, particularly in the wild can provide evidence that the scores measured in personality tests truly represent underlying personality traits and whether they are unique traits or the same trait measured in multiple tests.

Some correlations differed between the two traits suggesting they are unique personality dimensions. Boldness was correlated with defecation, which historically has been one of the key measures of ‘emotionality’ (Walsh and Cummins, 1976) the trait for which the open field test was originally designed to identify, described as a response to fear or anxiety (Carter *et al.,* 2013). Whereas Activity was strongly correlated with the score taken while mice were in the handling bag, which has previously been inversely used as a measure of docility (Dingemanse and Reale, 2005) and described as an effective measure of a proactive coping style (Careau *et al.,* 2008). However the traits also had some correlates in common providing some validity to the suggestion that they are both part of a proactive/reactive axis. Activity and boldness were both positively correlated with urination, thought to be linked with activation of the sympathetic nervous system (Walsh and Cummins, 1976), which is linked to a proactive stress response (Carere, Caramaschi and Fawcett, 2010).

Individual differences in behavioural flexibility are a fundamental component of the coping style concept (Koolhaas *et al.,* 2007). Proactive individuals consistently show less flexibility of behaviour in laboratory tasks (Coppens, de Boer and Koolhaas, 2010) and are more routine in their behaviour (Koolhaas *et al.,* 1999). If the scores here represent the coping style dimension it may then be expected that individuals scoring high in both boldness and activity would be less flexible in their behaviour and show lower rates of habituation to the testing environment. However the experimental tests used here did not pick up evidence for individual differences in habituation; although this may not rule out that they exist as power to detect individual differences in plasticity is often low (Martin *et al.,* 2011). Habituation is also only one form of behavioural plasticity, other measures of plasticity, such as how an individual adjusts its behaviour across different environments or in different situations, may have shown a different pattern.

Although no differences in habituation were seen at the individual level, some differences were seen between populations. In the full model activity reduced over repeated tests and this did not significantly differ between sites, demonstrating consistent rates of habituation to the testing environment as seen in previous studies (Martin and Reale, 2008; Mettke-Hofmann *et al.,* 2006). The full model showed no change in boldness scores over repeated tests but in the individual population models both Brackenhurst and Sherwood showed a significant increase in boldness, whereas there was no change over repeated tests at Silwood. At all three sites mice initially displayed a low level of boldness, potentially due to fear of the disturbance from the introduction of the novel object, and initial neophobia. Over subsequent tests, boldness increased at Sherwood and Brackenhurst, presumably from a decrease in fear and reduced neophobia allowing them to interact with the novel object more readily. However at Silwood boldness showed little change over subsequent tests, suggesting a lack of habituation to the novel object and the maintenance of a relatively high fear response. These differences could potentially be due to the differences in testing environment or handling protocol between study sites, but could demonstrate genuine population differences in behavioural plasticity due to adaptation to local conditions. However, this difference between sites was not significant in the full model, which leads to caution in its interpretation.

Habituation is usually ascribed to O'Keefe and Nadel's (1979) cognitive map theory. This theory suggests that when encountering novelty a map is created in the hippocampus. Once enough information has been collected for the cognitive map, habituation begins to occur, particularly when there are no biologically relevant reinforcing stimuli (Heise, 1984). Habituation to low level stressors in this way can provide a fitness advantage (Rodriguez-Prieto, Martin and Fernandez-Juricic, 2010). Studies suggest that in rodents, between-test changes in behaviour represent both adaptability (behavioural plasticity) and memory (Leussis and Bolivar, 2006). The three sites studied have different levels of disturbance and exposure to novelty. Previous studies have shown that anthropogenic disturbance can affect the behaviour of wild populations (Archard and Braithwaite, 2010) and the distribution of personality traits in an area (Martin and Reale, 2008). This makes adaptive differences in behavioural response to novelty a plausible suggestion, as habituation rates in other species are known to be higher in areas with greater levels of anthropogenic disturbance (Stankowich, 2008). Mice at Silwood are trapped at a site with limited access and less disturbance than at the other two sites. The increased boldness over repeated tests shown at Sherwood and Brackenhurst may therefore indicate adaptation to their local environment through greater adaptability or memory retention, allowing them to exploit novel resources and limit the negative effects of disturbance.

This kind of differing selection pressure can lead to contemporary evolution of behavioural traits (Hendry and Kinnison, 1999). Previously, different mouse strains have been shown to display differences in habituation patterns to an open field (Bolivar *et al.,* 2000), suggesting that habituation can be a heritable trait in mice and therefore open to differing selection between populations. Personality and plasticity may also partially be determined by natal environment or through maternal affects (Wolf and Weissing, 2010), with mice developing a level of plasticity during ontogeny appropriate to their local conditions. Data collected in this study is not able to distinguish between genetic and developmental effects, but tentatively suggests that habituation rate may differ between populations as a result of the local environment. However it is important to note that there may have been other factors differing between the populations studied here such as predation or food availability providing other sources of selection pressure, which may have caused the patterns seen.

Unlike in previous studies, this study found no difference in either mean boldness or activity between populations (Martins and Bhat, 2014). However, sex and age had a significant effect on boldness at Silwood but not at the other two sites, again suggesting there may be different selective forces acting on this population. At this site males were generally more active than females, which may suggest greater competition during the breeding season than at the other two sites causing stronger sexual dimorphism in behaviour. Male wood mice tend to have larger home ranges which overlap multiple female ranges which they regularly patrol during the breeding season (Tew and Macdonald, 1994) and previous studies have noted that more ‘vigorous’ males expend more energy maintaining large home ranges than other males (Tew and Macdonald, 1994). A greater difference in boldness at this site may therefore suggest more intense competition for females and territory than at the other sites.

At this site adults were also significantly less bold than juveniles; this implies greater selection for being bold as juveniles or against being bold during adulthood at this site. Different behavioural traits can be favoured at different life stages (Sih, Bell and Johnson, 2004). Higher boldness as a juvenile may allow higher access to resources during development which may outweigh the risks of higher rates of predation or unnecessary energy expenditure (Smith and Blumstein, 2008), whereas in adulthood caution may provide greater benefits and greater long term breeding success. These behavioural changes may be learnt during development, for example older individuals may see less benefit in exploring novel objects which do not present obvious rewards (Ensminger and Westneat, 2012). Alternatively, there may be an ontogenetic adaptation to being bolder while young which has been selected for at this site (Trillmich and Hudson, 2011). Another explanation for this pattern may be if bolder juveniles do not survive to adulthood due to an increased level of risk taking reducing their likelihood of survival.

In conclusion, this study has identified personality traits in the wood mouse using an open field and novel object test. These traits seem to accurately represent distinct personality traits described as activity and boldness. Data suggests these traits may be part of a higher order proactive-reactive behavioural syndrome. The study has also identified various covariates with these traits suggesting they correspond to behaviour in the wild. Between population differences in habituation rates may also exist, which may be due to differing levels of disturbance, however data for this is limited so conclusions are tentative.

2.5 Chapter Outcomes

- The open field and novel object tests carried out in the field describe activity and boldness behaviours respectively in the wood mouse.
- Activity and boldness are repeatable personality traits in the wood mouse.
- Activity and boldness are positively correlated with one another, potentially as part of a proactive-reactive behavioural syndrome.
- No individual differences in habituation were identified; there may be some differences between populations in habituation rates, although these were not significant.

- Handling scores can provide a good indicator of activity, which could be used as a proxy for personality in practical conservation projects.

The personality scores calculated in this chapter are used to assess the affect personality type may have on trapping bias and how this may impact translocation projects in Chapter Three. Here trapping success is also used to identify how these personality scores affect microhabitat use. In Chapter Four the scores collected here in the field are contrasted with scores taken from a captive bred population to investigate the impact of captive breeding on personality scores. Finally the testing procedures and models developed here are applied to explore the impact of personality on a simulated reintroduction in Chapter Five.

3 Chapter Three: Avoiding biases in behavioural studies; the effect of individual personality on trapping success and microhabitat use

3.1 Introduction

There is much previous evidence that individuals which occupy different ecological niches differ in a range of physiological and life history traits (Pearish, Hostert and Bell, 2013). Habitat use in particular can vary based on a large number of factors including; the individuals species (Schluter, 1993), sex (Cluttonbrock, Iason and Guinness, 1987), body size and other phenotypic features (Werner and Gilliam, 1984). However little attention has been paid to the interaction between habitat use and behaviour despite evidence that an animal’s behaviour affects how it uses its local environment (Mysterud and Ims, 1998). In the personality literature there is a growing suggestion that habitat use is likely to differ between individuals due to individual differences in behaviour. This is of particular interest to conservation science as it may affect how individual animals respond to differing release environments.

With a variety of approaches and trade-offs between personality types, some animals will do better or worse in an environment which changes both in space and time (Watters, Lema and Nevitt, 2003). More active individuals may have an advantage in highly heterogeneous environments as it will increase their chances of encountering resources (Wolf *et al.,* 2007), although may also have the disadvantage of an increased chance of encountering predators (Biro *et al.,* 2004) or contracting parasites (Boyer *et al.,* 2010). Bolder individuals are likely to have an advantage in low risk or low predation environments, where taking risks is likely to reap the maximum of rewards with minimum cost, but may suffer increased predation in higher risk areas (Reale *et al.,* 2007). When individuals of a certain personality type occur more often in a certain habitat type there is a personality type by environment correlation (Pearish, Hostert and Bell, 2013).These personality type by environment correlations may occur for a variety of reasons. Animals may manipulate their environment though niche construction to suit their personality (Donohue, 2005) or their environment may affect their personality, for example animals in safer environments may become bolder (Webster, Ward and Hart, 2007). Differences in mortality rates can also mean certain individuals are more likely to survive in particular locations. Alternatively, individuals with different personality types may seek out particular environments (niche picking; Stamps and Groothuis, 2010), which enhance their fitness (Edelaar, Siepielski and Clobert, 2008). Individuals may then select habitat for which they are more well suited (Edelaar, Siepielski and Clobert, 2008), which can be a mechanism for the maintenance of multiple personality types within a population as it will reduce competition. If this is the case then knowledge of individuals habitat preferences may allow conservation managers to aid in this niche picking behaviour by manipulating release location to a suitable habitat.

Previous data have shown that bold animals generally range further (Bremner-Harrison, Prodohl and Elwood, 2004), and are more likely to forage under risk of predation (Bell and Sih, 2007). Studies have also shown that personality type can affect territory size (Boon, Reale and Boutin, 2008). However the direct effect of personality on microhabitat use within a population has rarely been investigated. In the few studies in this area Pearish, Hostert and Bell (2013) found that more exploratory individuals were more likely to be found in open areas and Wilson *et al.* (1993) showed that pumpkinseed sunfish of different personality types inhabited different parts of a lake. A common expectation is that more shy individuals would be more likely to occur in safer habitats (Reale *et al.,* 2007), but this assumption has rarely been tested in practice.

Trap use can be considered an indicator of the trade-off between risk and reward, which is found through many aspects of an animal’s behaviour and often linked to personality. Entering a trap demonstrates an aspect of neophilia and risk taking often associated with boldness. Animals with different personality types may therefore be more or less likely to enter traps (Biro and Stamps, 2008). Wilson *et al.* (1993) showed that bold fish were more easily trapped than shy fish and since then a number of studies have shown that this phenomenon may be widespread (Carter *et al.,* 2012; Reale *et al.,* 2000; Tuyttens *et al.,* 1999).The propensity to enter traps has been shown to be repeatable (Reale *et al.,* 2000) and may be in part a heritable trait (Cooke *et al.,* 2007), but is also likely to be in part a learnt behaviour depending on the trapping experience (Tanaka, 1980). Biro and Dingemanse (2009a) suggested that passive trapping methods in particular will always be biased towards those more active and exploratory individuals. Most studies have assumed trappability is related to boldness (Wilson *et al.,* 1993; Boyer *et al.,* 2010; Reale *et al.,* 2000), suggesting that entering a trap demonstrates a high level of risk taking or neophilia (Reale *et al.,* 2000). However, few studies have tested out this assumption by estimating if trappability relates to measures of boldness collected using alternative methods (but see Carter *et al.,* 2012). Trapping bias is a concern in many studies as personality has been linked to various aspects of physiology and fitness (Biro and Dingemanse, 2009a). Personality based trap bias may therefore violate many of the assumptions made by previous studies utilising trapping regarding random selection of subjects. As trapping is a common way to assay small mammal populations and a few studies have demonstrated consistent differences in trappability between individuals in wood mice (Crowcroft and Jeffers, 1961; Tanton, 1965), any biases due to behaviour could therefore seriously affect the results of many experiments in this area (Biro and Dingemanse, 2009a), including aspects of this study. It may also be of concern to conservationists when aiming to trap a representative sample of a wild population for release elsewhere.

This study utilises wood mice, previously identified as having personality traits (see Chapter Two), to investigate personality type by environment interactions at the microhabitat scale within a single population. Small scale habitat structure has been shown to affect the behaviour of rodents in the wild (Vasquez, Ebensperger and Bozinovic, 2002) and wood mice have been shown to modify their foraging behaviour in areas in response to a predation threat (Diaz *et al.,* 2005). It is therefore likely that if personality affects habitat use then it would be seen at this scale in wood mice. Personality may also affect how individuals use the environment across a temporal scale, for example with changing weather conditions. Mouse movements can be affected by weather (Drickamer *et al.,* 1999), with fewer mice caught during wet conditions, or with sudden drops in temperature. Whereas more animals are caught when it is warm and cloudy or when a rainstorm occurred during the night (Tanton, 1965). Trapping success can also be affected by amount of moonlight, with fewer mice trapped on bright lit nights (Tanton, 1965; Plesner Jensen and Honess, 1995). These relationships may therefore also be modified by personality types, although this has never been explicitly tested. Entering more open areas on a moonlit night presumably indicates a level of risk taking, which would be consistent with what is usually expected from a bold behavioural type. Alternatively, activity levels may affect the need of individuals to collect food on wet or cold nights, as activity has often been linked with metabolic rate (Careau *et al.,* 2008). It may therefore be expected that animals with a higher activity levels would be more likely to venture out in less suitable conditions.

In addition, previous work has shown that small mammal trapping may be influenced by social cues, with mice usually being attracted to traps previously occupied by conspecifics (Stoddart and Smith, 1986). Wood mice generally prefer traps occupied by conspecifics over odourless or heterospecific odours, but show no preference between odourless and heterospecific odours (Stoddart and Smith, 1986). This may represent a level of risk avoidance, as encountering heterospecifics can lead to agonistic encounters and presumably the smell of conspecifics may indicate relative safety (Verplancke, Le Boulenge and Diederich, 2010). The propensity to avoid such risky encounters would then be expected to be affected by an individual's level of boldness (Reale *et al.,* 2007), it may be expected that bolder individuals to be more willing to enter traps with a heterospecific odour. Similarly, individuals with different levels of sociability may be more or less likely to enter traps previously occupied by a conspecific.

Showing that habitat use and behaviour in the wild corresponds to behavioural scores measured in experimental tests is important to provide ecological validity of personality traits (Reale *et al.,* 2007). However to accurately measure this effect, first potential bias in trapping probability needs to be measured and taken into account. This study investigates whether individuals with different personality types are more likely to occur in different environments, including the physical environment through microhabitat choice, the temporal environment through overnight weather conditions and moonlight, and through social cues of previous trap occupancy. Understanding how personality affects habitat use and trappability is particularly important to avoiding biases in many animal studies (Biro, 2013). The ultimate aim of this study is to focus on measures which could potentially cause bias in studies trapping animals in the field for transport into captivity or to be released in a novel location and the potential implications of this for translocation studies.

3.2 Methods

Trapping data from Chapter Two was reassessed to investigate what factors affected the trappability of wood mice and if there is a personality type by environment (physical, temporal or social) interaction in trapping probability. When calculating trapping success, data from Sherwood and Brackenhurst were analysed separately from data collected at Silwood, as trapping methods differed at Silwood Park. However, when investigating the effects of weather and habitat measures only mice trapped at Sherwood were used, so results were consistent and easily interpretable. Mice from Brackenhurst were in the most part trapped in hedgerows a much more linear habitat, making comparison to the woodland in Sherwood forest difficult. This type of linear habitat is likely to restrict mouse movement and be strongly affected by field management, which may mask any effects of microhabitat on trap use. Due to the scale of the study and the lack of restrictions on movement it is assumed that trapped mice had free choice of whether to enter a specific trap and therefore the local environmental conditions.

3.2.1 Habitat Assessment

Habitat was assessed at Sherwood in the immediate area surrounding each trap, consisting of a 5x5m grid square marked out when traps were placed. Habitat consisted of a bracken or bramble herbaceous layer and an oak or birch canopy. Measures consisted of; modal height of herbaceous layer (cm), modal canopy height (m), percentage canopy cover, number of trees, distance to nearest tree (cm) and percentage of open ground. Plant height and distance to nearest tree were measured to the nearest five centimetres whereas canopy height was estimated by eye to the nearest meter. Ground and canopy cover were estimated to the nearest 5%. Measures aimed to indicate various levels of ‘openness’, which mice may consider more or less risky habitat.

3.2.2 Weather Data

Weather data was gathered using the met office historical data website (http://wow.metoffice.gov.uk/), including data on overnight rainfall, temperature, humidity, visibility and cloud cover. Means or medians for each variable from the time the traps were set until 7am were calculated as appropriate. Moon phases were calculated based on a historical table.

3.2.3 Data Analysis

Estimates of individual personality (intercepts) were estimated from the best linear unbiased predictors (BLUPs) calculated using the restricted models developed in the previous chapter. These BLUPs were used in all further analyses as a proxy for individual personality scores.

3.2.3.1 The relationship between personality and trappability

Individual BLUPs for activity and boldness were used as independent variables to look at trappability at Brackenhurst and Sherwood. Three measures of trappability were used as dependant variables: *number of times trapped* (per trapping session), *number of locations trapped* (number of different trap locations in which the mouse was captured per trapping session), and *trap latency* (number of days traps were set in the trapping session before the mouse was first captured). A generalized linear model was created for each test with a poisson distribution and a log link. *Mouse Id* was included as a random effect to control for individuals caught over multiple trapping sessions. *Trapping success* (number of individuals trapped/number of traps), *trapping session, weight* (g), *sex* and whether the mouse had been trapped in a previous trapping session (yes/no) were included in all models as covariates. Only data from Sherwood and Brackenhurst were included in these models due to differences in sampling effort at Silwood and only individuals tested more than once were included in the analysis to ensure minimum bias in BLUP scores. The minimum adequate models were calculated by step-wise elimination of non-significant terms ($p > 0.05$).

A logistic regression model was also ran on data from Brackenhurst and Sherwood with whether the mouse was recaptured after its first trapping event (No=0, Yes=1) as the response and factor scores at first trapping as the predictor (*Boldness, Activity*). *Trapping success* (number of individuals trapped per night/number of traps), *weight* (g) and *sex* were also included as predictors *and trapping session* and *days from start of trapping session* were included as covariates.

Data on recaptures of mice before and after this study collected as part of ongoing research were used from Silwood to look in detail at long term trappability at this site. Again general linear models with a poisson distribution and log link were used with two separate measures of trappability *number of times trapped* and *number of locations trapped* as dependant variables. *Number of days on site* (days between first and last sighting) and *number of recaptures* were included as covariates as appropriate and *sex, weight* (g), *activity BLUP and boldness BLUP* were included as factors. Again the minimum adequate model was calculated by step-wise elimination of non-significant terms ($p > 0.05$).

3.2.3.2 Trap variables

Two sets of initial general linear models were created with activity and boldness BLUPs as the dependant variables. Each set of models initially separately analysed the temporal conditions during trapping including weather and moon phase, physical habitat surrounding traps consisting of microhabitat variables and social cues of previous trap occupants. Trapping session was included as a random effect in all analysis to control for general differences in habitat and climate between sites and seasons. Due to the results of the trapping bias models, *days since traps were set* was also included as a covariate. The first model looked at how weather affected the probability of trapping mice with different personality types. Overnight data of; *mean rainfall rate* (cm/minute), *mean humidity* (%RH), *mean temperature* (˚C), *weather conditions* (cloudy or clear), *visibility* (ranked from 1-very poor to 5-excellent), *moon phase* (%) and the interactions between *moon* and both *weather* and *visibility* were included as predictors. The second model looked at microhabitat in the 5m^2 surrounding the trap location and included *herb height* (cm), *canopy height* (m), *canopy cover* (%), *number of trees*, *distance to the nearest tree* (cm) and *openness* (%) as predictors. This model also included *moon visibility* (%) and all relevant interactions with habitat variables. The third model looked at whether previous occupancy of a trap affected capture and only included *previous occupant* (vole, mouse, shrew or none) as a predictor. Bank voles (*Myodes glareolus*) and occasionally field voles (*Microtus agrestis)* were regularly trapped at all three locations, however individuals were not always recorded to species level and so both have been included as 'vole'.

Only the first capture of each individual was included in each model to avoid pseudoreplication. A backwards stepwise procedure was used as a model selection criteria for each model, initially dropping factors with $p > 0.1$. Normality was assessed by visualising plots of the residuals. Once the above three models were computed the minimum adequate models were combined including all significant factors from the above models as well as all relevant interactions to create an overall model, which was again further reduced using a stepwise backwards procedure removing the least significant factors until all included variables were significant ($p < 0.05$).

All statistical analyses were performed using R 3.0.0 (Ihaka and Gentleman*,* 1996).

3.3 Results

Trappability analysis at Sherwood and Silwood comprised of data from 248 recaptures (Sherwood – 116, Brackenhurst 130) of 86 mice (Sherwood – 36, Brackenhurst – 50) trapped more than once (Table 3.1). Data from Silwood included 65 mice which were recaptured 12.11±7.19 (Mean±SD) times over a period of 154.82±102.3 days. Data for habitat analysis was taken from 13 trapping sessions including the first capture of 61 mice at Sherwood Forest.

Table 3.1. Summary of trapping data used to analyse the effect of personality on trapping success (Mean ± SD)

	Brackenhurst	**Sherwood**	**Silwood**
No. mice captured at least twice	31	57	62
Activity BLUP	1.42±0.12	1.41±0.11	1.4±0.14
Boldness BLUP	1.3±0.11	1.28±0.15	1.19±0.13
Mean Times Trapped	2.42±0.58	2.97±1.25	12.11±7.19
Delay to first capture	1.27±0.88	1.56±0.99	NA
Mean Locations Trapped	1.84±0.56	2.42±0.82	8.31±4.6
No. mice trapped at least once	116	59	65
Activity at first capture	0.52±0.71	0.46±0.99	NA
boldness at first capture	0.07±0.86	0.09±1.08	NA

3.3.1 The effect of personality on trappability

Number of times individual mice were trapped decreased with higher within session trapping success (β = -0.37±0.12, Chisq$_{1,218}$ = 9.38, $p < 0.005$), mice were also trapped more often if they had been trapped in a previous trapping session (β = 0.39±0.14, Chisq$_{1,218}$ = 8.13, $p < 0.01$). Number of locations trapped also increased if mice were trapped in a second trapping session (β = 0.43±0.9, Chisq$_{1,185}$ = 5.23, $p < 0.05$) and male mice were trapped in a greater number of trap locations (β = 0.26±0.1, Chisq$_{1,185}$ = 6.24, $p < 0.05$). Boldness had a significant positive relationship with days until first trapped (GLM: β = 1.58±0.79, $Chisq_{1,167}$ = 3.98, $p < 0.05$), suggesting that bolder individuals took longer to enter traps (Figure 3.1). The logistic regression model indicated that individuals which were more active on first capture were less likely to be recaptured (GLM: β = -0.7±0.26, Chisq$_{1,156}$ = 7.39, $P < 0.01$).

Data from Silwood showed no effect of personality on number of times trapped, or number of locations trapped

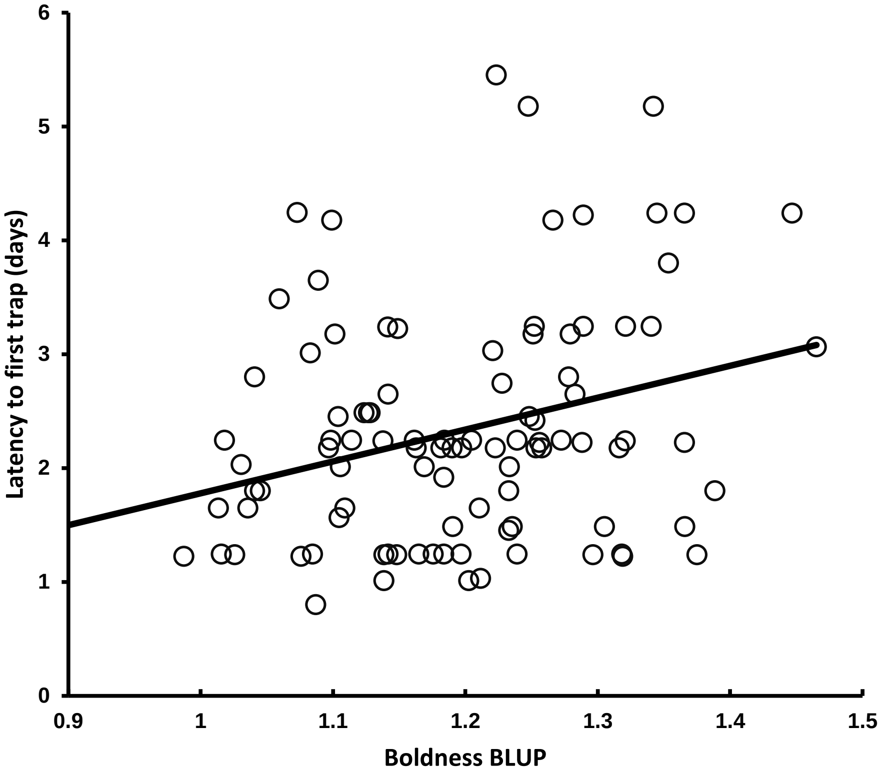


Figure 3.1. Boldness BLUPs of individual mice in relation to latency to first trapping in days with line of best fit (N=77). Data corrected for the effect of trapping session by subtracting the regression coefficient for respective trapping sessions from latencies.

3.3.2 Trap variables and personality

The restricted model for activity found that more active mice were caught when the moon was less full (β = -0.41±0.13, $F_{1,38}$ = 10.3, p < 0.01). The interaction between moon and canopy cover was also significant ($F_{1,38}$ = 6.31, p < 0.05). In areas with lower canopy cover less active mice were trapped when the moon was more full, whereas with high canopy cover activity was unrelated to moon visibility. The interaction between moon and openness was also significant ($F_{1,38}$ = 5.71, p < 0.05), in less open areas less active mice were trapped when the moon was more full, whereas in more open areas moon had little effect. The main factors of openness and canopy cover were not significant. Previous occupant was also significant ($F_{3,\ 38}$ = 3.21, p < 0.05), more active individuals were found in traps previously occupied by voles than an empty trap (p < 0.01) and tend to be more active than those entering a trap previously occupied by a mouse (p = 0.09; Figure 3.2), there was no difference in activity between individuals entering an empty trap and one previously occupied by a mouse.

None of the variables included in the model predicted the boldness of the mice trapped.

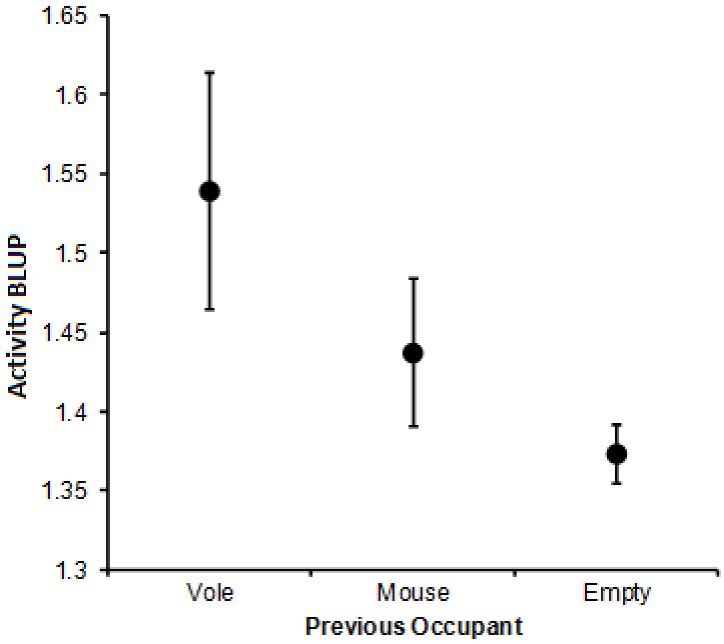


Figure 3.2. Mean activity BLUP (± SE) of individuals entering traps with different previous occupants (wood mouse, N=9; vole, N=5; or no previous occupant, N=46)

3.4 Discussion

Results here suggest that an animal's personality affects its probability of being trapped based on the habitat in the immediate vicinity of traps, weather conditions at time of trapping and the previous trap occupant. This study found limited effects of phenotypic factors on trap use suggesting that behaviour is a stronger indicator of habitat use that phenotypic factors, at least in wood mice. This study therefore provides evidence of a personality type by environment correlation in a natural population collected using standard trapping protocols. This suggests that microhabitat around traps and weather conditions at time of trapping may cause biases in the subset of a population trapped if not carefully controlled for. Personality also affected the latency to enter traps and an individual's likelihood of being retrapped at Sherwood and Brackenhurst, indicating this is another potential source of bias in personality and other behavioural studies utilising passive trapping methodology that needs to be taken into account.

Previous studies have reported that some animals are trap prone (trapped first or more often) or trap shy (trapped less often) and that this trait appears to be consistent over time (Tanton, 1965). This has led some studies to use trap proneness as a measure of personality, assuming that it is positively related to boldness. Contrary to this, the results presented here suggest that bolder mice in fact take longer to enter small mammal traps, but this had no effect on number of times trapped or number of locations trapped. This seems contradictory, as in previous studies 'bolder' animals are usually those more willing to enter novel environments and explore novel objects (Biro and Dingemanse, 2009b). However, passive trapping methods as used in this study and others (Reale *et al.,* 2000; Reale and Festa-Bianchet, 2003) may also be affected by factors such as routine formation and territory size. Previous studies have found that bolder individuals tend to have larger territories, and are more routine in their behaviour particularly through exploration (Carere *et al.,* 2005). This may reduce their likelihood of encountering or entering new traps. More active individuals were also less likely to be re-trapped than less active individuals. This may be because more active individuals range further decreasing the likelihood of their recapture (Dingemanse *et al.,* 2003). However this may be affected by number of traps laid or trap configuration as data at Silwood showed no relationship with number of times trapped, potentially as traps covered a wider area removing this effect. An alternative explanation may be if more active individuals find trapping more stressful as they struggle to escape more than less active individuals, as suggested by the handling scores in the previous chapter. More active individuals tend to be more proactive, meaning that in stressful situations they become agitated and attempt to escape (Careau *et al.,* 2008) and have higher metabolic rates (Huntingford *et al.,* 2010). A higher metabolism in these more proactive individuals requires high energy reserves (Stamps, 2007), when in a situation where food is restricted, such as while caught in a trap this may be a disadvantage and cause stronger negative associations with trapping than for more reactive individuals (Careau *et al.,* 2008). Stronger negative associations may make them more likely to avoid being trapped a second time.

This difference in trapping latency and recapture probability between personality types could potentially cause bias in which individuals are trapped if trapping sessions are too short to catch the boldest individuals. Tanton (1965) suggested that three days would be long enough to trap the most trap shy individuals in a population. The models developed here concur with this and suggest the boldest individuals take approximately 3 days to be trapped. As the trapping sessions used here lasted a minimum of 4 days this should have been sufficient to trap a representative sample of the population. After this initial trapping it is likely that latency to subsequent trappings would be shorter due to habituation (Reale *et al.,* 2007), however the trapping sessions used here were not long enough to test this.

The results from this study are the opposite result of those recently found in agamas (*Agama planiceps*), where bolder individuals were trapped faster (Carter *et al.,* 2012) or in North American red squirrels (*Tamiasciurus hudsonicus*), where more active individuals were more likely to enter traps (Boon, Reale and Boutin, 2008), both of which used similar passive trapping methods. This suggests a general trappability/personality rule may not exist, as different species respond to the experience of trapping in different ways. Within small mammals, even when using the same trapping methods, some species will avoid being trapped a second time whereas others will happily re-enter traps (Getz, 1961). It is likely that whether an animal is retrapped is less an indicator of boldness but more an individual's reaction to being trapped and how stressful the experience was. This would suggest that using trappability as a raw measure of boldness as in previous studies (Wilson *et al.,* 1993; Reale *et al.,* 2000; Reale and Festa-Bianchet, 2003) may not be reliable. To correct for potential biases caused by variation in trappability in this study, number of days after traps were set was included as a covariate in further analyses of habitat use.

After controlling for the effect of trap bias, this study indicated there is a personality type by environment correlation in wood mice. This correlation was seen by an interaction between the temporal and physical environment and through the choice of social environment. The model investigating microhabitat use in relation to activity score indicated that personality type affected the probability of being trapped based on conditions around the trap at time of trapping, particularly canopy cover, vegetation cover and moon phase. With low canopy cover less active individuals were trapped when the moon was full, whereas with high canopy cover moon phase had little effect. However, the interaction between moon and openness was also significant but in the opposite direction, in less open areas less active individuals were trapped when the moon was full, in more open areas moon phase had no effect. This may be explained as openness and canopy cover were negatively related, areas with dense canopy cover tended to have less dense vegetation and vice-versa. This suggests then that in areas with low canopy cover but high vegetation cover less active individuals are trapped when the moon was full. Whereas in areas with high canopy cover, openness or moon phase had little effect. Wood mice generally prefer areas with dense cover (Tanton, 1965; Drickamer *et al.,* 1999) and avoid areas with bare earth (Tew, Todd and Macdonald, 2000). Particularly under the risk of predation by owls, as in Sherwood Forest, wild rodents tend to forage near dense shrubs (Abramsky *et al.,* 1996). As shown previously activity is related to a more proactive, risk taking behaviour. Less active individuals in areas with low canopy cover may be more likely to shelter under dense vegetation when the moon is full as foraging in the open demonstrates an increased risk of predation (Abramsky *et al.,* 1996). More active individuals may remain in the open, taking the risk of predation to continue foraging as normal. In areas with dense canopy cover this effect was not seen as dense canopy would block moonlight creating a less obvious difference in risk between more and less open areas.

The cause and effect of personality type by environment correlations can sometimes be difficult to discern. Animals can potentially adjust their behaviour to the environment (Pearish, Hostert and Bell, 2013). However, here all animals from a trapping session were tested under identical conditions regardless of their trapping location; therefore any difference in behaviour due to the environment will not have confounded their habitat use within the session. Quadrats for this study were only 5m^2, whereas wood mice have home ranges in the range of 1151-10765m^2 in deciduous woodland (Harris and Yalden, 2008). Therefore wood mice are likely to use a wide range of microhabitats within a single night as they move extensively within this range each night (Wolton and Trowbridge, 1985), thus encountering varied levels of habitat cover. The results of this study may therefore represent where mice spend more of their time or are more likely to be trapped, rather than indicating that they spend all their time in this habitat type. This correlation between microhabitat use and behaviour therefore is likely to indicate a level of niche picking; animals intentionally selecting certain habitat types (Stamps and Groothuis, 2010) that may be adaptive if these environments increase their fitness. This behaviour may allow for the maintenance of different personality traits within a population if individuals are exploiting different niches, which reduces competition and may allow the population as a whole to better exploit the available resources (Michelena *et al.,* 2010).

This study assumes that open areas or more moonlit nights are perceived as more risky, an assumption that has been made in a number of previous studies (e.g. Jones and Dayan, 2000). Mice tend to avoid bright lit and open areas (Ibanez *et al.,* 2009), presumably as it is expected that predation rates would be higher under these conditions. Studies have shown that owls have greater hunting success on moonlit nights suggesting an adaptive significance to this behaviour (Clarke, 1983). However there is as yet little concrete evidence that ‘more risky’ habitat use leads to higher predation rates. There are studies that indicate bolder animals have higher mortality risk (Smith and Blumstein, 2008), but the reason for this mortality is sometimes not clear (Bremner-Harrison, Prodohl and Elwood, 2004). Future studies would benefit from empirical evidence that different habitats functionally present a differing level of risk, as this is often a key assumption of the trade-offs in personality traits.

The final part of this study looked at the effect of previous occupation on trapping success. Wood mice in general prefer traps occupied by conspecifics (Stoddart and Smith, 1986; Tew, Todd and MacDonald, 1994) although male mice may choose to enter traps previously occupied by heterospecifics (Stoddart and Smith, 1986). However, as shown in this study this can be modified depending on personality type. The models here demonstrate that more active individuals are more likely to enter traps previously occupied by voles. Voles and wood mice compete for both food and habitat (Canova, 1993) and so interactions between the two species are often intolerant (Lambin and Bauchau, 1989). It is therefore likely that active, more proactive individuals are more willing than less active individuals to run the risk of entering an area previously occupied by a vole for a food reward.

Data here suggests some bias in which individuals are trapped first and the likelihood of being re-trapped, however as overall trapping numbers did not vary, a trapping regime lasting at least four days would avoid this bias. The proportion of the population trapped also varied with amount of moonlight and habitat conditions around the traps. Again this can be mitigated by trapping on nights with different levels of brightness and different levels of vegetation, improving the chance of trapping a natural composition of wood mice.

This study demonstrates that populations of wood mice are unlikely to be randomly distributed across the habitat. This has implications for studies that restrict their trapping regime to only a portion of the habitat available to a particular population. Personality type by environment correlations are likely to be pervasive in wild populations (Stamps and Groothuis, 2010). Therefore future studies should consider carefully the trapping methods used, the study species and how trappability may be affected by differences in habitat, weather and personality. Trap bias is unlikely to make the results of personality studies erroneous but may reduce the power of studies to detect an effect of personality, due to a reduction of the range of personalities trapped and tested. However non-personality related studies may be more seriously affected, as ignoring personality during trapping will cause biases in other features correlated with personality such as metabolism, sex or size and the trapped population may not accurately represent the wild population in these features. There may also be practical problems with trap bias. For example, evidence suggests that badger culling methods are causing selection in the population for more trap-shy individuals (Tuyttens *et al.,* 1999) and in fish farms bolder, faster growing fish are harvested faster leading to selection for slower growing fish (Biro and Post, 2008). This may be a serious consideration for translocation studies when trapping individuals for conservation projects, either for transportation to another site or for taking animal into captivity, as biases in trapping regimes may lead to only a subset of the population being trapped. This may reduce the success of the population upon release by limiting the behavioural strategies adopted by the population.

To conclude, this study has identified variations in trapping success due to individual personality type. Bolder individuals take longer to be trapped, this may be because they are more routine in their behaviour or because they tend to range more widely and therefore are less likely to enter traps. Active individuals were less likely to be retrapped which may indicate they find trapping a more stressful experience. Personality also interacted with both weather and microhabitat to affect trapping success, suggesting that more active individuals are more willing or have a greater need to enter more open areas on moonlit nights. This study indicates that personality needs to be considered to avoid bias in any project involving trapping.

3.5 Chapter Outcomes

- Personality can cause trapping bias in wood mice; bolder mice take longer to be trapped and more active mice are less likely to be re-trapped.
- Personality affects habitat use depending on weather conditions; in areas with low canopy cover more active mice are more likely to enter open space when the moon is full.

- Previous trap occupant can affect the personality of individuals willing to enter traps; active mice were more willing to enter traps previously occupied by voles.
- To avoid trapping bias trapping should take place in a variety of weather and habitat conditions for suitably long periods of time to ensure an accurate representation of personality distributions in a population.

The potential confounding factors and biases identified in this chapter are used to avoid some of these problems in Chapter Five and to rule out the possibility that patterns identified there are due to differences in trapping success. Patterns of habitat use identified here are also used to support and further inform conclusions drawn about the impact of personality type on behaviour after a translocation. Due to the potential effect of voles on retrapping success, previous occupant is included in models of recapture dispersal used in Chapter Five.

4 Chapter Four: The effect of captive breeding on wood mouse personality and the implications for translocation

4.1 Introduction

Bringing animals into some form of captivity is an unavoidable part of most reintroduction or translocation projects. The length of this captivity can vary from a few hours, to generations. This can include animals in captivity for transportation, a quarantine period, or long term captivity for breeding. Unfortunately this period in captivity can affect an animal's behaviour, which can subsequently negatively impact its success upon being released (Griffin, Blumstein and Evans, 2000). Short term captivity can increase stress levels due to activities such as trapping, handling and transport (Teixeira *et al.,* 2007), which can cause problems when measuring personality traits (Wilson *et al.,* 1993), but these short term effects on behaviour are mostly reversible. However, long term captivity can have more serious effects, as individuals released from long term captive bred populations can be unsuited to life in the wild due to behavioural changes whilst in captivity. For example previous studies have found that captive bred grey partridges (*Perdix perdix*), once released, showed poor vigilance behaviour compared to wild individuals, feeding throughout the day not just at dawn and dusk like wild individuals, exposing themselves to predation (Rantanen *et al.,* 2010). Similarly captive reared Northern water snakes (*Nerodia sipedon*) showed restricted activity, abnormal habitat use, inappropriate body temperatures and poor body mass, which were related to factors evident in the captive rearing environment such as small cages and under floor heating causing them to develop inappropriate behaviours (Roe *et al.,* 2010).

Captivity can affect behaviour in a number of ways; through learning, development and evolution (McDougall *et al.,* 2006). Contemporary evolutionary change refers to selective forces acting on heritable traits which relate to an animal's fitness in timescales under a few hundred years (Stockwell, Hendry and Kinnison, 2003), which can occur within the time span of a human lifetime (Ashley *et al.,* 2003). For this to occur genetic variance must underlie the variance in the trait under selection (Lynch and Walsh, 1998). The genetic basis of many personality traits has been confirmed in the wild and captivity (Drent, Oers and Noordwijk, 2003). Captive conditions often relax natural selection whilst simultaneously imposing unnatural selection conditions (Archard and Braithwaite, 2010). Relaxing natural selection may allow inappropriate behaviours to emerge that would otherwise be selected against (McPhee, 2004) as captive animals are released from selective pressures such as predation and disease (Huntingford, 2004). A study comparing the behaviours of mice that had been bred in captivity to their wild bred counterparts found that the mice stopped showing appropriate anti-predator behaviour after several generations in captivity and variation in behaviour within the population increased over this time (McPhee, 2004). To compensate for this increase in variation during captivity some studies have recommended releasing more individuals (McPhee and Silverman, 2004). However releasing more individuals generally increases the logistic problems and the cost of reintroductions, particularly when dealing with larger species. It also goes against the recent focus on individual welfare based conservation, where releasing individuals with little chance of survival is not recommended (Reynolds, 2004).

Captive animals can also encounter directional selection pressures not naturally encountered, as conditions in captivity differ from those in the wild; animals in captivity are regularly disturbed by humans, need to spend little time foraging and are often placed in unnatural social situations (Huntingford, 2004). In addition, humans can directly affect the behaviour of animals in captivity through selective breeding (Stockwell, Hendry and Kinnison, 2003). Animals bred in captivity can often be consciously or unconsciously selected for behaviours suited to conditions in captivity (Snyder *et al.,* 1996), which can cause directional selection for more tame or less wary animals (Snyder *et al.,* 1996). As those individuals more suited to life in captivity are more likely to survive and breed, these traits will increase over subsequent generations. This is evident in captive lab strains of rodent which tend to be more docile than wild strains (de Boer, van der Vegt and Koolhaas, 2003, Kunzl *et al.,* 2003). Personality plays a strong role in this as personality traits can affect how an animal responds to the stress of captivity. Generally it is the extremes e.g. overly active or aggressive individuals which are poorly adapted to captivity, reducing their fitness and chance of breeding in captivity, resulting in the increased docility and tameness in laboratory strains (McDougall *et al.,* 2006). These effects can be further enhanced by inbreeding due to small founder populations (Woodworth *et al.,* 2002). In addition, some studies have shown that more behaviourally plastic individuals have lower rates of survival in captivity, leading to selection for less plastic individuals which can be a cause of stereotypical behaviour (Mason *et al.,* 2013).

Behaviour can also be shaped during an animal lifetime. Stamps (2003) suggests that individuals have a reaction norm of possible behavioural reactions, but that being raised in different environments causes them to select a personality type from within this range during ontogeny. This selection can be affected by the individuals' physical or social environment, and parental effects can strongly influence behavioural development (Wolf and Weissing, 2010). As conditions in captivity differ from those in the wild this may cause large divergences in behaviour in captive populations. Rearing in captivity may provide a lack of environmental stimuli essential for animals to develop certain behaviours such as predator recognition (Griffin, Blumstein and Evans, 2000), causing severe behavioural deficits. In some cases personality traits may be more varied in wild populations, as individuals can select different habitats and niches, which subsequently affect their behavioural development (Stamps, 2003).

Personality traits have been repeatedly linked to a number of behaviours vital to life in the wild (anti-predator, foraging etc.; Dingemanse *et al.,* 2004) and so it has been suggested that maintaining a suitable range of personalities in a release group, and therefore in captive populations prior to release, is a priority (Watters and Meehan, 2007). A lack of variation in behaviour reduces a population's ability to respond to changes in the environment (Lynch and Walsh, 1998; Falconer, 1989) and different behaviours may be important at different times or stages of an introduction (Dingemanse *et al.,* 2003). To fully understand what is causing changes in behaviour in captivity studies need to look at the effects of heritability, the developmental environment and the current environment on behaviour. This is particularly important for conservation as it will affect how translocation projects prepare captive animals for release. For example, whether projects should focus on selective breeding to maintain and promote behavioural strains, or should they aim to affect behaviour during an animal’s life by varying rearing conditions or providing pre-release training (Watters, Lema and Nevitt, 2003).

This study investigates the effect of captivity on the behaviour of wood mice. Wood mice are naturally nocturnal, territorial and have high rates of predation (Harris and Yalden, 2008). In captivity however these pressures are relaxed, which may cause an increase in personality variation. Individuals used for this study are also part of a captive breeding program and those best suited for life in captivity are most likely to successfully breed, which may lead to inadvertent directional selection for tameness.

The first aim of this study is to confirm mice retained in captivity maintain consistent personality traits. The second is to compare the personality distribution of wild caught mice to those maintained in captivity for over 30 generations. The amount of behavioural plasticity through habituation to repeated tests will also be estimated and compared between the wild and captive populations to observe if mice in captivity have less ability to adapt behaviour due to a lack of environmental stimuli. The final aim is to then identify factors affecting this change in personality in captivity by estimating heritability and the effects of the current environment and factors during ontogeny on behaviour. Findings from this study will be discussed in the context of the implications of captive breeding on future translocation.

4.2 Methods

4.2.1 Study Subjects

This study utilised a population of wood mice maintained in captivity at the Food and Environment Research Agency, Sand Hutton, York. The mice used for the study were kept in an environmentally controlled room (temperature 17-21 ˚C, humidity 40-70%) in single sex cages of mice from the same litter (cage size; 530mm X 375mm X 160mm), number of mice per cage varied from one to six. Cages contain wood shavings and paper wool bedding and are furnished with a cardboard tube and chew sticks for enrichment. Mice are provided an *ad libitum* supply of water and a laboratory pellet feed. Mice are selectively bred to maintain genetic diversity every 2-3 months, at which point all of the oldest generation are euthanised. Mice tested were the 36/37th generation in captivity. Data was also collected on the age and parentage of tested mice. Details of data collection methods for wild mice used for comparison are described in Chapter Two.

4.2.2 Behavioural Testing and Scoring

Mice were transferred from their home cage to the testing apparatus in a handling bag during which they were weighed to the nearest half gram, sexed and their handling score measured (1-docile to 4-highly agitated). Mice were tested using the same apparatus and methods discussed in previous chapters, consisting of an open field test, followed by a novel object test before being returned to their home cage. Behaviours were then scored from the videos using the same protocol as in the second chapter. Mice were tested between 9am and 4pm.

In total fifty-five mice were initially tested over two days (20-21st June 2013). Twenty-seven days later (18th July 2013) twenty of these mice were then retested; the remainder of the mice initially tested either could not be individually identified or had been euthanized under normal husbandry practices at FERA so could not be retested. 1-2 mice were tested from each cage.

4.2.3 Data Analysis

4.2.3.1 Creating personality scores

Factor analysis was used to condense the behaviours measured in the tests into a limited number of factors summarising the behavioural variation. Bartletts test of sphericity and KMO tests indicated the covariance matrix was adequate for factor analysis. Bartlett's test was highly significant ($p<0.001$) and KMO exceeded 0.6 (OF – 0.65, NO – 0.65). A combination of the MAP criterion and scree test was used to select the number of factors to extract.

4.2.3.2 Modelling personality and behavioural plasticity

General linear mixed modelling was used to investigate the key hypotheses. Two sets of models were created the first with the score from the open field test (Activity) as the dependant variable and the second with the score from the novel object test (Boldness) using the same procedure. *Mouse Id* was used as a random intercept to examine the significance of individual repeatability (personality) and *trial number* as a random slope to examine if individuals differ in their behavioural plasticity (habituation).

The model with the best random effect structure (selected through model comparisons using likelihood ratio tests) was refined to only contain significant fixed effects. *Time* (minutes from 6am), *date* (relative to first day of testing) and *test number* were included as covariates. Significance of fixed effects was calculated using type III sums of squares. Backwards elimination of non-significant fixed effects ($p > 0.05$) was used as a model selection criteria.

Adjusted repeatability (r; the intraclass correlation coefficient) of scores was calculated from the final models as the ratio of the between-individual variance over the sum of the between- and within-individual variance (Nakagawa and Schielzeth, 2010). All individuals were included in the analysis, even those that had only been tested once as this has been shown to increase the power of analyses (Martin *et al.,* 2011). To meet assumptions of normality residual plots were used to visually assess distributions and both activity and boldness scores were log transformed to improve fit.

For the final part of the analysis individual specific estimates (BLUPs) of intercepts (personality score) and slopes (plasticity score) were calculated from the final restricted models calculated above. Urine spread has been linked to dominance in lab mice, to investigate if this correlated with boldness a Spearman's rank correlation was carried out between boldness BLUP and urine spread in the first test of each individual.

4.2.3.3 Factors affecting personality traits

4.2.3.3.1 Individual traits/current environment

To calculate if personality or plasticity were due to static traits a linear model was ran with *sex*, *age* (days), *weight* (g) and *density* (number of mice in cage) as factors. When testing the effect on personality scores all individuals were included even those that had only been tested once, whereas when testing plasticity it could only be accurately calculated for those individuals tested multiple times. The minimum adequate model was calculated by removing non-significant factors ($p > 0.05$) until all factors included in the model were significant.

4.2.3.3.2 Heritability

To estimate narrow sense heritability (h^2) of boldness and activity slope a sibling analysis was performed using a simple linear model with *litter* as a factor was used and heritability calculated as twice the intraclass correlation coefficient. This heritability estimate does not take into account potential environmental or developmental effects and so may be inflated if those effects are significant (Falconer, 1989). To test for this using available data, *number of mice in litter at birth* and *litter weight* (mean weight in grams of mice in litter shortly after birth) were included in the model to see if they significantly affected personality. Residuals were visualised to confirm data met normality assumptions.

4.2.3.4 Comparison to wild populations

To investigate how personality scores differed in captivity from those of individuals in the wild, comparable factor scores were created using a combined factor analysis including data from all personality tests carried out at FERA and previously in the wild (KMO: OF-0.76, NO-0.76). A further mixed model was then created using data from the mice tested at FERA and mice tested in the wild in the same season at Sherwood and Brackenhurst. The mixed model included *ID* as a random effect and *sex*, *weight* (g), *time* (since 6am), *test number* and *location* (FERA, Sherwood or Brackenhurst) as fixed effects as well as the interaction between *location* and *test number*. Again a stepwise backwards elimination procedure was used to identify significant effects. This was repeated for both Activity and Boldness. Only data from the first two tests for each individual were included and only individuals tested during the summer at Brackenhurst, Sherwood and FERA.

Following McPhee (2004) variance in activity and boldness behaviours were compared between the lab population and both Brackenhurst and Sherwood separately using a Levenes test. Bonferonni adjustment was applied for multiple comparisons and $p < 0.025$ was considered significant. Only the first test from each individual was used in this case to avoid pseudo-replication.

As handling scores have previously been used as a measure of docility (Dingemanse and Reale, 2005), which may be affected by time in captivity, handling scores recorded in the first test of each individual were also compared between the lab and the field using a Kruskal-Wallace test.

4.3 Results

Details of mice included in the study are shown in Table 4.1

Table 4.1. Details of mice included in the study for the initial test and the retest 27 days later. Data given in counts or Mean ± SD.

	Initial Test	**Retested**
no. mice	55	20
male/female	26/29	8/12
Weight (g)	16.3±4.3	18.25±3.6
Age (days)	49.22±32.94	75.8±44.43
activity score	0.02±0.88	-0.19±1.62
bold score	-0.02±0.82	0.2±1.52

4.3.1 Factor Scores

Following the MAP criterion two components were obtained from the open field test and one from the novel object test (Table 4.2 and Table 4.3). The first factor retained from the Open Field test explained 41% of the total variance, again referred to as ‘Activity’ (Table 4.2). A second factor was also obtained which may have represented levels of stereotypical jumping/back-flipping behaviour, but was difficult to interpret and was not included in further analyses. The factor obtained from the novel object test explained 55% of the total variance, again referred to as ‘Boldness’ (Table 4.3). The factor structure was very similar to that calculated previously for wild mice.

Table 4.2. Factor loadings for results from Open Field factor analysis with eigenvectors and percentage variance explained, variables loading stronger than 0.3 in bold (N=76 tests of 57 individuals)

	Factor 1 (Activity)	**Factor2**
Lines crossed	**0.84**	0.17
Enter middle squares	**1.09**	-0.21
Rears	-0.17	**1.26**
Latency to enter centre	**-0.39**	-0.18
Time grooming	-0.05	**-0.42**
Jumps	0.20	**0.34**
Time in centre	**0.92**	-0.09
Eigenvector	2.85	1.86
Variance Explained	41%	27%

Table 4.3. Factor loadings for results from Novel Object factor analysis with eigenvector and percentage variance explained, variables loading stronger than 0.3 in bold (N=76 tests of 57 individuals)

	Factor 1 (Boldness)
Latency to touch	**-0.89**
Number of touches	**0.79**
Latency to approach	**-0.85**
Actual approaches	**0.61**
Time frozen	**-0.63**
Time spent touching	**0.72**
Time spent near	**0.65**
Eigenvector	3.84
Variance Explained	55%

4.3.2 Personality

Individuals were consistent in Boldness ($p < 0.01$) confirming that wood mice in captivity also have personality traits (Table 4.4) with a high repeatability of 0.56±0.13 for Boldness (Figure 4.1). Activity was not repeatable ($p = 0.057$), although this may have been due to the small number of repeats providing a lack of statistical power. There was no effect of any of the main effects included on personality scores.

Activity and boldness scores for the first test of each individual were not significantly correlated in captivity (Spearmans Rank Correlation: $r_s = 0.15$, N = 57, $p = 0.27$).

4.3.3 Habituation

There was no main effect of test number on activity or boldness suggesting that overall mice did not habituate to the testing apparatus over repeated tests. However, the inclusion of test number as a random slope did improve the fit for Activity (Table 4.4, Figure 4.1), suggesting that individual mice respond differently to repeated testing, most mice decreased their activity from the first to the second test but to varying degrees. There were no fixed factors affecting Activity or Boldness scores.

Table 4.4. Log likelihoods of models and results of model comparisons investigating individual consistency and plasticity for both Activity and Boldness scores. Model comparisons with different random effects carried out using likelihood ratio tests (N=76 tests of 57 individuals)

Model			**Likelihood Ratio Test**			
	Random Factors	**Log L.**	**Test**	**LRT**	**df**	***p*-Value**
Activity						
a	None	-32.75				
b	Intercept	-31.5	a vs. b	2.51	1	0.057
c	Slope	-28.72	a vs. c	8.08	1	**<0.01**
Boldness						
a	None	-59.62				
b	Intercept	-56.36	a vs. b	6.52	1	**<0.01**
c	Intercept*Slope	-55.82	b vs. c	1.01	2	0.46

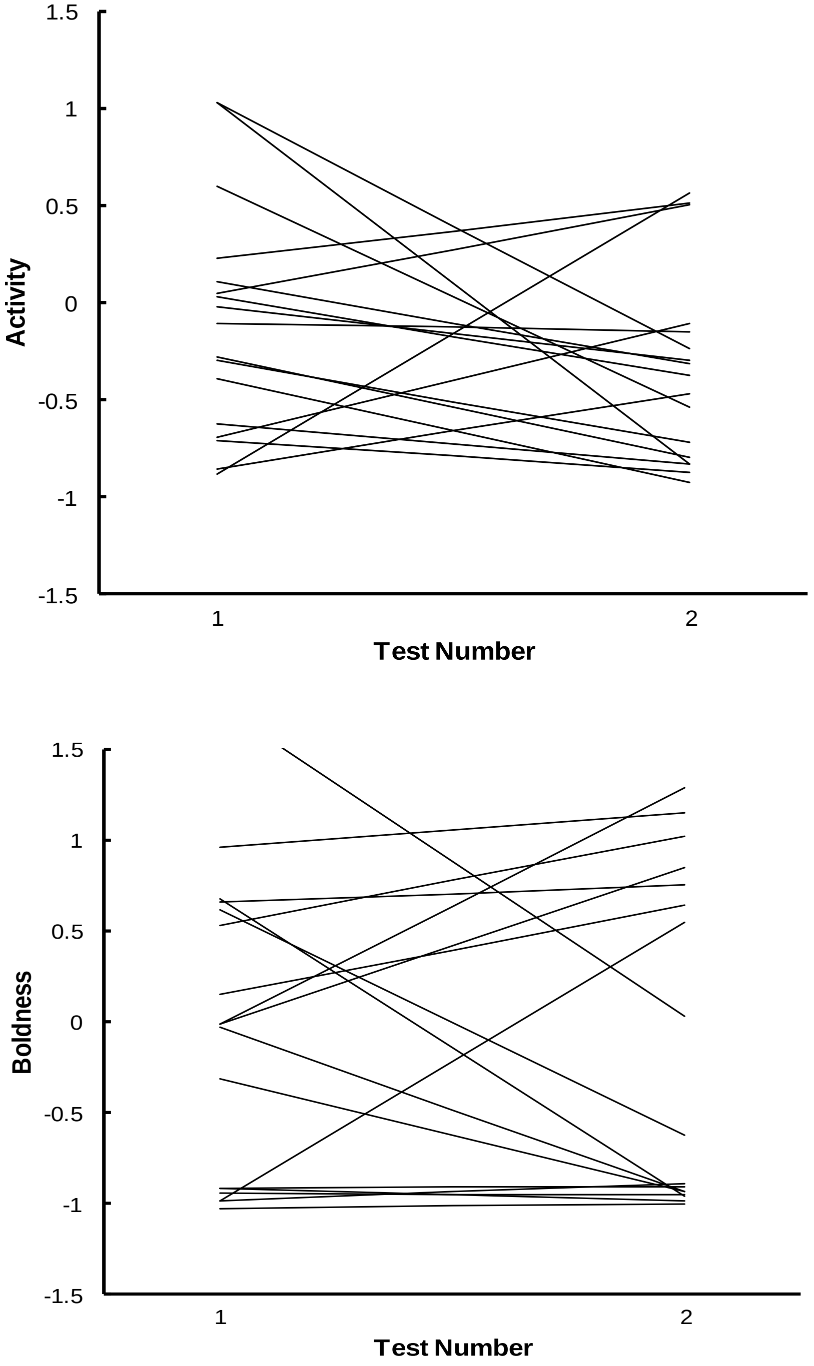


Figure 4.1. Individual activity scores (top) and boldness scores (bottom) of mice tested in captivity over repeated tests (N=18).

4.3.4 Factors affecting personality scores

The BLUP models found no effect of *sex, weight* or *density* on boldness scores; however activity slope changed with *age*. Older mice were less plastic in their behaviour and decreased their activity score less from test one to test two than younger mice (β = 0.002±0.001, $F_{1,16} = 8.56$, $p < 0.01$). When the score from the first activity test was used as a proxy for activity score, activity increased with age (β = 0.01±0.003, $F_{1,53} = 5.03$, $p < 0.05$) and with number of mice in cage (β = 0.18±0.09, $F_{1,53} = 4.3$, $p < 0.05$). The heritability analysis showed a strong trend towards the heritability of boldness scores with a significant difference in scores between litters ($F_{23,33} = 1.81$, $p = 0.051$) with a heritability estimate for boldness of h^2= 0.53±0.32, the first activity score was not significantly heritable. This heritability estimate based on siblings may be inflated due to environmental factors, however when *number of mice in litter* and *litter weight* (mean weight shortly after birth in grams) were added to the model neither were significant, suggesting these ontogenetic effects played little role in causing differences in behaviour. Most other environmental factors were consistent between litters.

Boldness was significantly positively correlated with urine spread ($r_s = 0.278$, N = 57, $p < 0.05$). There was no correlation between urine spread and activity score ($r_s = 0.05$, N = 57, $p = 0.69$).

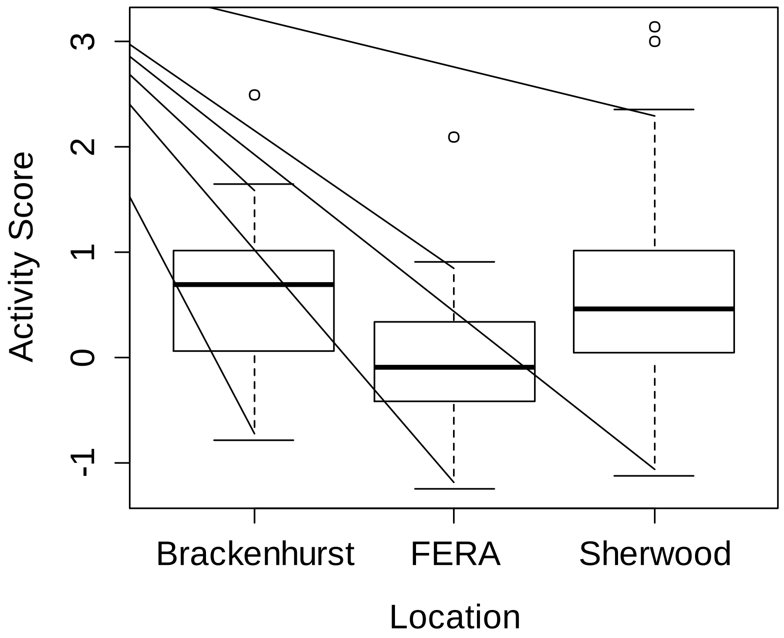
4.3.5 Comparison to wild populations

The factor analysis of wild populations produced similar factor scores to those produced in Chapter Two (Table 4.5). The only significant effect in the Activity model was location ($F_{1,189} = 8.98$, $p < 0.001$), with activity at FERA being significantly lower than either Brackenhurst or Sherwood ($p < 0.001$) and no difference between Sherwood and Brackenhurst (Figure 2). Boldness did not differ significantly between captivity and the wild. No evidence was found for a difference in behavioural variance between groups (Levenes Test: Brackenhust/FERA; $F_{1,106} = 0.006$, $p = 0.94$, Sherwood/FERA; $F_{1, 137} = 0.4$, $p = 0.53$).

Table 4.5. Factor loadings for results from the combined open field and novel object factor analyses with eigenvector and percentage variance explained, variables loading stronger than 0.3 in bold (N=260 tests of, 190 mice).

Open Field Test	**Factor 1 (activity)**	**Novel Object Test**	**Factor 1 (boldness)**
No. Lines Crossed	**0.97**	Latency to Touch	**-0.89**
Enter Centre Square	**0.96**	Number of Touches	**0.87**
Rears	**0.81**	Latency to approach	**-0.83**
Latency to Enter Centre	**-0.56**	Actual Approaches	**0.77**
Time Grooming	**-0.5**	Time Frozen	**-0.77**
Jumps	**0.43**	Time Touching	**0.74**
Time in Centre	0.24	Time Near	**0.51**
Eigenvector	3.34	Eigenvector	4.25
Variance Explained	48%	Variance Explained	61%

The Kruskal-Wallis test showed that there was a significant difference in handling scores between Sherwood, Brackenhurst and FERA for the first test (chi-squared = 19.63, df = 2, $p < 0.0001$, Figure 4.2). Pairwise Mann-Whitney U tests showed this difference was significant between FERA and Brackenhurst ($W = 453.5$, N = 139, $p < 0.0001$), FERA and Sherwood ($W = 919$, N = 108, $p < 0.01$) but not Sherwood and Brackenhurst ($W = 2101.5$, N = 135, $p = 0.78$).



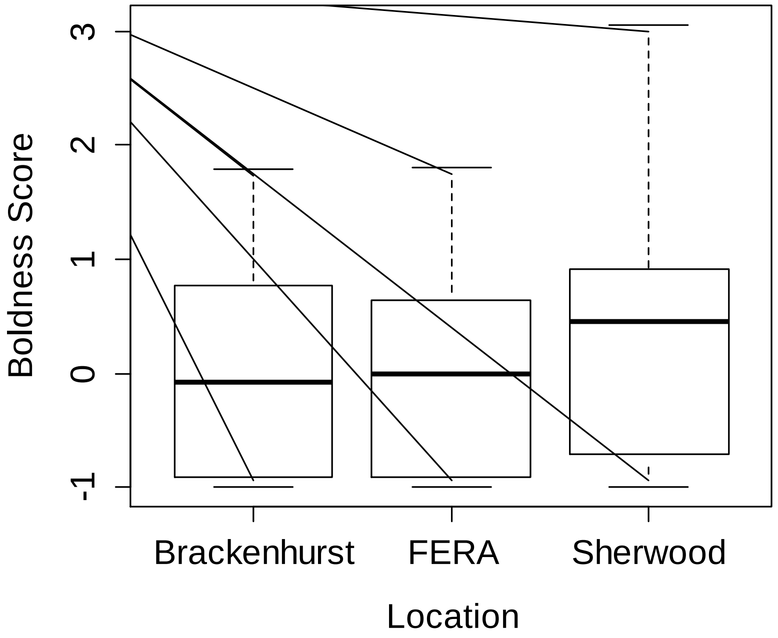


Figure 4.2. Activity (top) and boldness (bottom) scores in the first open field and novel object test respectively, from mice living in the wild (Brackenhurst, N=52; and Sherwood, N=83) and captive bred in a lab for 36/37 generations (FERA, N=55).

4.4 Discussion

This study has shown that consistent personality traits remain evident in wood mice after a long period of breeding in captivity. Data suggests that the boldness trait remained repeatable, was highly heritable and was not significantly affected by any of the state or environmental effects measured. Although activity was not found to be repeatable in the captive population, this is most likely due to the small number of repeats not providing enough power for significance to be detected. Previous studies have also noted that personality traits are often less repeatable in captivity than the wild (Bell, Hankison and Laskowski, 2009). Data comparing behavioural scores showed that activity was lower in mice maintained in captivity for multiple generations than wild populations, but that boldness remains consistent. This may suggest selection against high levels of activity in captive populations.

Activity and boldness behavioural scores of mice tested in captivity remained similar to those measured in wild populations with a similar factor structure. This again confirms the consistency of these traits in wood mice populations. However, one major difference was seen as rearing behaviour loaded negatively on the activity trait in captivity, whereas rearing loaded positively in the wild. This may be due to the second factor identified in the open field test in captivity, which was not shown in wild mice. This factor was positively related to both rearing and jumping and possibly represents the stereotypic jumping behaviour seen in some of the captive individuals tested. Stereotypies are linked with an inflexibility of behaviour (Campbell, Dallaire and Mason, 2013), which can be exacerbated by un-enriched housing conditions often found in captivity (Mason *et al.,* 2013). The existence of this second stereotypy factor may have caused rearing to be more strongly associated with this trait than normal activity.

Data here suggest that personality traits, or at least boldness is heritable in the wood mouse, whereas data for activity were inconclusive due to the small sample size. Estimates of heritability for boldness were high; however heritability's are often higher when measured in the captivity rather than the wild (van Oers *et al.,* 2005). This may be due to captive conditions being more uniform than that in the wild, allowing little divergence in behaviour during development (Dingemanse *et al.,* 2004). Other factors in addition to genes can affect the development of different behaviours (Trillmich and Hudson, 2011), such as pre-natal maternal effects or gene-environment interactions which can artificially inflate estimates of heritability. This estimate of heritability measured here therefore sets an upper limit to that which may be expected in the wild (van Oers *et al.,* 2005). The study found no evidence for litter size or brood weight on boldness scores. However this does not rule out other unmeasured developmental factors which may affect personality such as maternal effects on behaviour. Environmental factors remained constant between litters, suggesting that rearing environment has little effect on the development of behaviour in wood mice, particularly as the variance of scores was similar between the wild, with a potentially wide range of environmental conditions, and captivity where conditions were relatively uniform.

Rapid adaptation to life in captivity (within tens of years) is likely to reflect a combination of selection, behavioural plasticity and developmental plasticity (Mason *et al.,* 2013). This study found lower levels of activity in captivity to that in the wild, but similar levels of boldness, potentially demonstrating a directional selection for activity in captivity and no selection for boldness. Mice retained at FERA were less active and showed no greater variance in behaviour than in the wild populations. As this study found no evidence for environmental effects on behaviour and strong support for the heritability of these traits it seems likely that there is directional selection for animals that cope better in captivity. The breeding programme at FERA involves pairing males and females based on genetic history to maintain diversity, however if mice fail to breed then one of the partners is replaced with a different individual. This method is a classic pattern seen in many captive breeding studies and can easily result in inadvertent selection on the population for individuals better suited to captivity and therefore more willing to breed (Frankham, 2000; Allendorf, 1993; Loebel *et al.,* 1992). Previous studies have demonstrated that it is usually individuals who suffer least from stress and are less active and aggressive who show greater breeding success in a captive environment (McDougall *et al.,* 2006). Over generations this leads to a population with reduced activity scores and increased tameness as seen here. A high tendency to explore may also be disadvantageous in captivity where conditions are constrained and stable, where a need to explore may lead to restlessness (Mason *et al.,* 2013). Handling scores were also compared between groups as a proxy for docility (Reale *et al.,* 2000). Handling scores were significantly lower at FERA than either of the other two sites suggesting a higher level of docility. This may indicate selection for docility, which may be correlated with low levels of activity. However, docility during handling at FERA may have been a learned response due to higher rates of interaction with humans rather than an inherited one. High docility and tameness is likely to cause decreased success in released populations (Frankham, 2008). Docile individuals are less likely to explore their environment and compete for resources, tameness may also lead to additional problems with human-animal conflict if individuals do not naturally keep away from human activities.

Data used in this study to compare captive reared to wild populations may not be directly equivalent as various external environmental conditions differed from being tested in the field to being tested in the lab, which may have affected behavioural responses during testing. However the lack of significant difference between the mean or variance in boldness scores measured in the wild populations and the captive populations provides confidence that these differences were not major and some inference can be drawn from the differences seen in activity score. It is perhaps surprising that boldness was not higher in captivity as it is usually seen as a balance between risk and reward, yet life in captivity has little risk reducing any selection against excess boldness. Potentially boldness is selectively neutral within the population if it has no significant costs or benefits associated with it in captivity. Due to its strong heritable component this may cause levels of boldness to remain consistent over many generations in captivity.

Activity and boldness were not correlated in captivity, whereas they were found to be consistently correlated in wild populations. This is similar to other studies where behavioural syndromes broke down in captivity (Bengston, Pruitt and Riechert, 2014) or in areas where there was no predation (Bell and Sih, 2007). This suggests there is some selective advantage to these traits remaining correlated in wild populations, which is not evident in captivity. This also provides evidence that behaviours measured in an open field and a novel object test represent two different personality traits under differing selection pressures. As high activity was selected against in this study, this may have disrupted the correlation between boldness and activity if there was some benefit to remaining bold. Alternatively, behavioural syndromes may develop due to the rearing environment (Bengston, Pruitt and Riechert, 2014) and different rearing environments of wild and captive reared mice may have affected the correlations between these behaviours. This again may cause problems when releasing individuals back into the wild. If there is a selective advantage to certain traits being correlated, as previously suggested in studies of sticklebacks (Dingemanse *et al.,* 2007), then this decoupling in captivity could cause behaviourally disadvantageous pairings of behavioural traits in captive reared animals.

There was no difference in habituation rates for either boldness or activity between captivity and the wild which was in some ways surprising. It was expected that captive mice would show lower rates of habituation to novelty either due to a previous lack of exposure to novelty and disturbance, as conditions in captivity are relatively constant, or because some previous studies have shown selection against behavioural plasticity in captivity (Mason *et al.,* 2013). For example, data from African striped mice (*Rhabdomys pumilio*) has shown that animals reared in captivity are less behaviourally flexible (Jones, Mason and Pillay, 2011). Alternatively, previous studies have found that domesticated animals (Desforges and Woodgush, 1975) or those exposed to humans (Ellenberg, Mattern and Seddon, 2009) habituate quicker to novel stimuli. However neither of these patterns were seen in this study and mice habituated at a similar rate across sites. This suggests that habituation rate is a trait maintained in captivity and was not affected by prior experience or learning in response to novelty or disturbance, although no definitive conclusion can be drawn as number of repeats in captivity was small so a difference of habituation in captivity may have been missed. This at least provides some hope that although population mean levels of personality traits differed in captivity, individuals remain behaviourally flexible and so may be able to adjust their behaviour to some extent once released into the wild. However, habituation is only one form of behavioural plasticity and may not be representative of the ability to adjust behaviour in different environments.

Additional results seen comprised; activity increasing with both age and density within cages, and older mice demonstrating less plasticity in their behaviour than younger mice. Activity may have increased with age if the lack of movement in younger mice demonstrated a fear reaction which reduced in older mice through experience or if there is a selective advantage to being less active as a juvenile creating an ontogenetic behavioural change (Trillmich and Hudson, 2011). Freezing is a common anti-predator response seen in mice (Eilam, 2005) and in some cases has been shown to be more common in young animals (Smith, 1991). Older individuals are likely to be more habituated to life in a laboratory environment and handling reducing their stress response during testing, making them less likely to freeze. This increase in activity was not seen previously in wild populations of wood mouse, suggesting that in the field increased activity may not develop due to experience or may be actively selected against through forces such as predation. Previous studies have also suggested that behavioural plasticity should change with age as the trade-offs related to being plastic change (Komers, 1997). In this study older mice reduced their activity less between tests than younger mice, potentially as the costs of being flexible in behaviour increase with age or there was little benefit in remaining flexible.

The fact that individuals from higher density cages were more active potentially points to a developmental aspect affecting activity scores. More active individuals have been shown to be more social in previous studies (Myers and Krebs, 1971). Being reared in high densities potentially forces an animal to be more social which may also increase activity if the two behaviours are coupled. Alternatively, as increasing densities will increase competition activity levels may diversify to avoid competition with conspecifics (Groothuis and Trillmich, 2011). This kind of within family competition can encourage niche selection through the social environment despite the lack of heterogeneity in the physical environment (Trillmich and Hudson, 2011). Keeping animals in groups in captivity and encouraging competition may help retain variance in behavioural traits which may aid success once released (Watters and Meehan 2007).

An additional result to come out of this study is evidence that boldness in wood mice may be linked to dominance. Previous research has shown that more dominant mice are usually those that spread their urine over a greater area (Drickamer, 2001). In this study the spread of urine in the testing arena was estimated and had a strong correlation with boldness. As there was no correlation with activity score it suggests this result is not due to how much the mouse moved around the arena. As groups of animals tend to have dominance hierarchies, this correlation with personality may explain the variance in some personality traits seen within litters (Bremner-Harrison and Cypher, 2011) and again may provide a tool to increase behavioural diversity in captivity.

This study emphasises the need to record behaviour in individual studies, as patterns of behavioural change in captivity here differed from those measured elsewhere (McPhee, 2004). Behavioural change is likely to depend upon the selection pressures applied to a particular population. After behavioural variation is lost in a population it may be impossible to get it back, so monitoring and reducing behavioural change in captive populations should be a priority (Kleiman, 1989). Individual captive breeding studies would therefore benefit from recording behaviour across time in their populations to ensure they are maintaining diversity. This data can also be used to compare behavioural scores to wild populations measured using similar techniques to identify any divergence. Ensuring that all individuals have a chance to breed in captivity should maintain behavioural diversity, however some individuals may respond to the stress of captivity differently either enhancing or reducing their longevity or reproductive success. Although no effect of ontogeny was seen in this study, few data were available, in other studies developmental conditions have been shown to have a strong impact on behaviour and so varying rearing environment may be useful in promoting a variety of behaviours in captive populations (Watters and Meehan, 2007), which is particularly important to those populations destined for release back into the wild.

In conclusion, patterns of behaviour in the open field and novel object tests are similar in a captive bred population to that measured in the wild, indicating that boldness and activity are personality traits retained in captivity. Data indicates that boldness is a heritable trait, activity may also be heritable but data was limited due to small sample sizes. Evidence suggests that activity is selected against in captivity, potentially due to the husbandry procedures used in this population. This suggests that captive populations due for release back into the wild need to be carefully managed to avoid losing vital behavioural variation.

4.5 Chapter Outcomes

- Boldness remains a repeatable behavioural trait in captivity, activity may also be repeatable but here it was not significant likely due to small sample sizes.
- Litter was a significant predictor of boldness, suggesting it is a heritable trait in captive wood mice.
- Activity was lower in captivity suggesting directional selection against activity through the captive breeding scheme.
- Handling scores indicated greater docility in captivity, which may either have been a learnt or inherited behaviour.

Data on the effect of captivity in this chapter is used to contrast with the effects of short term captivity seen in Chapter Five. As personality is confirmed to be at least partially heritable this can be used to interpret patterns of personality scores seen between populations in Chapter Two in light of natural selection. Results here provide a number of suggestions regarding the management of captive populations to maintain behavioural diversity, discussed in Chapter Six.

5 Chapter Five: The effect of individual personality and group composition on dispersal and mortality in a simulated reintroduction

5.1 Introduction

Increasing evidence shows that personality traits can have a strong influence on an animal's life history and fitness, including its likelihood to disperse, mating success and mortality rates (Dingemanse *et al.,* 2004). This has led to interest in the conservation biology literature in how personality traits may affect the results of translocation projects and if they can be utilised to improve reintroduction success (Watters, Lema and Nevitt, 2003). Introductions often fail due to high post release dispersal (Mihoub *et al.,* 2011) and low survival (Armstrong and Seddon, 2008). Both of these factors effectively reduce the size of the introduced founder population and therefore the probability of successful breeding and establishment. Personality research potentially provides the tools to tackle these problems without the need for extensive pre-release training, post release management or intensive selective breeding, or at least allows more tailored programmes to suit individual animals.

However, most studies on the effect of personality on fitness related traits have looked at behaviour in either free ranging animals or those maintained in a laboratory. How individuals of different personality types respond to forcibly being placed in a novel environment as in a translocation is not clear. Adaptation to a new environment can be a highly stressful process, particularly if the animal has been held in captivity for a long time and has become acclimatised (Baker, Gemmell and Gemmell, 1998). Success at a release site may relate to how well individuals deal with the stress of a new environment. This stress response can differ within a group (Davis and Parker, 1986) and can reduce survival post release, particularly by impairing memory (Teixeira *et al.,* 2007).

Boldness has been described as a fundamental aspect of human behavioural variation and this may also be the case in animals (Wilson *et al.,* 1994). Boldness has been measured in a number of different ways, but generally a bold animal is defined as more likely to approach novel objects (Bremner-Harrison, Prodohl and Elwood, 2004) and take risks (Reale *et al.,* 2007). Boldness has been repeatedly linked to both dispersal (dispersal probability; Dingemanse *et al.,* 2003; Brandt, 1992; Drent, Oers and Noordwijk, 2003, dispersal distance; Fraser *et al.,* 2001) and survival (Smith and Blumstein, 2008), suggesting it could be a key avenue to improve the success of reintroduction studies. Recommendations in this area suggest that studies follow animals with different personality types after release to determine their success in relation to ecological contexts (Watters and Meehan, 2007). Bremner-Harrison, Prodohl and Elwood (2004) investigated this by looking at dispersal and survival rates in the swift fox (*Vulpes velox*) during a reintroduction in the US. The study found that bold swift foxes (those more willing to approach a novel object) dispersed farther and had a much higher probability of mortality in the 6 months after release (Bremner-Harrison, Prodohl and Elwood, 2004). In the longer term reproductive success also plays a strong role in the outcome of translocations and has also been positively related to boldness (Smith and Blumstein, 2008). However, this study focussed on the critical short period after release and so measuring reproductive success was not within the scope of the project.

Studies such as that by Bremner-Harrison *et al.* (2004) may lead to the recommendation that only those individuals most likely to survive or least likely to disperse are selected for release (Stockwell, Hendry and Kinnison, 2003). However, trade-offs have been found in many studies of personality, with traits beneficial in one situation having a cost in another e.g. boldness has been repeatedly linked to increased levels of mortality but also high reproductive success (Smith and Blumstein, 2008). Therefore, only releasing shy individuals may increase survival and decrease dispersal but may also limit the growth of that population. This has led to the suggestion that release groups should be selected to give the greatest variety of personality traits possible to increase their chances of success (Watters, Lema and Nevitt, 2003). By creating release groups with animals displaying a range of personality types managers may improve their chances of success against environmental uncertainty, as the costs and benefits of different personality types will vary over time and between situations (Watters and Meehan, 2007). Models have since shown that groups with mixed personality types have increased behavioural flexibility (Michelena *et al.,* 2010) and colonization success (Fogarty, Cote and Sih, 2011). Colonizing a new environment may require a mix of personality types as different stages of colonization may favour different individuals. Traits for increasing population size may be different from those required to initially settle in a novel habitat, or different traits may be required to thrive in varied environments such as with different population densities or predation levels. Personality traits regularly interact with the environment resulting in a behavioural response (Dingemanse *et al.,* 2010) and this may be particularly true for dispersal (Fogarty, Cote and Sih, 2011). An important part of an animal's environment is made up by interactions with conspecifics and so dispersal may be affected by the behavioural composition of the group (Cote *et al.,* 2010) or population density (Fogarty, Cote and Sih, 2011). Some studies have demonstrated that a homogenous group may have adverse effects; such as all aggressive individuals reducing mating success (Sih and Watters, 2005) or all bold individuals inflating dispersal probability (Cote *et al.,* 2011). However empirical data is lacking and currently a lot of work in this area is theoretical or carried out on captive animals in unnatural conditions.

The previous chapters have shown that wood mice (*Apodemus sylvaticus)* have repeatable personality traits of activity and boldness. This study aims to investigate if these traits affect the success of individuals in a simulated reintroduction by looking at how they relate to the two main factors affecting the initial success of a founder population; dispersal and survival. This study will also assess if varying the composition of release groups by boldness has any effect on individual or group success, with the particular aim of observing if mixed groups have higher success as suggested by previous models. This study simulates a hard release, one that does not provide any post release shelter or food (Clarke, Boulton and Clarke, 2003).

Many previous studies investigating personality in wild populations regularly take animals into captivity before behavioural testing. However this practice has been brought into question due to a lack of information on how this may affect measured personality traits (Archard and Braithwaite, 2010; Biro, 2012) and whether personality in the lab corresponds to behaviour in the wild (Niemelae and Dingemanse, 2014). This study therefore aims to examine this effect by scoring behaviour both in the field and after mice have been taken into captivity. By using a random regression approach it is possible to analyse if the response to captivity differs between individuals and if behaviours measured in captivity are an accurate representation of behaviour in the wild.

5.2 Methods

5.2.1 Study species and Study area

Wood mice were trapped at Sherwood Forest National park (53˚ 12’ 31.9”N, 01˚ 04’ 04.8”E) before being transported by car to Brackenhurst campus (approx. 14 miles, 30 minutes; See Appendix for map of release sites). Details of the study species can be found in Chapter Two.

5.2.2 Trapping and transport

Mice were trapped over a 10 day period (3rd - 12th September 2013) using standard small mammal trapping techniques and Longworth Traps (Gurnell and Flowerdew, 2006). Traps were baited with rolled oats, a small piece of carrot and casters (fly pupae) and contained hay for bedding. Three grids of twenty-five traps each were placed in varying locations at Sherwood Forest for either one or two nights before being moved to a new location, this was so the maximum number of mice could be caught over the shortest amount of time, as the probability of trapping new mice rapidly decreased over subsequent trap days. However due to this short time span, data from Chapter Three suggest that the boldest individuals were not trapped and brought into captivity, the implications of this are discussed later. Traps were placed in the evening within a few hours of sunset and checked again shortly after sunrise.

Upon trapping, mice were weighed to the nearest half gram, sex and reproductive status was noted (the presence of descended testes was recorded in males and pregnancy, visible nipples or perforate vagina, were recorded in females). Juvenile mice (<10g) and obviously pregnant or lactating females were released at point of capture and not taken into captivity. Mice that were to be brought into captivity were first behaviourally tested (following the protocol below), then returned to the trap and provided with extra food and clean bedding if required. Mice were then taken by car to Brackenhurst campus (approx. 14 miles, 30 minutes).

5.2.3 Housing and marking

Mice were housed in a secure room at Home Farm on Brackenhurst campus for up to two weeks in individual plastic cages measuring 18cm x 28.5cm x 12.5cm deep as recommended by Malo *et al.* (2010). Cages contained wood shavings and shredded paper as bedding, *ad libitum* water and a varied feed scattered in the cage to simulate a natural foraging environment. A small piece of tubing and a chew stick were also included to provide enrichment and encourage natural behaviours. The room was maintained at ambient light intensities and temperature to ensure mice retained their natural routine during temporary captivity. Husbandry procedures exceeded the ASPA guidelines.

All mice were PIT tagged for identification before release (Francis Scientific Instruments, Cambridge, 1.41x9mm, glass, 0.035g, <0.4% body weight), except for two mice which were deemed too small for PIT tagging and were instead given unique fur clips. PIT tags were injected into the scruff of the neck while mice were manually restrained and a small quantity of superglue was used to seal the hole. Thirteen of the mice were also fitted with VHF radio collars (Biotrack, Pip Ag376, weight approximately 1g, <6.5% body weight). Radio collared individuals were all male mice over 15 grams and were selected from across the personality spectrum. Radio collars were attached using a cable tie while mice were manually restrained, excess cable was removed. Radio collars had a battery life of approximately 32 days and contained a temperature sensor so mortality events could be identified. All mice were collared a minimum of 24 hours before release to allow time for any adverse effects be observed or collar fit to be adjusted if required.

5.2.4 Behavioural Testing

The testing protocol and apparatus were identical to those described in Chapter Two. The same observer carried out all tests and scored all videos. All mice were tested twice, once in the field upon trapping and once in the lab after 24 hours in captivity. The same testing equipment was used in both situations.

5.2.5 Release and Tracking

Mice were released in three groups at a novel location in Sherwood Forest after 5-15 days in captivity dependant on capture date, at least 500m from original capture location. Release sites were selected from the space available at Sherwood Forest so they were equally spaced and were a minimum of 100m from the closest path. Habitat at Sherwood Forest is an oak and birch woodland with a bracken and bramble ground layer; however sites were initially visually assessed to ensure they had similar habitat conditions. Mice were released in three groups of fourteen individuals composed of; all bold individuals (boldness greater than the median), all shy individuals (boldness less than the median) and a mixed group (see Table 5.1 for mean group personality scores and details of mice in each group). Four mice were radio-collared in each of the bold and shy group and five in the mixed group. Release groups were transported by car to the release site in Longworth traps and were released one at a time, leaving a few meters and a few minutes between releases to reduce the risk of aggressive encounters.

Following release a trapping grid was set up at each location centred on the release sites consisting of 25 traps set at, 20m intervals covering a total of 6400 square metres. Traps were set 4 nights a week for 6 weeks following release. Captured mice were weighed, sexed and checked for PIT tags and collars before being released. Traps were closed and left in place when not in use to encourage habituation to their presence. Radio collared mice were tracked during the day to their nest 6 days a week and tracked at night a minimum of 2 nights a week. At night mice were located to within a couple of metres and the location logged on a GPS device (Garmin eTrex, Garmin Ltd., Hants, UK). Location fixes were taken 2-4 times per tracking night leaving a minimum of 30 minutes between fixes, long enough for data points to be considered independent.

5.2.6 Habitat Measures

Ten habitat measures were estimated within the $5m^2$ grid surrounding each trap and each GPS location for radiotracked individuals. These included: % bracken cover, % bramble cover, % grass cover, modal height of herbaceous plants (cm), modal canopy height (m), % canopy cover, number of oak trees, number of birch trees, % cover of dead wood and % open ground. Height of plant layer was measured to the nearest 5cm, canopy height was estimated to the nearest metre, and percentage cover was estimated to the nearest 5%.

5.2.7 Data Analysis

5.2.7.1 Creating personality scores

Personality scores were calculated using the same method as previously used in Chapters Two and Four. Factor analysis was carried out independently on the open field and novel object data. For all analyses Bartlett's test was highly significant ($p<0.001$) and KMO exceeded 0.7 (OF – 0.82, NO – 0.74) suggesting that the data is sufficient for factor analysis. The number of factors extracted was selected by applying the Minimum Average Partial analysis (Velicer, 1976). Regression was used to calculate factor scores.

5.2.7.2 Modelling personality

Restricted maximum likelihood general linear mixed models (R; library nlme) were again used to model personality and behavioural plasticity. Two sets of models were created the first with 'Activity' as the dependant variable and the second with 'Boldness' using the same procedure.

Mouse Id was used as a random intercept to examine the significance of individual repeatability (personality), and location (lab/field) as a random slope nested within mouse Id to measure individual plasticity to the change in test environment.

The following fixed effects were added to the model: *location* (lab, field), *date* (centred around mean), *time* (minutes from 6AM), *temperature* (˚C) and *weight* (grams). While keeping all the fixed effects in the model, random effects were varied to produce the best fitting model (models compared using likelihood ratios) following Zuur (2009). Initially *individual ID* was added as a random effect, if this was significant *location* was included as a repeated measure within individual ID (random slope/regression model; Dingemanse *et al.,* 2010). Once random effect structures were determined, significance of fixed effects was calculated using type III sums of squares. Backwards elimination of non-significant fixed effects (*p*>0.05) was used as a model selection criteria.

To meet assumptions of normality residual plots were used to visually assess distributions and activity was log transformed to improve fit. Adjusted repeatability (r; the intraclass correlation coefficient) of behavioural scores was calculated from the final models as the ratio of the between-individual variance over the sum of the between- and within-individual variance (Nakagawa and Schielzeth, 2010).

As activity was repeatable, the activity BLUP was calculated from the activity model and used as an estimate of activity score for each individual. However as boldness was not repeatable, both boldness in the lab and boldness in the field were included in further models to examine which gave a better predictor of behaviour. Activity slope (the change of behaviour from the field to the lab) was also included to examine if this predicted future behaviour.

5.2.7.3 Dispersal and survival

Radio tracking data indicated that immediate post release dispersal continued for approximate 5 days, based on increasing mean daytime distance from release site, after which point further dispersal was limited. To test whether the personality of individuals that dispersed before day 5 differed from those that remained a logistic regression model was created with immediate dispersal (1- before day 5, 0- day 5 and after) as the dependant variable and *activity BLUP, activity slope, field boldness, lab boldness, release group* (bold shy or mixed)*, sex, weight* (grams) and *days in captivity* as independent variables.

The following analyses looked at dispersal after this point and used results from days 5 onwards. The first two models looked at overall recapture numbers in each grid over time using a generalized linear model with a poisson distribution and log link. The first model used raw capture numbers for tagged individuals on each trapping day and the second model used a calculation of 'minimum released mice remaining in trapping area' a count of individuals caught that day and at any future time used as an estimate of how many mice likely remained within the release site. *Release group (*shy, bold, mixed), *days since release*, *number of resident mice trapped* and all relevant interactions were included as factors, *number of traps occupied by other species* and *number of falsely triggered traps* were also included as covariates in both models.

The next two models used radiotracking data to investigate how dispersal distance related to individual personality and release group composition using a mixed model approach. The first model used daily mean interfix distance recorded while mice were active at night, as a dependant variable to look at amount of movement after release and the second daytime nest distance from release point as a dependant variable as a measure of dispersal distance. Both models used *mouse ID* as a random factor and *days since release, days in captivity, release group activity BLUP, activity slope, field boldness* and *lab boldness* as fixed factors along with all relevant interactions.

A Cox's proportional hazard survival model was used to investigate the probability of individuals with different personality types leaving the release site. *Field boldness, lab boldness, activity BLUP, activity slope* and *release group* were included as fixed effects and the day individuals were last seen at the release site was scored as a positive event, mice still on the site after 28 days were scored with a negative event as data was right censored.

For all of the above models, where appropriate, normality was assessed by subjectively assessing residual plots. Stepwise elimination of non-significant factors ($p > 0.05$) was used as a model selection criterion in all cases.

To investigate if there was any difference in personality between radio collared individuals that died during the 30 days of the study and those that survival a binary logistic regression model was carried out with *activity BLUP, lab boldness, field boldness* and *activity slope* as predictors and *mortality* (0 - survived, 1 - died) as the response. A stepwise backwards procedure was used to restrict the model until only factors with $p < 0.1$ remained in the model. This was done to identify trends in the data which may not have been significant due to the small sample size (N=10).

5.2.7.4 Weight change after release

As a measure of success after release a mixed model was created with weight at each recapture as the dependant variable. Individual ID was included as a random effect to control for repeated measures. *Group, activity BLUP, boldness in the field, boldness in the lab, age, sex* and *days since release* were included as predictors along with the interaction between *days since release* and all the other factors. Stepwise elimination of non-significant factors ($p > 0.05$) was used as a model selection criteria.

5.2.7.5 Habitat

Radiotracking and recapture data were used to investigate differences in habitat between the three release sites and to build up a picture of habitat use by radio-collared individuals. A principle component analysis with Promax rotation was ran on all trap locations and GPS locations to condense habitat measures in to a smaller number of components. Number of components to extract was selected using a combination of Cattells scree test and the MAP criterion.

5.2.7.6 Habitat differences

Habitat differences between sites were compared using a one-way ANOVA with each principal component as the dependant variable and release grid as the factor. Due to multiple comparisons differences were only considered significant if $p < 0.0166$. Normality of data was verified using a Shapiro-Wilk test.

5.2.7.7 Habitat Use

Using a mixed model approach habitat components were also compared to personality scores of individual mice found in these locations, to identify any habitat preferences between mice with different personality types. *ID* was included as a random effect to control for repeated measures, *field boldness, activity BLUP, activity slope, weight* and *days since release* were included as fixed effects. *Release group* was kept as a covariate in all analyses to account for any differences in habitat composition between sites. A different model was ran for each habitat component. Assumptions of normality were verified by visualising residual plots. Models were selected by stepwise elimination of non-significant figures ($p > 0.05$).

5.2.7.8 Home Range Size

GPS data were used to create home range estimates for each radio collared mouse using 95% Minimum Convex Polygons (ArcGIS 10.0; ESRI, Inc. Redlands, CA). Only individuals who had been located at over 5 points were included in the analysis (mean±SD = 15.3±6.62). Home range estimates were calculated using points collected after mice had a stable daytime nest (moved <5m since previous day). A linear model was then used to look at factors affecting home range size including; *release group, weight, activity BLUP, activity slope, field boldness* and *lab boldness* as fixed effects. Again normality of residuals was verified using residual plots and stepwise elimination of non-significant factors was used as a model selection criterion.

All statistical analyses were performed using R 3.0.0

5.3 Results

In total forty-two mice were behaviourally tested and brought into captivity, thirty-one male and eleven female (See Table 5.2 for details). Mice were retained in captivity for an average of 11.17±2.82 (mean±SD) days before release. After release 23 of the mice were recaptured at least once (bold - 8, shy - 5, mixed - 10), with those mice remaining at the release site for an average of 18.26±10.35 days (bold – 16.5±9.49, shy – 15.2±11.28, mixed – 21.2±10.85). Radio tracked mice were tracked for an average of 21.92±11.57 days. Contact was lost with one mouse after the first day, one died from trap related mortality and 4 mice died from unknown causes but suspected to be due to predation.

Table 5.1. Details of individuals included in release groups. Data Shows Mean ± SD

Group	Bold	Mixed	Shy
Activity	0.24±1.1	0±0.9	-0.25±0.95
Boldness	0.41±0.85	-0.08±0.9	-0.33±1.05
Male/Female	10/4	8/6	13/1
Adult/Sub-adult/Juvenile	10/4/0	8/4/2	13/0/1
Weight (g)	19.54±3.35	17.61±3.84	19.93±3.5

5.3.1 Factor Analysis

As in Chapter Two only one component was retained from each test (Table 5.3, Table 5.4). The factor retained from the Open Field test explained 62% of the total variance and represents activity and exploration, with number of lines crossed, number of centre squares entered and number of rears loading positively, further referred to as ‘Activity’ (Table 5.3). The factor obtained from the novel object test represents aspects of neophilia and fearlessness with number of touches and approaches to the novel object loading heavily, and aspects of predator response with a negative loading of time spent frozen, further referred to as ‘Boldness’ (Table 5.4).

Table 5.2. Details of mice included in study.

age	sex	weight (g)	group	field boldness	lab boldness	activity BLUP	activity slope	times trapped	days at release site	mean distance from release	mean movement distance	died?
Adult	Male	20.5	Bold	1.49	0.99	1.59	-0.30	9	17	37.57	49.96	yes
Sub-Adult	Male	15.5	Bold	0.80	-0.26	1.75	-0.83	8	10	40.00	67.98	yes
Adult	Male	18.5	Bold	1.69	-0.28	1.51	-0.67	1	7	186.97		yes
Adult	Male	18	Shy	-1.13	-1.13	1.71	-0.86	0	0	147.57	62.90	yes
Adult	Male	20	Shy	-0.45	-0.57	1.40	-0.39	5	7	65.30		unknown
Adult	Male	20.5	Mix	-0.28	0.14	1.38	-0.41	11	29	43.17	35.42	no
Adult	Male	21	Mix	-1.18	-0.62	1.83	-1.10	15	29	51.37	53.59	no
Sub-Adult	Male	15	Mix	-1.02	-1.18	1.54	-0.57	0	0	76.11	33.75	no
Adult	Male	20	Mix	0.53	-0.09	1.50	-0.60	0	0	121.02	29.10	no
Adult	Male	22	Mix	-1.13	-0.52	1.63	-0.78	1	2	121.24	21.91	no
Adult	Male	22	Shy	0.80	-1.20	1.72	-0.90	7	22	45.41	58.79	no
Adult	Male	23.5	Shy	-0.99	-0.67	1.45	-0.93	0	0	194.92	52.04	no
Adult	Male	18	Bold	-1.13	0.00	1.31	-0.60	0	0	21.21		
Adult	Male	18.5	Bold	0.72	0.19	1.60	-0.57	5	24			
Adult	Female	22.5	Bold	1.33	-0.25	1.66	-0.50	0	0			
Sub-Adult	Male	15	Bold	0.30	0.03	1.73	-0.80	0	0			
Adult	Male	20.5	Bold	0.38	-0.02	1.34	-0.56	0	0			
Adult	Male	23	Bold	1.27	0.24	1.08	0.02	9	29			
Sub-Adult	Female	16	Bold	0.63	-0.28	1.52	-0.46	9	28			
Sub-Adult	Female	15	Bold	-1.19	0.51	1.82	-0.92	7	12			
Adult	Male	22.5	Bold	0.48	0.28	1.39	-0.71	0	0			
Adult	Male	24	Bold	0.86	1.34	1.71	-0.84	0	0			

Table 5.2. Details of mice included in study cont.

age	sex	weight (g)	group	field boldness	lab boldness	activity BLUP	activity slope	times trapped	days at release site	mean distance from release	mean movement distance	died?
Adult	Female	24	Bold	-1.10	2.34	0.91	-0.02	4	5			
Sub-Adult	Female	16.5	Mix	1.30	1.75	1.16	-0.05	0	0			
Sub-Adult	Female	15	Mix	0.91	-1.13	1.52	-0.52	11	28			
Sub-Adult	Female	14.5	Mix	0.85	0.12	1.03	-0.14	8	21			
Juvenile	Male	11.5	Mix	-0.66	-0.47	1.64	-0.86	10	24			
Adult	Male	20.5	Mix	-0.31	-0.71	1.65	-0.77	14	28			
Juvenile	Female	10	Mix	0.67	-1.16	1.52	-0.76	13	29			
Adult	Female	19.5	Mix	0.91	-0.13	1.52	-0.57	0	0			
Adult	Male	21	Mix	0.03	-1.20	1.22	-0.62	1	1			
Adult	Female	19.5	Mix	1.42	0.88	1.88	-0.77	5	21			
Adult	Male	18.5	Shy	-0.86	-0.46	1.58	-0.96	0	0			
Adult	Male	20	Shy	-1.04	-1.12	1.76	-0.78	10	29			
Adult	Male	20	Shy	0.53	-1.19	1.76	-0.87	0	0			
Adult	Male	18.5	Shy	1.71	-1.14	1.44	-0.54	0	0			
Adult	Male	18.5	Shy	0.78	-1.15	1.64	-0.61	0	0			
Adult	Male	27	Shy	-0.51	-1.18	1.78	-1.22	1	17			
Adult	Male	18.5	Shy	0.60	-0.59	1.63	-0.67	0	0			
Juvenile	Female	11.5	Shy	-0.13	-0.63	1.46	-0.66	0	0			
Adult	Male	20	Shy	1.39	-1.17	1.59	-1.11	1	1			
Adult	Male	23	Shy	2.95	-0.58	1.72	-0.62	0	0			

Table 5.3. Factor loadings for results from Open Field factor analysis with eigenvector and percentage variance explained, variables loading stronger than 0.4 in bold, N=84

Variable	**Factor 1 (Activity)**
Lines crossed	**0.97**
Enter middle squares	**0.92**
Rears	**0.85**
Latency to enter centre	**-0.61**
Time grooming	**-0.74**
Jumps	**0.62**
Time in centre	**0.7**
Eigenvector	4.31
Variance Explained	62%

Table 5.4. Factor loadings for results from Novel Object factor analysis with eigenvector and percentage variance explained, variables loading stronger than 0.4 in bold, N=84

Variable	**Factor 1 (Boldness)**
Latency to Touch	**-0.92**
Number of Touches	**0.91**
Latency to approach	**-0.76**
Actual Approaches	**0.85**
Time Frozen	**-0.72**
Time Spent Touching	**0.71**
Near Touching	0.38
Eigenvector	4.14
Variance Explained	59%

5.3.2 Mixed Models

5.3.2.1 Personality

Individuals were consistent in their behaviour between being tested in the field and the lab for activity ($p < 0.01$, Figure 5.1) but not for boldness ($p > 0.05$; Table 5.5, Figure 5.2) with adjusted repeatability for Activity of 0.37±0.1.

5.3.2.2 The effect of captivity

Testing location (lab/field) was significant as a random slope for Activity suggesting that individual mice responded differently to being brought into captivity (Table 5.5, Figure 5.1). The only significant fixed effect for Activity was location with mice generally reducing their activity once taken into captivity (β = -0.65±0.08, $F_{1,41}$ = 74.64, $p < 0.0001$). The only factor affecting boldness scores was time, with boldness reducing later in the day (β = -3.44±0.98, $F_{1,82}$ = 12.22, $p < 0.001$).

Table 5.5. Log likelihoods of models and results of model comparisons investigating individual consistency and plasticity for both Activity and Boldness scores.

Model			**Likelihood Ratio Test**			
	Random Factors	**Log L.**	**Test**	**LRT**	**df**	***p*-Value**
Activity						
a	None	-58.45				
b	Intercept	-55.67	a vs. b	5.56	1	**<0.01**
c	Intercept*Slope	-51.35	b vs. c	8.64	2	**<0.01**
Boldness						
a	None	-116.62				
b	Intercept	-116.29	a vs. b	0.68	1	0.21
c	Intercept*Slope	-114.59	b vs. c	3.39	2	0.12

Despite not being significantly repeatable between the lab and the field, boldness in the lab was positively correlated to activity in the lab ($r_s = 0.32$, N = 42, $p < 0.05$) and boldness in the field was positively related to activity in the field ($r_s = 0.44$, N = 41, $p < 0.005$). Activity slope was positively related to boldness in the field ($r_s = 0.34$, $p < 0.05$), as bolder individuals reduced their activity less in captivity, but negatively related to activity BLUP ($r_s = -0.67$, N = 42, $p < 0.0001$), the most active overall individuals reduced their activity most in captivity.

When tested no features of the animal (sex, age, reproductive status, weight) or the test situation (temperature, humidity, time) predicted the level of change in behaviour once taken into captivity.

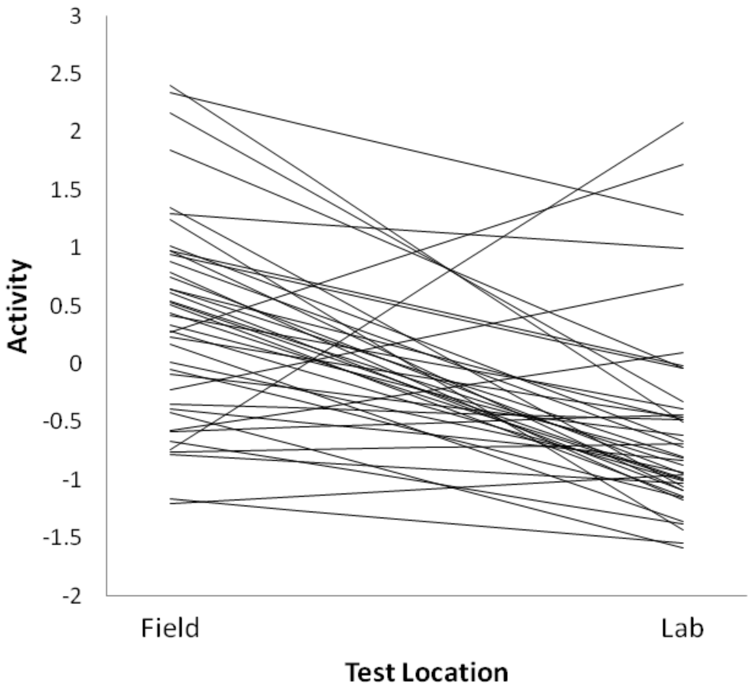


Figure 5.1. Individual activity scores from the open field test recorded in the field and in the lab (N=42)

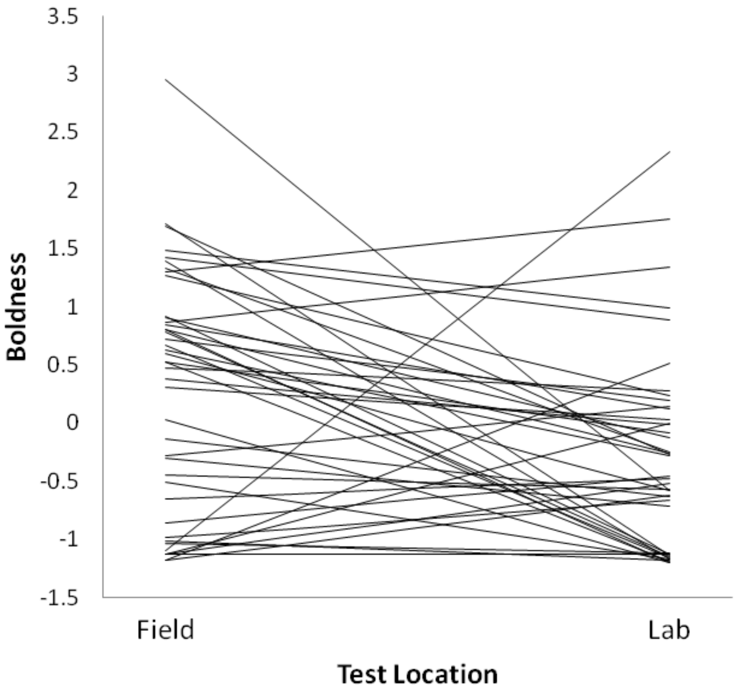


Figure 5.2. Individual boldness score in the novel object test recorded in the field and in the lab (N=42)

5.3.2.3 Effect of personality post release

Overall 5 of the 13 radio tracked mice died during the study as recorded by the mortality sensors in the collars; however one of those deaths was due to trap related mortality. On average tracked individuals continued to move away from the release site for approximately 5 days after release at which point they settled 88.48±59.58m from the release site, although this was higher for the shy group and slightly lower for the bold group (Bold, 45.82±29.82; Mix, 77.71±37.5; Shy, 128.33±79.45). This is similar to Miller (1958) who found that 86% mice moved less than 120m after release. As the radio tracked individuals dispersed little after this point it seems likely that further reduction in trapping numbers after this point are mostly due to mortality rather than further dispersal. However mortality rate after this point for radio tracked individuals was 36% whereas losses from trapping sites was 55% (bold - 62.5%; shy - 75%; mix - 37.5%), suggesting there may be some additional dispersal.

5.3.2.4 Dispersal from release site

Mean daily captures of all mice, released and resident were lower at the shy group, which suggests population densities were lower in this area (Mean±SD; Bold:8.42±2.55, Mixed:9.58±2.78, Shy:3.53±1.98). This difference was significant when a poisson regression model was ran with date included as a covariate ($Chisq_{2,53}$=22.71, $p<0.0001$). Number of resident mice captured per day was generally lower at the shy group (shy – 2.26±1.59, mix – 4.58±2.32, bold 5.37±1.54) and this difference was also significant when a poisson regression model was ran ($Chisq_{2,53} = 26.5$, $p < 0.001$) with the shy group having significantly lower recaptures ($p<0.001$).

The logistic regression model found no significant factors predicting which individuals dispersed in the first 5 days.

The only significant effects from the poisson model looking at absolute number of marked mice trapped were group ($Chisq_{2,44} = 17.27$, $p < 0.001$), the bold group had significantly greatest recaptures than the shy group ($p < 0.005$), and the interaction between group date as the number of recaptures decreased faster at the shy group than the mixed group (β = Chisq$_{1,44}$ = 6.2, $p < 0.05$).

The poisson model for minimum number of mice remaining at each release site showed a significant decrease in mice over days since day 5 after release at all groups (β = -0.19±0.01, Chisq$_{1,35}$ = 8.78, $p < 0.005$). Again group was significant (Chisq$_{2,35}$ = 18.1, $p < 0.001$), both the bold and shy group had significantly lower recaptures than the mixed group ($p < 0.005$, Figure 5.3).

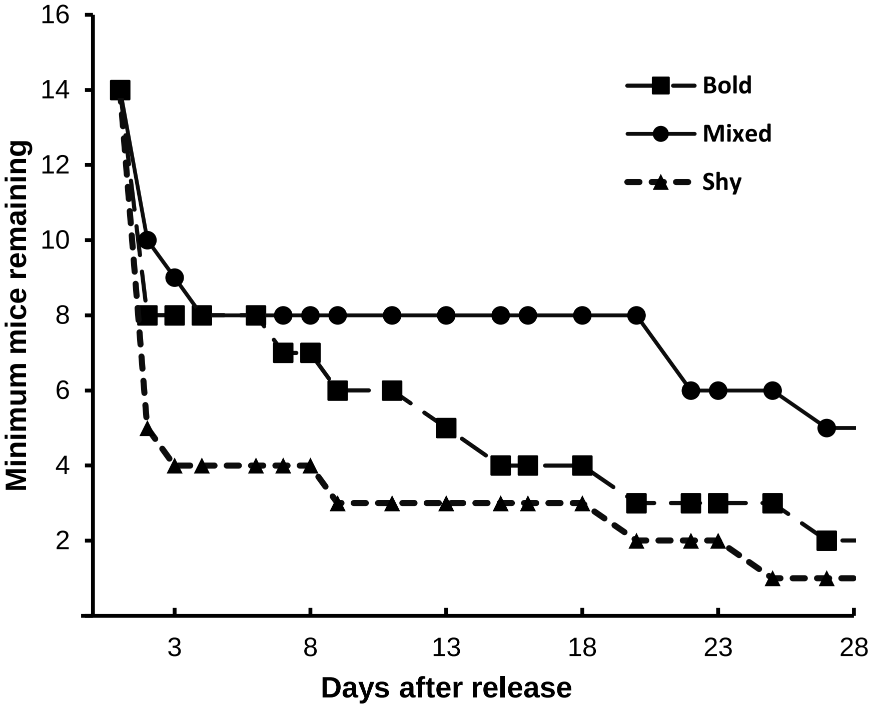


Figure 5.3. Minimum number of mice remaining at each trapping grid (bold - squares, mixed - circles, shy - triangles) over days after release.

5.3.2.5 Radiotracked Mice

The first model looking at mean interfix distance each 24h found that Activity BLUP was positively related to mean movement ($\beta = 53.06 \pm 20.9$, $F_{1,6} = 6.45$, $p < 0.05$). Distance moved increases over days since release ($\beta = 1.23 \pm 0.46$, $F_{1,41} = 7.2$, $p < 0.05$) and that release group had an effect on movement distance ($F_{1,6} = 5.95$, $p < 0.05$), with the bold group having the greatest interfix distance and the mixed group the least ($p < 0.0001$, Figure 5.4).

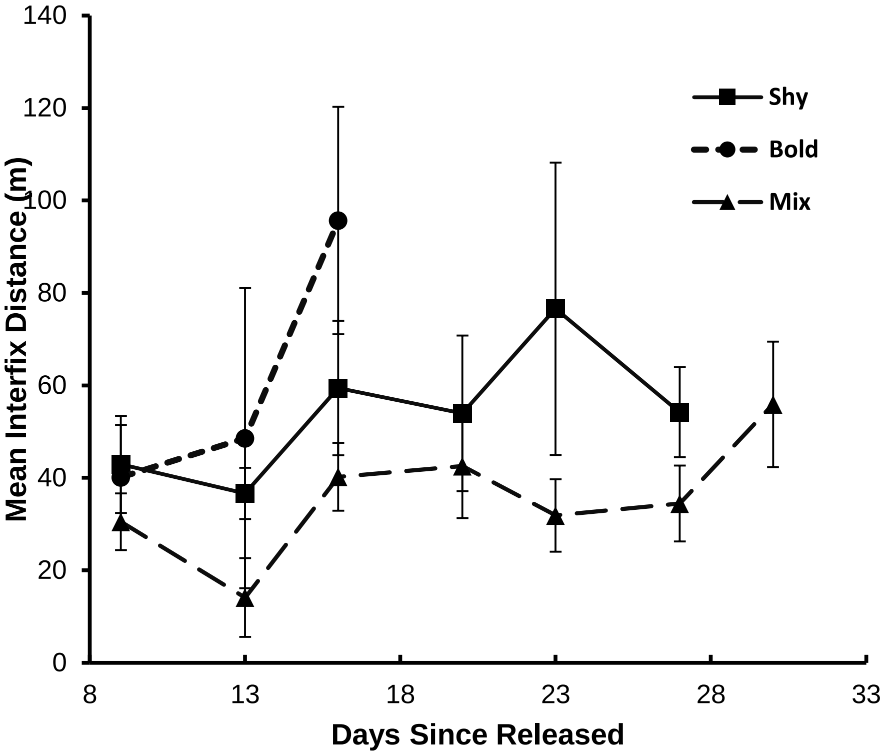


Figure 5.4. Mean interfix distance for each release group (bold – squares, mixed – circles, shy – triangles) over days from release with standard error bars. Points indicate when data from at least 2 released individuals was available.

The second model looking at nest distance from release point over time from day 5 found a significant relationship with Activity score ($\beta = -385.69 \pm 140.41$, $F_{1,9} = 7.55$, $p < 0.05$) although this had a negative relationship with distance (Figure 5.5) with the most active individuals dispersing the least far. Activity slope score was also negatively related to nest distance (β = -195.1±82.47, $F_{1,9} = 5.6$, $p < 0.05$) those that decreased their activity most once taken into captivity dispersed further. Dispersal distance also decreased over days since release (β = -0.34±0.17, $F_{1,191} = 4.16$, $p < 0.05$) although this is likely due to the death of some of the individuals that had dispersed furthest (Figure 5.6).

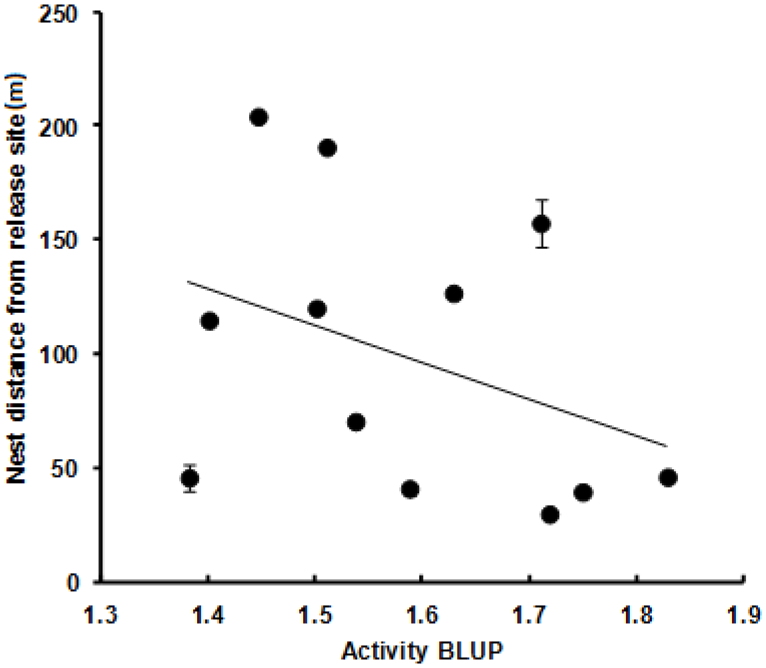


Figure 5.5. Activity BLUP of individuals against their mean daily nest distance from release site, with standard error bars and line of best fit.

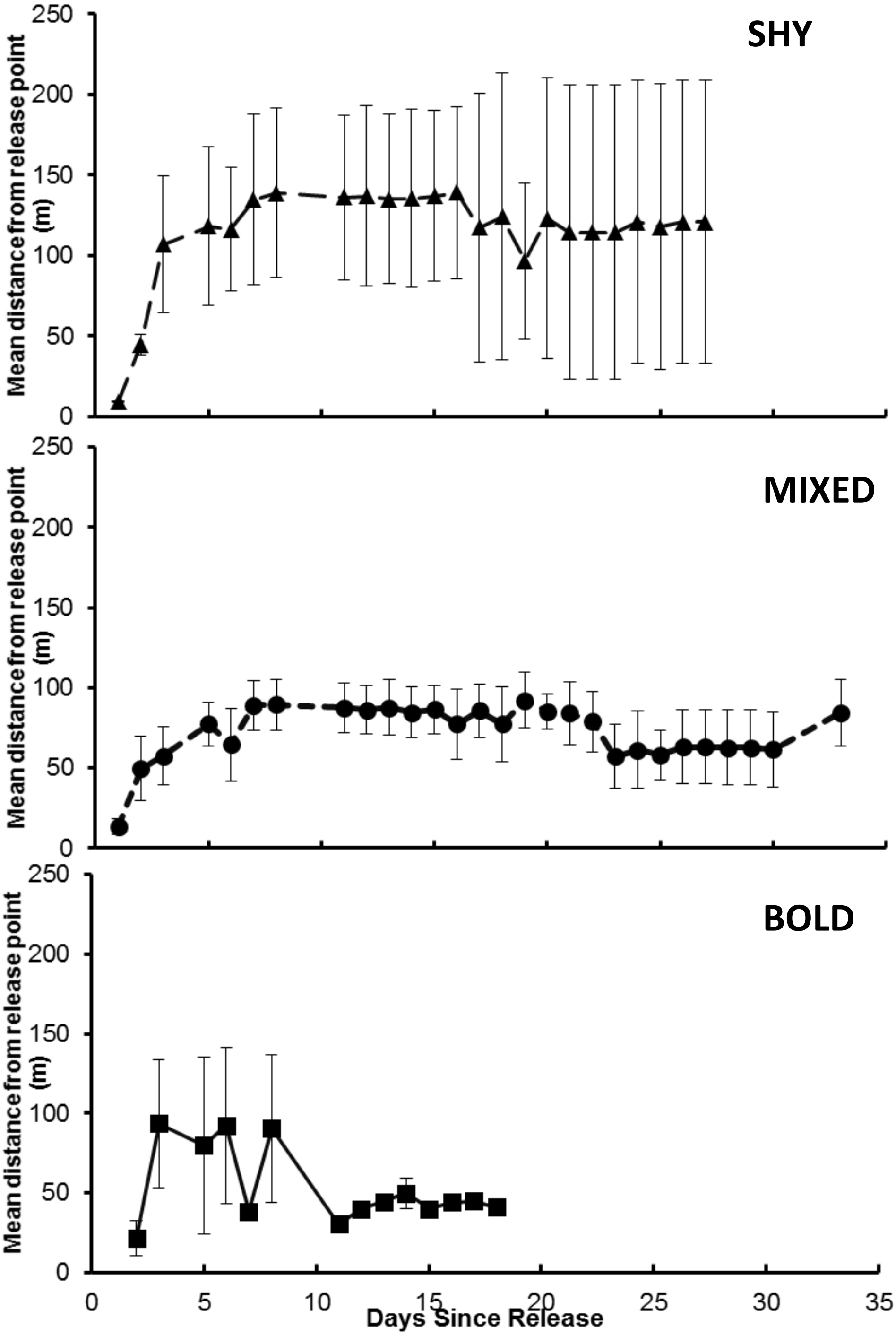


Figure 5.6. Mean distance from release point over time for each of the three release groups (Shy – top, mixed – middle, bold - bottom). Includes data when at least 2 radio tracked individuals remain.

The final logistic regression model suggested that bolder radio collared individuals tended to have a higher probability of mortality after release (β = 1.18 ± 0.74, chisq$_{1,9}$ = 3.26, p = 0.07) (Figure 5.7).

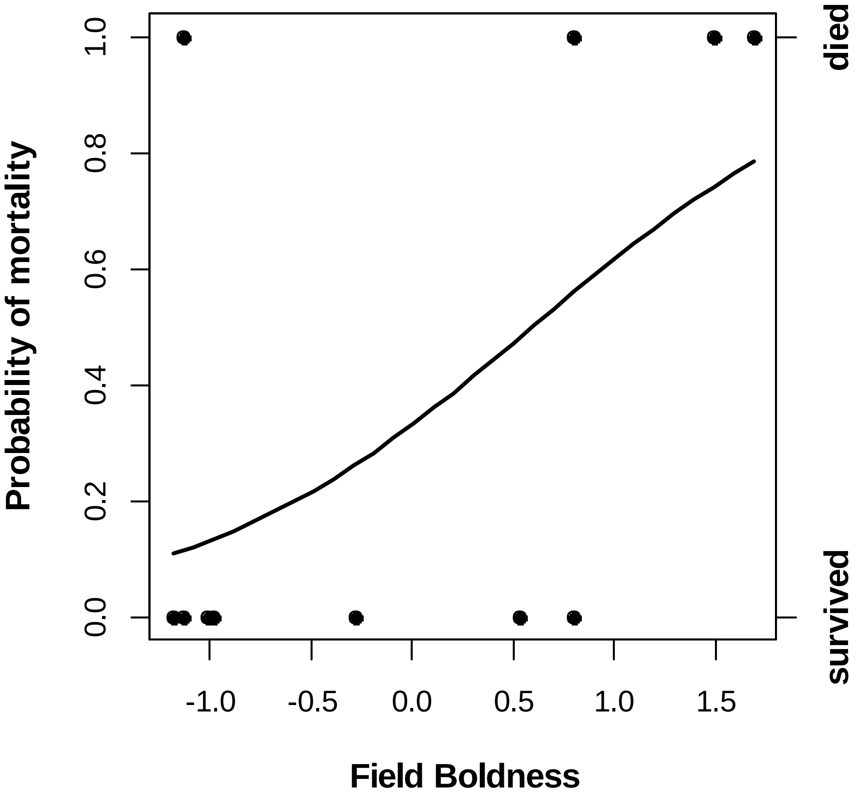


Figure 5.7. Plot of field boldness against mortality during monitoring period after release (0 - survived, 1 - died). Line shows logistic regression model result predicting mortality probability (N=11).

The Cox's proportional hazard survival model suggested that boldness in the field increased the probability of leaving the release area (Risk Ratio = 1.84, 95%CI = 1.02 to 3.31, $p < 0.05$), whereas activity BLUP decreased it (RR = 0.06, 95%CI = 0.004 to 0.77, $p < 0.05$). A risk ratio of 1 suggests no change in risk due to factor. Release group had no effect on probability of dispersal.

5.3.2.6 Weight after release

Male mice were significantly heavier than female mice (β = 2.95±0.93, $F_{1,19}$ = 17.17, $p <$ 0.01) and juvenile mice were significantly lighter than adult mice (β = -4.32±1.04, $F_{1,19}$ = 17.17, $p < 0.001$). Weight generally increased over time after release (β = 0.62±0.14, $F_{1,138}$ = 15.22, $p < 0.0001$). The interaction between sex and days was significant ($F_{1,138}$ = 6.54, p < 0.05), male mice put on less weight after release than female mice. Finally, the interaction between activity and days was significant as more active mice put on less weight than less active mice (β = -385.69±140.41, $F_{1,138}$ = 5.79, $p < 0.05$).

5.3.2.7 Home range size

Home range sizes ranged from 0.6 to 3.75 hectares and were largest at the mixed group and smallest at the bold release site (Mixed, 2.67±1.2, N=5; Shy, 2.27±1.06, N=3; Bold, 1.06±0.57, N=2). However home range size showed no significant link with personality, release group or any of the factors included in the model. This may be due to the limited number of data points included in estimating home range sizes and the limited number of individuals tracked. However these results are similar to (Lodewijckx, 1984a) who also found no link between home range size and open field behaviour.

5.3.2.8 Habitat Differences

The PCA reducing the number of habitat variables gave a KMO of 0.63 suggesting data were adequate (N=10 variables in 403 locations). Three components were retained; PC1 which had high positive loadings on open ground and number of oaks and negative loadings on bracken cover and herb height, PC2 with positive loadings on open ground and grass cover and negative on canopy cover and bramble, and PC3 with high positive loading on percentage cover of dead wood and negative on number of birches.

Habitat differed significantly between grids with the mixed release site having a higher proportion of bare open ground with low oak canopy (PC1: Kruskall Wallace; X^2 = 13.57, df = 2, $p < 0.01$), the shy release site also had significantly less dead wood with more birches (PC3: Kruskall Wallace; X^2 = 18.3, df = 2, $p < 0.001$; Figure 5.8).

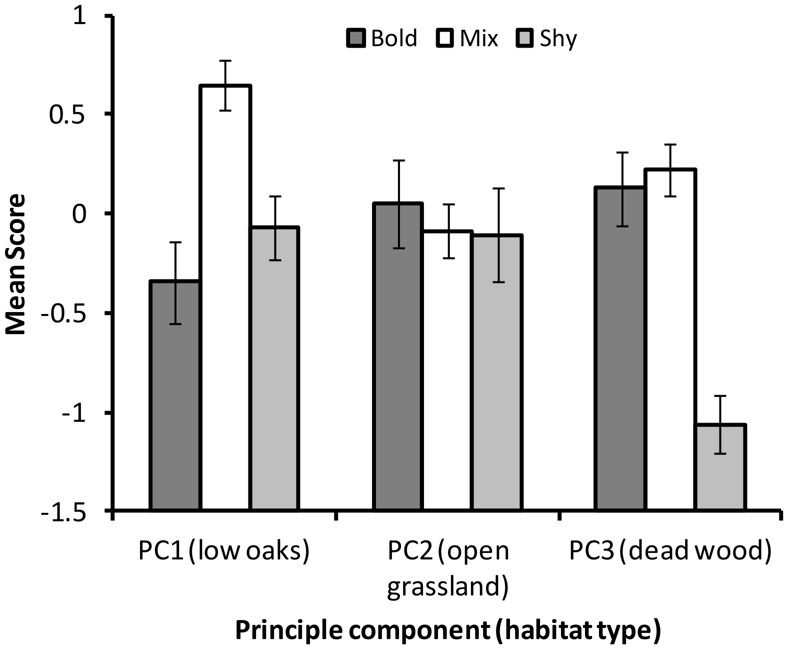


Figure 5.8. Mean habitat scores for each habitat component for each grid with standard error bars (N=25 for each grid).

5.3.2.9 Habitat Use

PC1 use was predicted by date (β = 0.03+0.01, $F_{1,177} = 7.78$, $p < 0.01$) with the use of open ground increased over time. Use of PC2 also increased over time (β = 0.2+0.07, $F_{1,197}$ = 8.37, $p < 0.005$), was positively related to both lab boldness (β = 0.58+0.17, $F_{1,7} = 11.14$, $p < 0.05$) and activity BLUP (β = 3.75+0.87 , $F_{1,7} = 18.53$, $p < 0.005$), and was negatively related to the date by activity BLUP interaction (β = -0.12+0.04 , $F_{1,197} = 7.64$, $p < 0.01$), as the more active individuals increased their use of PC2 over time more than less active individuals. None of the included variables predicted use of PC3.

5.4 Discussion

Results from this study show that personality traits affect behaviour after a reintroduction to a novel habitat. More active individuals moved around more after release but settled closer to the release site, whereas bolder individuals were more likely to leave the release area and had a higher probability of mortality. The data also showed some evidence that releasing all shy individuals led to inflated short term dispersal. These results are consistent with the recommendation that releasing a mix of personality types leads to greater reintroduction success. In addition, data suggest that even short term captivity has a strong impact on behaviour and that behaviours measured in captivity may not directly relate to behaviours measured in the wild, even when using the same testing procedure.

This study again confirmed the repeatability of activity as a personality trait in wood mice and suggests that the trait may be context general, with consistent behavioural scores when tested in both the field and in the lab. However this was not the case for boldness, as individual boldness scores in the lab and in the field were unrelated. This highlights the issues surrounding the effects that environment and the stress of captivity may have when performing behavioural tests. Many personality studies transport animals to the lab before behavioural testing (e.g. Dingemanse *et al.,* 2003), but this may distort the measures of behaviour taken in unpredictable ways (Niemelae and Dingemanse, 2014). In this study there was no relationship between the boldness scores measured in the field and in captivity, suggesting that the boldness trait measured here is context specific. This change in behaviour may either be due to the stress and experience of captivity affecting behavioural responses to the stimuli or because individuals are responding to different cues during the test which changed between the field and the lab and weren't controlled for.

Time in captivity may provoke different behaviours even in response to the same stimuli (Butlers *et al.,* 2006). If an individual's response to behavioural tests is due to their stress response (as discussed in Chapter Two) longer periods in captivity can drastically change this response. Being tested in the field may provoke a short term stress response, potentially a Cannonian fight or flight response used to escape from an immediate threat (Cannon, 1929), whereas long term stress may provoke a different conservation or withdrawal pattern (Selye, 1950). Potential negative effects of captivity were evident, even in the first 24 hours in captivity before testing, as mice tended to lose weight in this time (mean±SE; -0.28±0.24 grams).

Alternatively, personality traits can be highly context specific. Subtly different cues encountered while in captivity and removal from a familiar context may change or skew behavioural responses (Butlers *et al.,* 2006). Testing in captivity may simulate a high predation risk environment compared to the field due to the presence of humans, isolation from conspecifics and inhibition of movement during transport to the testing apparatus (Tanas and Pisula, 2011). Risk taking behaviour as seen in the novel object test can be highly modified by the threat of predation (Bell and Sih, 2007). Perception of this level of risk will change over time in captivity and due to the stressors encountered which can subdue normal behavioural responses (Butler and Dufty, 2007) and affect individuals to different extents (Kock *et al.,* 1990). Niemelae and Dingemanse (2014) suggest that testing animals in the lab may not give true impression of behaviour if the stimuli experienced are outside the normal range experienced in the wild. Due to either of these causes (internal changes due to captivity or external cues prompting different responses), the novel object test in the lab appears to be reflecting a different behavioural trait than when measured in the field. Due to this, both lab boldness and field boldness were included in further analyses to identify which provided a better measure of wild personality. Field boldness was a better predictor than lab boldness for most behaviours measured post release except habitat use, suggesting that behaviours measured in the lab were further divorced from wild behaviours than behaviour measured in the field.

Despite being repeatable, the random regression models also identified differences in how individuals changed their activity score from the field to the lab. The majority of individuals had lower levels of activity in the lab than the field but to different extents, representing variation between individuals in their behavioural plasticity between these two contexts.

These changes in behaviour once taken into captivity may represent variation between individuals in their ability to habituate (Butlers *et al.,* 2006) or to cope with captivity (Mason *et al.,* 2013) or potentially their attention to external cues (Titulaer, van Oers and Naguib, 2012). There was a stable correlation between boldness and activity in both locations, which may represent a stable behavioural syndrome (Bell and Stamps, 2004) in wild mice. Field boldness was negatively related to plasticity in the activity score which suggests that either bolder individuals are less plastic in their behaviour and are unable to change their behavioural response between different situations, or that they are less affected by the stress of captivity causing less change in their behaviour. As shyer individuals reduced their activity more once taken into captivity this may represent them taking longer to recover and adjust to capture and captivity (Wilson *et al.,* 1993; van Oers *et al.,* 2004). This correlation between boldness and activity but reduced plasticity in behaviour is again consistent with a higher order proactive-reactive behavioural syndrome as suggested in previous chapters. The proactive-reactive syndrome is focused on an individual's response to stress, which can play a key role in success after a reintroduction (Teixeira *et al.,* 2007).

Due to time and manpower constraints on the project it was not possible to remove resident wood mice living in the release area before the release. Although this makes the data more difficult to interpret it represents the situation common in translocations for reinforcement used to bolster numbers in struggling populations (IUCN/SSC, 2013).

Stamps and Swaisgood (2007) recommend measuring post release travel distance as a measure of preference for habitat, and an animal's rapidity of departure from the release site as a measure of rejecting the new habitat. At all three groups there was an initial drop in numbers at the release site as some individuals were never retrapped, and this drop was much greater at the shy group than at the other two groups. Data in Chapter Three assessing trap bias showed the opposite pattern, where more active (usually more bold) individuals were less likely to be retrapped, suggesting that the pattern seen here is not just due to trapping bias. Data from radio tracked individuals indicates dispersal was higher during the first five days after release so this drop is likely to reflect dispersal rather than mortality. Individual reaction to novelty can affect the probability of an animal rejecting its new habitat in a release as well as their reaction to human activities (Pinter-Wollman, 2009). However, none of the individual level factors were a good predictor of this short term dispersal suggesting there may be some group effect. Myers and Krebs (1971) found that shy voles were the least socially tolerant and similarly more asocial individuals have also been shown to disperse further in mosquitofish (Cote *et al.,* 2010) and grey-sided voles (Ims, 1990). This sociability dependant dispersal can either depend on the least social becoming aggressive and dispersing, or the most social choosing to stay with the group (Blumstein, Wey and Tang, 2009). If this pattern is also true for wood mice this may have caused individuals from the shy group to disperse when initial population densities were high as populations with more asocial individuals tend to have more dispersers, regardless of individuals personality type (Cote *et al.,* 2011). Sociability dependant dispersal should vary with population density (Cote and Clobert, 2007) as density of conspecifics provides an obvious dispersal cue (Clobert *et al.,* 2009). This is reflected in this study as after population density decreased after around 5 days post release numbers plateaued to some extent at all three sites. If shy mice generally prefer lower densities, this may also explain why recapture numbers were consistently lower at the shy group.

Some studies have found physiological differences (age, sex, weight etc.) between dispersers and non-dispersers in a potential ‘dispersal morph’ (O'Riain, Jarvis and Faulkes, 1996; Sinn, Gosling and Moltschaniwskyj, 2008), however that was not seen here and the only significant predictors of dispersal was through behaviour. Data collected here are consistent with the classical ‘social subordination hypothesis’ (Christian, 1970), which suggests that less aggressive, subordinate individuals are more likely to disperse when population densities are high as they become social outcasts and suffer from aggression from more dominant individuals (Brandt, 1992). Individual tracking data reflected this as the most active individuals (often bolder or more dominant) showed the shortest dispersal distance, whereas less active individuals dispersed further. More aggressive individuals (often correlated with activity in a proactive/reactive syndrome) tend to hold higher quality territories (Scales, Hymanb and Hughes, 2013) and so may be less willing to disperse. The social subordination hypothesis also describes a second mode of dispersal when densities are lower; at this point dispersers are higher quality individuals dispersing of their own free will for potential fitness benefits (Gaines and McClenaghan, 1980), choosing to risk moving through a dangerous unknown habitat (Fraser *et al.,* 2001). This study found bolder individuals had a higher probability of not being retrapped after the initial dispersal. This is likely to represent a combination of both increased dispersal and increased mortality. The increased dispersal may be due to bolder individuals being natural dispersers, due to higher levels of neophilia causing them to be more willing to settle in a novel environment (Stamps and Swaisgood, 2007). Neophilia may also explain why bold mice tended to move around more at the release site seen here through higher mean interfix intervals. Mean interfix distances increased over time at all release groups suggesting that neophobia had at least some part to play in initial reaction to the release environment. However this greater level of movement and dispersal may be traded off with and cause high mortality rates (Bremner-Harrison, Prodohl and Elwood, 2004). Unfortunately none of the dead mice were able to be recovered to discover the cause of death, a problem found in other release studies (Letty *et al.,* 2002). High activity levels may be caused by high metabolic rate which has been previously linked to high mortality (Biro and Stamps, 2010). This trade off may be reflected in the fact that more active individuals put on less weight after release than less active individuals, potentially due to this higher energy throughput (Careau *et al.,* 2008). Additionally more bold individuals may be more likely to expose themselves to predators, by entering more open areas (as discussed below) providing additional mortality risk, as boldness was negatively related to the probability of freezing in response to potential predation during the novel object test.

Dispersal entails major risks and costs to the disperser (Stamps, Krishnan and Reid, 2005), such as hostile environments and the time and energy required (Cote *et al.,* 2010). Settling in a new patch also runs the risk of poor habitat choice (Edelaar, Siepielski and Clobert, 2008), but some of these costs can be reduced by being specialized for the job either physically or behaviourally (Clobert *et al.,* 2009). Dispersal involves three stages; departure from the current patch, movement between patches, and settling in a new patch (Clobert *et al.,* 2009). Personality has the potential to act independently on each of these three stages (Cote *et al.,* 2010). Introductions remove the first step to some extent by forcing animal into a new environment; which introduces a new challenge through the stress of forced introduction. Initial dispersal may represent the response of the individual to the initial stress of release into a novel environment. Bolder individuals are better able to cope with the novelty of their new environment and better able to compete with other released individuals and resident animals to settle at the new site, whereas shy animals may reject the site and disperse away from it due to competition in the local environment (Cote *et al.,* 2010). The ongoing dispersal in bolder individuals seen after this point may be more due to a willingness to take risks moving between sites (Stamps, Krishnan and Reid, 2005) due to predation, energy expenditure and the probability of not finding a suitable patch.

To confirm if differences in behaviour between sites were not just due to habitat differences, a series of habitat measures were taken and used to create habitat scores reflecting major habitat types. This indicated there were differences in some of the habitat measures between sites which may have affected dispersal and survival. Habitat consisting of low dense oak canopy was higher at the mixed release site, whereas there was less dead wood at the shy release site. Dense oak trees may provide high resource load supporting larger numbers of mice and reducing dispersal at the mixed release site. Dead wood can also be an important part of small mammal habitat (Fauteux *et al.,* 2012), so significantly lower recaptures at the shy release site may indicate poor habitat quality. However, Stamps and Swaisgood (2007) suggest that population density is a poor estimator of habitat quality and instead it may reflect the preferred density of those individuals who live there. This would be consistent with the low sociability of shy individuals preferring low densities. Due to logistical constraints it was not possible to survey the habitat before release except for ensuring a similarity of major habitat variables. Ideally to confirm that behavioural patterns were not due to habitat the study would be repeated using different release locations. However release group was not significant for the majority of analyses when included as a covariate suggesting that the majority of behaviour was affected by individual personality score not release group location.

The model looking at how individuals used habitat also revealed some interesting patterns. The use of open ground under oaks gradually increased over time suggesting that this was an environment initially avoided by all individuals but was more used once individuals became settled. Data also showed that the use of open grassland was related to both activity and boldness which may demonstrate increased risk taking. Habitat use demonstrates a balance between risk and reward (Partridge, 1978) and small mammals tend to avoid open areas, presumably to reduce predation risk (Simonetti, 1989). Studies have shown particularly when under the risk of owl predation, as at Sherwood Forest, wild rodents tend to forage near dense shrubs (Abramsky *et al.,* 1996). More active and bold individuals may be more willing to take risks in order to exploit resources found in these open areas or to avoid long detours around them. This is similar to patterns found by Pearish, Hostert and Bell (2013) where more exploratory stickleback were more likely to be found in open areas. This difference in habitat use may also help explain the low population densities at the shy release site and the higher retention at the mixed site. If few of the individuals at the shy site were willing to enter parts of the habitat this effectively reduces the space available and increases population densities, potentially leading to higher levels of dispersal. Whereas in the mixed release group this dividing up of resources by different niche exploitation may have allowed higher numbers of mice to co-occupy the release site and increase the local carrying capacity.

Sample sizes in this study were not huge; however the relationships between individual personality traits and release behaviour were evident. The data at the group level was more difficult to interpret as there was only one repeat of each group, which may lead to caution in extrapolation of group level effects. Potential group level effects may also be affected by confounds due to habitat as discussed above. Normally it is the juveniles that disperse during the breeding season in wood mice (Jensen, 1996), however here adult mice were used for practical and ethical reasons. Data may therefore not reflect patterns of dispersal in the wild, although it is a reflection of practice common in many translocations. All of the radio collared individuals were male to increase comparability between groups. This means the inferences for females are limited as in wood mice males and females show different patterns of territory holding and dispersal (Harris and Yalden, 2008), however few sex differences in behaviour were identified in other parts of the study.

Some of the effects in this study may have been caused by group mean personality score (Cote *et al.,* 2011). However in most of the models individual behaviour was a better predictor of dispersal/survival than group level predictors. This does not rule out that there may also be a group level effect, but due to the experimental design it was not possible to pull this effect apart from the individual level effect without repeating the study. Overall the data shows that the mixed release group had highest overall retention of individuals and lowest number of mortalities. This is in line with previous suggestions that a mix of individuals makes the best release group. In this study the mixed group was not only an intermediate between the other two groups but showed lower initial dispersion than the other two sites. These effects of reduced mortality and dispersal could potentially be caused by social niche differentiation. It has been suggested that different personalities arise from individuals utilizing the habitat in different ways creating their own niche (Bolnick *et al.,* 2003). In areas with high competition for the same resources even small changes in the use of the environment can reduce competition and potentially agonistic encounters (Trillmich and Hudson, 2011). Supporting this, a model by Michelena *et al.* (2010) showed that mixed groups were better able to exploit environmental resources; Hessing *et al.* (1994) also found that pigs from groups with a mix of personality types had higher weight gain.

A mix of personality types may also increase success when colonizing a new environment. As discussed previously, if shy individuals are less socially tolerant it may explain why they dispersed from high density populations but were successful when densities lowered (Cote *et al.,* 2010). Asocial individuals are usually the first to colonise empty habitats (Cote *et al.,* 2011). However as they prefer low densities this may cause populations to increase slowly, which may reduce the success of a translocation (Cote *et al.,* 2010). Populations with a mix of personality types (asocial and social) can therefore speed up invasion (Cote *et al.,* 2010). The mixed personality group may contain a good mix of those socially tolerant individuals who can maintain population densities and less social individuals who are willing to disperse into a novel area making them ideal for successfully colonizing a new environment (Cote *et al.,* 2010). However, only one replicate of each release group was created in this study which leads to some caution in the interpretation of these findings.

A number of studies have shown that the relationship between behaviour and survival can change both through time and across environments (Dingemanse *et al.,* 2004; Mathot *et al.,* 2012; Sinn *et al.,* 2010). Where one behaviour may improve survival for one species, in one situation or in one particular year this may not be the case in other contexts. Particularly the relationship between boldness and survival may be moderated by the environment. In some situations being bolder, more aggressive and neophilic may actually increase chances of survival in a novel environment (Sinn *et al.,* 2014), potentially if competition is high, resources scarce or survival strongly depends on exploring new environments. Although general rules may be found regarding how certain personality traits affect success these may not always hold. Therefore when no other information is available, releasing a variety of individuals would seem to be the best option, but where possible additional data should be collected about the specific species in question and how they respond to the proposed release environment.

In conclusion this study has successfully shown that behavioural scores measured in a novel object and open field test can to some extent predict the behaviour of mice after release into a novel environment. Shyer individuals tend to show high initial dispersal from a release site, potentially due to low competitive ability, whereas bold individuals show higher levels of ongoing dispersal. This study also showed that bolder individuals tend to be more willing to enter open habitats, potentially indicating higher levels of risk taking. Finally, there is some evidence that changing release group composition based on personality type may have an effect on reintroduction success and when in doubt mixed release groups may provide the greatest success

5.5 Chapter Outcomes

- The novel object tests carried out in the field and after twenty four hours in captivity identified different behaviours, suggesting that even small changes in the state of the animal or testing environment can affect behavioural scores.
- Bolder individuals showed less plasticity in activity behaviour, consistent with a proactive-reactive behavioural syndrome.
- Data indicated two modes of dispersal, first shy/subordinate/asocial individuals dispersing when densities were high followed by a gradual dispersal of bold/dominant/social individuals.
- Bolder individuals tended to use more open habitat, consistent with displaying risk taking behaviour.
- Bolder individuals had higher rates of mortality, potentially due to higher levels of activity either using up energy reserves or through predation.
- The mixed group had the lowest rates of mortality and dispersal possibly suggesting a group level effect, through a mechanism such as niche partitioning. Although due to a single repeat of each group and potential habitat confounds this conclusion is tentative.

This chapter builds on data collected in the previous chapters about the existence and consistency of personality traits in wood mice. Data collected from radio collared individuals agrees with trapping data from Chapter Three about the effects of personality on habitat use. Data also shows that captivity affects personality in the short term as well as the long term as indicated in Chapter Four. This chapter provides further data used to discuss practical recommendations for translocation studies discussed in Chapter Six.

6 Chapter Six: Evaluation of results and practical recommendations for translocation projects

The aim of this study was to assess the practical applications of personality research to translocation procedures using a non-endangered model species. Wood mice were chosen as an easily captured, mammalian species. The large quantity of previous research on rodent species also allowed the application of tried and tested experimental methodology. The first step addressed in Chapter Two was to confirm that wood mice had repeatable personality traits. The methods used were versions of personality tests used commonly in rodents in laboratory environments, but applied using portable equipment in the field, to avoid some of the suggested biases of bringing animals into captivity prior to testing (Niemelae and Dingemanse, 2014). This was repeated across three sites to confirm the consistency of the personality traits identified in this species. Additional areas examined were individual plasticity and habituation rates as these can affect the calculation of behavioural scores if not considered (Dingemanse *et al.,* 2010). Other potential causes of bias such as trapping success and environment-behaviour correlations were assessed in Chapter Three, to ensure that the traits measured were accurate and not confounded by other effects. Chapter Three also aimed to highlight some practical considerations need to be taken into account to effectively carry out this kind of trapping and testing procedure in other species. To relate the data practically to translocation procedures the interaction between captivity and personality was investigated, both in the long term in Chapter Four and the short term in Chapter Five. During translocations animals necessarily need to be kept in captivity for at least a short duration during transport but potentially for generations as in captive breeding programmes. Therefore a captive bred population of wood mice was assessed in Chapter Four to ensure personality traits are maintained in captivity and are not just caused by rearing environment. This also allowed the identification of potential selection pressures on personality scores in captivity. In Chapter Five the short term effect of captivity on personality scores was assessed and some concerns were identified suggesting studies may need to be careful of when and where animals are behaviourally tested, as the testing situation may cause changes in behaviour or assess entirely different traits. Finally in Chapter Five, the effect of individual personality traits and group composition of personality traits on reintroduction success was assessed using a simulated release, focusing on short term success through dispersal and mortality rates. In all, this study has produced some recommendations regarding translocation practice and identified some concerns and pitfalls when measuring personality which need to be considered if personality scores can be practically utilised to increase translocation success.

This chapter begins by discussing the methods used here to measure behaviour, identifying any possible confounding factors and how these may be avoided. Next it outlines the methods used to define the behaviours measured and goes on to attempt to validate these definitions by discussing additional correlates with these behaviours. Only once this has been done is it possible to discuss patterns in the behaviour, through behavioural syndromes, behavioural plasticity and the heritability of behaviour. Finally, the chapter discusses the practical effects of these personality traits through trap and habitat use and how this affects behaviour during a translocation. To conclude it discusses how these results may be practically applied and future directions of the research.

6.1 Identifying personality traits

The initial step for any study aiming to apply personality research to a population is to confirm that the study species display consistent behaviours that meet the criteria for being considered personality traits. To do this consideration needs to be taken over the methods used to measure behaviour, the potential confounds affecting behavioural scores, and to validating those behaviours to confirm which personality traits the recorded scores reflect. This validation is also required so results can be compared and contrasted with the wider personality literature.

6.1.1 Measuring behaviour

The initial step of the project was to confirm the existence of personality traits in wood mice to ensure they could be used as a suitable model species. This study used a simple version of the open field and novel object tests. These tests are well used and relatively robust when used on laboratory animals in a controlled setting (Hall, 1941). However this level of control was not possible during this study as one of the key aims was to utilise animals in the wild, to avoid undue stress and the potential biases caused by transporting animals into captivity (Archard and Braithwaite, 2010). Using a field adapted testing method, Chapter Two showed that mice displayed repeatable behaviour in both the novel object and open field tests at all three sites studied. The behaviours displayed were not affected by external conditions such as temperature, humidity and time of day and where potential sources of bias were identified, they were controlled for statistically.

There are a number of different designs of open field and novel object tests used in previous studies. One of the main considerations is whether the animals are forcibly placed into the arena, or allowed to emerge from a refuge; this refuge can then be left in the arena as a retreat during the test or blocked off after the animal emerges. The decision was made in this study to place the animal directly into the arena on mostly practical grounds. To repeatedly test a large number of individuals this provided more viable data as emergence times from a refuge can be long (>5mins). This potentially means that behaviours displayed may represent more of a stress response from being forcibly placed in a novel arena, rather than exploratory behaviours (Carter *et al.,* 2013). However, this was taken into account during interpretation and neither trait was considered as voluntary exploration.

As recommended by a number of recent personality studies (e.g. Dingemanse *et al.,* 2010), potential plasticity of behaviour through habituation to the testing environment was taken into account. This study made the decision to deal with habituation statistically rather than by varying the arena and/or novel object between tests. This was done because simple habituation through repeated exposure could be relatively easily quantified, whereas introducing new objects each test introduces numerous sources of stimulation and variation such as different colours, shapes or smells. These different features of an object can affect how quickly and how long it is explored for (Mettke-Hofmann *et al.,* 2006) and individuals may respond differently to each of these different stimuli, thus introducing numerous sources of noise to the data (Mettke-Hofmann *et al.,* 2006). The added benefit of controlling for habituation in this way is that it made testing animals in the field significantly more logistically viable, as numerous different objects did not need to be transported to the field and a record of which stimuli each individual had previously been exposed to did not need to be kept.

Other environmental variables during testing, such as the location of the testing arena e.g. under trees or in the open, did differ between trapping grids and were not controlled for. However, previous studies suggest this does not affect behaviour during these kinds of standardised tests (Martin and Reale, 2008). This suggests that subjects are responding to the local environment of the testing arena, rather than the external environment. Any bias that may have been caused by testing location should only have been between trapping sites as testing locations were kept largely standardised within each trapping site; therefore trapping site was controlled for statistically when possible. This lends reasonable confidence that the behaviours seen in the tests was a response to the test stimuli and patterns and significances seen were not an artefact of any external factors.

One factor which was not taken into account during testing and analysis was potential non-linear changes in behaviour over repeated testing. This was not done due to the difficulties of modelling potential individual differences in non-linear patterns of behavioural change. However it is plausible that patterns of behaviour would not be linear. Habituation to the tests as used involved two factors, first a fear response or neophobia, which may have initially reduced activity or boldness scores and second experience, which may also reduce activity and boldness as novelty wears off. The interaction between these two patterns of behaviour may induce an initial increase in boldness and activity as fear and neophobia wear off, but once the object and arena have been fully explored a later reduction in activity and neophobia from habitation may occur. The timescale of this interaction could change within a single session or between tests and this pattern could differ between individuals creating a complex pattern, which would be difficult to model and interpret. However, future studies may benefit by designing methods which can accurately identify non-linear changes in behaviour, as potentially this pattern could differ between individuals.

In this study separate oblique factor analyses were run for variables recorded in the novel object and the open field tests. This is slightly different to some previous studies using similar techniques which have either combined data from multiple tests and ran one factor analysis or used an orthogonal rotation method. It was decided to run separate factor analyses so the results of each personality test could be considered under their own merit. As the aim of the project was to look at the applicability of personality testing in practical translocation projects, running separate analyses allowed the identification of which test would give a better indicator of relevant personality traits. Second, some studies have used an orthogonal rotation method; this method prevents multiple identified factors from being correlated, creating clear unambiguous independent personality scores. However, this method presupposes the possibility of finding multiple correlated factors which may be separate traits but part of a higher order character or behavioural syndrome. Despite this, in the majority of analyses in this study only one factor was extracted so different rotation methods would have produced identical results.

6.1.2 Defining Behaviour

Once behavioural tests have been ran and all confounding variables have been accounted for, the next step is to score and define the behavioural scores recorded. This may depend on the testing methods used, but is inherently subjective to a degree. However, this subjectivity can be mitigated by clearly identifying what behaviours each trait represents.

The behaviours measured here can be generally described as a reaction to a novel arena for the open field test and a novel object in the novel object test. However it is important to identify what stimuli the mice are responding to and how this relates to the natural behaviour of the mice in the wild. The tests were designed to provoke and identify activity and boldness behaviours, following definitions used in previous studies, where the response to a novel object was described as boldness (e.g. Bremner-Harrison, Prodohl and Elwood, 2004) and the response to the open field as activity (e.g. Boon, Reale and Boutin, 2008).

The factor identified in the open field test was identified consistently across the chapters by a strong factor loading of the number of squares the mouse crossed, an obvious indicator of activity and one used in many previous studies (Montiglio *et al.,* 2010). A short latency to enter the centre squares and amount of time spent within the centre of the arena also often loaded strongly on the activity factor. Rodents generally avoid the centre of an open arena, which has been linked to a higher predatory risk and a lack of shelter (Eilam, 2003). Some previous studies have therefore defined entering the centre of an arena as a measure of boldness and it is possible there may have been elements of that here as activity and boldness were usually correlated. However, entering the centre of the arena may just be an artefact of the high movement of more active individuals causing them to enter the centre of the arena as they crossed it more regularly. Due to the small size of the arena used here and the fact the arena was usually covered by an umbrella to prevent glare on the camera, it is unlikely that the centre was perceived as significantly more dangerous than the outside edge, making entering the centre a not particularly risky behaviour.

Boldness was defined by a willingness to approach a novel object, a behaviour which on numerous occasions has been defined as risk-taking and bold (e.g. Bremner-Harrison, Prodohl and Elwood, 2004; Carere and van Oers, 2004; Frost *et al.,* 2007). Exploration of a novel object represents information gathering about the animals environment, but is often traded off with costs through time and energy expenditure and potential hidden risks such as predation (Mettke-Hofmann *et al.,* 2006). Boldness was defined not only by a short latency to approach the object but also time spent near the object, which suggests that the behavioural score is not just an artefact of increased movement from activity as the object was placed in one corner of the arena to prevent accidental approaches. Mice were also seen qualitatively to actively sniff touch and explore the object when they approached, suggesting approaches were intentional. Boldness behaviour was identified as risk taking and not just neophilia as bolder mice also tended to freeze for less time when the object was placed into the arena. Freezing is an antipredator response (Smith, 1991), typified by the animal remaining immobile with the aim of avoiding detection by a predator (Eilam, 2005), and was likely provoked in response to the disturbance caused by the experimenter opening the lid and placing the object into the arena. Freezing in this situation when the ‘predator’ is in such close quarters would not seem to be an adaptive strategy as it is only a viable strategy if the prey has not been spotted by the predator (Eilam, 2005) and so may indicate a strong reactive or shy response, potentially creating a maladaptive behavioural carryover in this situation.

This study measured the duration of the repeatability of behavioural scores, a feature lacking in many studies of personality. The implications of repeatability over hours, days or years may be very different. When applying personality research in a translocation, confirming that personality traits are consistent over periods of time relevant to the project may be key. Measuring personality traits over a few short days may not be representative of behaviour if animals are not released for week or months later. Even when animals are released after only a short period of time in captivity, managers may want to be able to predict individual behavioural responses weeks or months after release. This is only possible if personality traits are known to be consistent over this period of time. Therefore confirming personality traits are consistent over time periods appropriate to the study and study species should be a first step in applying personality research to translocation projects.

6.1.3 Validating Behaviour

Studies such as Trillmich and Hudson (2011) have encouraged the distinction between behavioural profiles as those behavioural scores measured in a personality test, and personality traits as the unseen underlying cause of behaviour. To confirm the definition of the behavioural scores measured here as boldness and activity further testing was required

(Trillmich and Hudson, 2011), to establish their convergent validity through correlations with other behaviours considered to represent activity and boldness (Carter *et al.,* 2013). Evidence for the clarification of the definition of each behavioural score as a personality trait came from each of the chapters. Chapter Two looked at correlates with each of the behaviours in the attempt to provide some validity of the traits as described. Activity and boldness both increased during the breeding season. This is consistent with what would be expected from wood mice in the wild as dispersal increases over this period which may increase activity, competition is also high which would be expected to lead to increased levels of aggression and boldness (Montgomery, 1978; Lodewijckx, 1984b). General activity may also be lower in the winter due to limited resources and energy reserves (Lodewijckx, 1984b). Activity was higher in males than females, which would also be expected as males tend to hold larger territories and move around more than females (Harris and Yalden, 2008) as was seen by the larger number of trapping locations for males in Chapter Three.

In Chapter Three boldness but not activity was linked with urine spread within the testing arena. Urine spread in captive mice is an indicator of dominance; boldness has been frequently linked with aggression and dominance in a number of studies (Dahlbom *et al.,* 2011; Norton and Bally-Cuif, 2012). Risk taking in habitat use was also seen in the fifth chapter when bolder individuals were more likely to enter open spaces; a behaviour previously linked with boldness and increased risk of predation (Simonetti, 1989). This may have led to their increased rate of mortality also seen in Chapter Five.

Mice in captivity in Chapter Three that were in cages with a higher density tended to be more activity, suggesting that activity may develop in higher density populations. In Chapter Five higher initial dispersal and generally lower densities were seen in the shy release group consistent with evidence that shyer individuals tend to be more asocial, as found in a previous study of small mammals (Myers and Krebs, 1971).

Evidence for the validity of activity measured in the open field test came from Chapter Five which showed that more active individuals had higher interfix distances once released into the wild, similar to Bremner-Harrison, Prodohl and Elwood (2004). The handling bag test also suggested that activity was negatively related to docility (Reale *et al.,* 2000). This was supported by results in Chapter Four which showed that activity scores were greater in wild populations than captive, which may be due to increased tameness and docility in captivity, either as a learnt or inherited trait.

Validating personality traits measured in standardized behavioural tests is important to confirming these traits reflect behaviour in the wild. For translocation studies there would be little value in measuring a trait which purely reflects behaviour in captivity and has no bearing on how individuals respond to natural stimuli. Measuring personality traits using multiple methods may be a good way to validate behaviours in animals destined for translocation. When behaviour in the wild is not directly observable, carrying out ethograms of behaviour alongside standardized tests, to confirm that behaviours that are expected to be correlated the measured personality traits are, which should give a good indication of behavioural responses in the wild.

6.1.4 Are activity and boldness scores part of the same trait?

Although there is some debate about whether a novel object and open field test actually measure the same behaviour (Fox *et al.,* 2009). The differing associated traits and behaviours discussed above, suggests they are different personality traits. However both traits were repeatedly correlated across the populations measured in Chapter Two. This suggests that the two traits may be either expressions of a higher order behavioural character (Araya-Ajoy and Dingemanse, 2014) or reflections of a behavioural syndrome (Sih, Bell and Johnson, 2004).

Activity and boldness were both correlated with the amount of urination events during the test, in addition boldness was related to the number of faecal boli left after the test. Both amount of urination and defection have been linked to activation of the sympathetic nervous system and a proactive behavioural response (Carere, Caramaschi and Fawcett, 2010; Hessing *et al.,* 1994). Furthermore, activity was negatively related to the score from the handling bag test, previously been suggested as a good measure of reactivity (Careau *et al.,* 2008). These correlates, with the addition of the fact that activity and boldness were correlated, suggests that these personaltiy traits may be part of a proactive-reactive behavioural syndrome, similar to that discussed in the coping styles literature. When faced with a stressor proactive individuals will explore, interact or manipulate events, whereas reactive individuals will withdraw, hide or freeze (Koolhaas *et al.,* 1999).

Many studies have discussed the existence of key axes of behaviour, which different personality traits may tie into. These have been discussed as behavioural syndromes (Dingemanse, Dochtermann and Nakagawa, 2012), coping styles (Coppens, de Boer and Koolhaas, 2010) or fast/slow exploration strategies (Careau *et al.,* 2009). If these higher order behavioural patterns exist and are consistent across species it may allow the possibility of developing simple tests which give a good indication of where individual animals fall along this continuum. Although there may be variation in how strongly they display individual traits in specific scenarios, this may provide an excellent short cut for studies wanting a fast but informative indicator of behaviour. Very simple tests have been shown to give an accurate indicator of heritable personality traits (e.g. Hansen, 1996). This may be what is required for translocation practice where potentially funds, time and scientific expertise are limited. Data here demonstrate that scores in an open field and novel object are strongly correlated, which suggests that carrying out only one of these tests, potentially whichever is a better indicator of responses to a novel environment (discussed below) is required. In practical projects there may be a trade-off between the time and effort required and the amount of extra information it provides. Therefore identifying a single relatively simple test that gives a reasonable indication of reintroduction response may be ideal.

However, the correlation between activity and boldness was not found in the captive bred and reared mouse population in Chapter Three. Sample sizes from the captive population were fairly small which could lead to type II error. Alternatively, the selection pressure produced by the breeding program used at FERA could have broken the link between activity and boldness. Trait correlations can be shaped by natural selection (Sih, Bell and Johnson, 2004). Selective breeding in captivity can break these functional links leading to non-adaptive trait combinations (McDougall *et al.,* 2006). Data from Chapter Three suggested that activity was being selected against in captivity as rates of activity were significantly lower than in the wild populations. This selection could have been caused by more active individuals coping less well in captivity. Boldness however, was not significantly different in the wild populations from those in captivity suggesting a decoupling of the two traits. Several models have been produced to explain how the correlations between different traits may become decoupled (Trillmich and Hudson, 2011). Although without further knowledge of why the traits were linked in the wild, either physiologically or because of some selective advantage, it is difficult to interpret why they were not linked in captivity.

If this decoupling of these two traits is a real effect it may be a concern to translocation projects. Previous studies suggest that personality traits may be correlated because they provide a selective advantage (Dingemanse *et al.,* 2007), potentially through providing alternative tactics (Dingemanse *et al.,* 2007). Changing these correlations may therefore have severe implications for the success of captive reared individuals released into the wild. It may also cause problems when attempting to apply simple tests as discussed above if the behaviour measured is no longer correlated with the personality trait of interest. Managers of captive breeding facilities of animals destined for release should therefore keep a close eye on the effect captive breeding is having on key behavioural traits, in mean level, variation and correlations between traits.

6.2 Avoiding Biases

6.2.1 Individual behavioural plasticity and habituation

Using consistent stimuli between tests allowed a measure of individual habituation rate to be taken, which can be considered a type of behavioural plasticity (Martin and Reale, 2008). Taking account of between test variation in responses in personality studies is important to avoid potential biases (Sih *et al.,* 2004) particularly if individuals are tested a variable number of times.

This study found no individual differences in habituation response to repeated testing in the same environment in the wild, although it did find consistent habituation rates to both tests in most situations. This would suggest that in future a single test of behaviour could be used to give a good indicator of personality type as all individuals changed their behaviour in a similar manner between tests. When practically utilizing personality tests, ensuring that individuals show similar patterns over repeated tests would allow confidence that in future a quick and simple test could reliably give an indicator of behaviour, without requiring repeated testing. If individual differences in plasticity are identified then this may need to be taken into account when investigating what affect this has on post release success.

Data from Chapter Two did suggest possible differences in habituation between populations. Between population differences in habituation but not personality are possible if habituation rate is a separate character under selection (Martin and Reale, 2008). Data suggested that individuals at Silwood Park showed lower levels of habituation to the novel object test than at the other two sites. However, the majority of data at Silwood was collected by a different experimenter using slightly different methods which may have skewed results. Experimenter and the experimenter by test number interaction were included as a covariate to control for this potential confounding effect in statistical analyses. Unfortunately this may have had the adverse effect of removing the significance of any actual effect of population differences as a between experimenter effect. However, any potential differences between sites may also have just been an artefact of differing methodology. The methods used to trap, handle and test mice at Silwood differed in a number of ways from those used at Brackenhurst and Sherwood (discussed in Chapter Two). It is therefore not possible to rule out the possibility that all differences in behaviour at this site were due to these differences in methodology. Mice at Silwood were generally kept for longer in traps before processing, although they were kept at thermo-neutrality for this time, and were handled for longer as a number of additional measures were taken. Mice here were also PIT tagged, which could have caused additional stress. Taken together these effects may have caused the trapping and handling process to be a more stressful experience, reinforcing a greater fear response in the test situation and preventing habituation. Therefore no definite conclusions could be drawn about differences in personality or behavioural plasticity scores between sites. Few studies have measured between population differences in personality and plasticity and so this may warrant further investigation.

6.2.2 Trapping bias

The third chapter investigated the potential effects of personality type on trap bias, which provides some practical suggestions and warnings for future studies, even those not specifically looking at personality traits. This study found that personality affected when and where different individuals were trapped. Namely, that bolder individuals took longer to enter traps and more active individuals were less likely to be recaptured. This has strong implications for studies of personality, but also many other areas where animals are regularly trapped for study or for conservation reasons. In a personality study, only trapping a subset of the population will give a biased view of the effects of personality as the subset of individuals trapped will not be a true representation of the wild population. This could potentially underestimate the effect of personality traits and will reduce the power of analyses. For other animal studies utilising wild caught animals, trap bias could cause more serious problems. Personality has been linked to many features of an animal's life history, physiology and behaviour including size, weight, gender, metabolism, reproductive success (Sih, Bell and Johnson, 2004; Careau *et al.,* 2008; Stamps, 2007; Wolf *et al.,* 2007; Biro and Stamps, 2008; Reale *et al.,* 2010). Therefore any bias in the personality subset trapped will also cause bias in the representation of these factors in the captured sample, affecting the assumptions and conclusions made by these studies.

Of particular relevance to this study, trap bias could also cause problems during translocations. Animals are often trapped prior to transport, either to be taken into captivity or to be released at another location to bolster populations. As expressed previously, having a range of personality types is important for the success of a population (Watters and Meehan, 2007), if a particular subset of the population is not trapped initially this is reducing the probability of success from the outset. This may also mean that a subset of the population that may differ physiologically, behaviourally or genetically from the whole population may be trapped. This may lead to the creation of a founder population which is not behaviourally or physiologically representative of the initial source population, which could have implications for future conservation.

These problems may be difficult to overcome. This study has shown that the effect of personality on trappability may not be the same between species. For example other studies have found that bolder or more active individuals were caught quicker or more often (Carter *et al.,* 2012; Boon, Reale and Boutin, 2008), but that was not the same pattern as seen here. This makes estimating what proportion of the population has been trapped difficult. However as shown here, trapping for a reasonable period of time and under different conditions and habitats can improve the likelihood of trapping the full range of personality types. Utilising different forms of trapping may also assist in this, as active trapping methods may target a different proportion of the population than passive methods (Biro and Dingemanse, 2009a).

6.2.3 Personality type by environment correlations

This study has provided some empirical evidence for a personality type by environment correlation in wood mice (Pearish, Hostert and Bell, 2013). Little empirical evidence has previously been collected on individuals with different personality types using habitat differently, particularly at the microhabitat level (but see Wilson *et al.,* 1993; Pearish, Hostert and Bell, 2013), despite a general assumption in the personality literature that this should be the case (Reale *et al.,* 2007). This study demonstrated in Chapter Three that where individuals of different personality types were trapped depended on not only habitat conditions in the trap vicinity but also environmental conditions at time of trapping. In other populations it has been proposed that behaviour by environment correlations may occur when developmental habitats affect behaviour (Bell *et al.,* 2011). However, it seems probable that the cause and effect in this situation was individuals with different personality types choosing to select different habitats, as there were a wide variety of microhabitat conditions to select from within each individuals home range. This conclusion was backed up by the radio tracking data collected in Chapter Five, which showed that bolder and more active individuals were more willing to use open habitats, even when initially released in the same location. This may demonstrate differences in risk taking as wild rodents usually prefer to forage near cover, particularly under the risk of predation (Abramsky *et al.,* 1996).

Personality type by environment interactions may cause trapping bias if trapping is not carried out in the full range of habitat conditions used by the target populations. Serious consideration should be given to the trapping method used for particular species and how they could potentially interact with personality type to create bias. Collecting personality data on animals in the wild and comparing this distribution to the population in captivity may help to identify biases caused in a particular study using a particular method.

6.3 The effect of captivity on personality traits

All translocation studies require taking animals into captivity for either the long term for captive breeding, or the short term for transport and quarantine etc. This study attempted to identify some of the problems that captivity can cause when applying personality traits to translocation studies.

6.3.1 Long Term Captivity

Data in the third chapter taken from the mice in captivity at FERA implied that personality traits are heritable in wood mice. This is consistent with previous studies measuring the heritability of personality traits in other species (van Oers *et al.,* 2005). Despite fairly limited data, parentage was a good predictor of boldness, although not activity. However this study only measured narrow sense heritability looking at the correlations between individuals with the same parentage, it also did not take into account potential confounding variables such as maternal effects or rearing environment. Prenatal maternal effects and gene-environment interactions can artificially inflate measures of heritability (Trillmich and Hudson, 2011), through factors such as epigenetics or gene induced environment selection (Trillmich and Hudson, 2011). Heritability rates of personality traits may therefore be lower in more diverse natural environments (van Oers *et al.,* 2005).

Despite this, data suggested there was selection against activity in captivity, a pattern seen in other captive bred populations (Mason *et al.,* 2013), but not against boldness. This highlights an important practical point regarding personalities and captivity. Husbandry methods in captivity often inadvertently select for certain personality types (McDougall *et al.,* 2006). Usually those more suited to life in captivity, such as those more tame and docile individuals (Snyder *et al.,* 1996). This is often, as is likely in the population at FERA, due to selective breeding. In these breeding schemes animals are selected as breeding pairs using parentage data and stud books to retain genetic diversity in the population. However if individuals fail to breed they are paired with different individuals with the aim of improving breeding success. Unfortunately this type of scheme inevitably leads to selection for individuals more likely to breed in captivity (van Heezik and Seddon, 2001), again often those more tame and docile individuals (de Boer, van der Vegt and Koolhaas, 2003; Kunzl *et al.,* 2003). This was seen here with individuals bred in captivity having higher docility (through a lower handling score) and lower activity levels.

This can be a problem when aiming to reintroduce a population to the wild as it reduces the behavioural diversity of the released population and therefore the flexibility of that population on release in response to different factors (Watters and Meehan, 2007). However having captive bred individuals which thrive in captivity yet show the same behavioural compositions as wild populations may be an impossible combination (Mason *et al.,* 2013). Even when closely managing breeding through studbooks, personality and particularly individual response to stress may interfere with pregnancies or offspring survival (Zhang, Swaisgood and Zhang, 2004). By identifying individuals which respond to certain types of stressor it may be possible to manage their effects in susceptible individuals.

Suitable enrichment in captive populations may be one important way of reducing stress across the population and therefore maintaining variation in personality types (McDougall *et al.,* 2006).

6.3.2 Short Term Captivity

In the short term, although behavioural changes may be reversible, captivity may cause problems in accurately measuring personality traits. In Chapter Five the same individuals were tested in the field and retested after 24 hours in captivity. This is rarely done in personality studies despite the fact that previous studies have suggested that the length of time spent in captivity can affect stress levels (Teixeira *et al.,* 2007) and therefore behaviour (Butlers *et al.,* 2006). In this study significant individual differences in behavioural plasticity in activity scores between the two situations were identified. As suggested previously, the majority of this difference in behaviour was likely to have been due to the animals' response to being taken into captivity rather than differences in testing apparatus or procedure. The majority of individuals reduced their activity between being tested in the field and after a day in the lab, which may be due to the mice treating the lab as a higher risk situation due to being restrained, experimenter presence and other factors. However, there was some individual variability in how much they reduced this behaviour, which could be largely predicted by the individuals' level of boldness in the field. Bolder individuals reduced their activity less than shyer individuals when tested in captivity. This suggests that either bolder individuals were unable to adjust their behaviour as much due to being more inflexible and routine (Koolhaas *et al.,* 1999), or alternatively may have been less affected by the stress of captivity and so retained similar levels of behaviour to that in the wild. However, boldness scores in captivity were not related to boldness scores in the field and these changes in behaviour in the novel object test were not predictable. This suggests that boldness in the field and boldness in the lab were context specific and may reflect entirely personality behavioural traits (Coleman and Wilson, 1998). This difference could potentially be interpreted as investigating novelty in a low risk environment and investigating novelty in a high risk environment, which can provoke different behavioural responses (Bell and Sih, 2007).

As a practical recommendation this leads to caution in the interpretation of behavioural responses from behavioural tests carried out in differing environments. For example numerous studies have discussed the difference between encountering a novel object in the home environment and encountering a novel object in a novel environment (Reale *et al.,* 2007). Understanding which behaviour is expected to be correlated to the response to being released into a novel habitat is not currently clear. In this study bold behaviour in the field gave a better indicator of dispersal and mortality rates after release, but boldness in the lab gave a better indicator of habitat use. Initial behaviour upon release may be interpreted as the response to novelty within a high risk novel environment, similar to testing boldness shortly after captivity. After a certain time post release the environment will be less novel but individuals may still encounter novel food, conspecifics and predators, so testing boldness in a familiar environment may give a better indicator of these later responses. The majority of unwanted dispersal and mortality in reintroduction studies happens shortly after release (Armstrong and Seddon, 2008) and so testing animals in a novel environment and with novel objects/foods may give the best indicator of behaviour in these situations, despite potentially being more difficult to interpret due to multiple stimuli affecting behaviour. This may also indicate that pre-release training carried out in a familiar environment may provoke different responses than if it were carried out in an unfamiliar environment.

6.4 Applying personality traits to translocation success

The key aim of this study was to use a model system to investigate how previously identified personality traits affect the behaviour of individuals after being introduced to a novel environment, with the aim that these may be manipulated to improve the success of translocation projects in the future. Managers have previously tried to prepare animals for release through ‘pre-release training’ used with the aim of changing animals behaviour to meet a pre conceived target trait range (McPhee and Silverman, 2004). This trait range is intended to give the release animals the best probability of success in certain behaviours. However in real wild environments there are many different situations for which an animal needs to respond adequately, and in each of these situations there is rarely one optimum way of behaving in any given circumstance (Watters and Meehan, 2007). Often because of limited behavioural plasticity some animals may excel in one situation but do poorly in another. Therefore it has been suggested that manipulating personality types may be a key avenue to improve reintroduction success (Watters and Meehan, 2007), and some evidence has previously been collected through real reintroduction projects to support this (Bremner-Harrison, Prodohl and Elwood, 2004; Sinn *et al.,* 2014). This study therefore used a model system to attempt to confirm some of the patterns seen previously and in addition manipulate release group composition to examine its effect on release success (discussed below).

Reintroductions have three main aims; survival of animals after release, settlement of animals in the release area and successful reproduction in the release area (Teixeira *et al.,* 2007). This study focused on the more short term indicators of reintroduction success through dispersal and survival rates. Clear patterns were seen at the individual level which support results shown in previous projects about the trade-offs in personality and fitness and also how individuals behave in a reintroduction. More bold and active individuals (more proactive) tended to initially settle close to the release point. This study suggests this may be because they coped better with the stress of being released into a novel environment or were better able to compete with both resident mice already in the environment and other mice released simultaneously. After this initial period however, more proactive individuals had a greater tendency to leave the release area. This loss was likely both through higher rates of mortality, brought on by risk taking and higher movement rates provoking predation and potential exhaustion, but may also have been caused by increased dispersal, although these two mechanisms are difficult to separate from trapping data. The shyer, less active (more reactive) individuals on the other hand dispersed quickly after release (suggested by lower recapture numbers) and tended to disperse further (indicated by radiotracking fixes). This study suggests this may be because more reactive individuals tend to be less aggressive, dominant and competitive and may have been forced out of the immediate release area (as in the social subordination hypothesis; Christian, 1970). There is also some evidence that these individuals tend to be more asocial and prefer lower densities, therefore may have been moving away from the high initial population densities (Myers and Krebs, 1971). After this initial emigration, more reactive individuals tended to have lower mortality rates. This demonstrates a trade-off now frequently found in personality studies. Bolder individuals may be more dominant allowing them to claim better territory and potentially better mating opportunities (Duckworth and Badyaev, 2007a), particularly as male wood mouse territories cover multiple female ranges (Harris and Yalden, 2008). Bolder individuals are also often more willing to explore novel environments allowing them to exploit novel food sources and take risks (Boon, Reale and Boutin, 2008), demonstrated here by their willingness to forage in the open (Chapter Five) and in bright moonlight (Chapter Three), increasing their resource gathering ability. However this risk taking comes at a cost of increased rates of mortality (Watters and Meehan, 2007). Unfortunately the cause of death was not able to be discovered in this study as corpses were not recovered, but here is suggested to be due to predation due to risk taking (entering open area) and ranging behaviour (greater interfix distance) or due to energy expenditure from the greater activity patterns (indicated by lower weight gain after release).

These trade-offs would agree with the suggestions made by Watters, Lema and Nevitt (2003) that ensuring a mix of individuals would give a balance of different strategies and potentially improve success at the population level. If little is known about the effects of the release habitat on individuals, then releasing a mix of personality types would ensure that at least some individuals would thrive in all environments. Potentially releasing a mix of individuals also allows increased colonisation and invasion success. Previous studies suggest a mix of more social (here bold) and asocial (here shy) increases colonization success (Cote *et al.,* 2010). However this again highlights the problems of using captive bred populations such as those measured in Chapter Three. These individuals had much lower rates of activity, but similar rates of boldness to wild populations. It is therefore unclear how this would affect the trade-offs seen as this correlation had been decoupled. Previous studies have also shown that particularly when animals are raised in a captive environment there is less heterogeneity and so less opportunities for niche differentiation and the development of different personality types (Stamps and Groothuis, 2010).

Some of the results here differ from those found by Bremner-Harrison *et al.* (2004, 2013) when observing fox behaviour after release, upon which this study was initially based. These studies on three species of fox found that across all species bolder individuals travelled further and had higher rates of mortality, as was seen here in mice, but showed no evidence of the high initial dispersal seen in the shy mouse group. This difference is likely due to differences in release procedure, as here individuals were released relatively close to one another and in an area already containing resident mice. As discussed earlier this dispersal likely resulted from these individuals dispersing away from this initial high density population. In the studies by Bremner-Harrison *et al.* release sites were chosen to avoid competition between individuals, which may have avoided this inflated dispersal. There may also have been species differences, but how general or species specific these patterns in behaviour after release are is difficult to assess at this point. Previous studies have found consistent correlates with personality between a wide range of species in other situations (Smith and Blumstein, 2008).

The third aim of reintroductions was not assessed here, namely how reproductive success after release relates to personality type. This was due to restrictions on the project i.e. radio collars of a suitable weight only lasted 30 days and the study species chosen mainly reproduces during the spring/early summer. The probability of recapturing the relatively small number of wood mice which were released towards the end of the breeding season during the next breeding season was slim. There was also not scope to include genetic analysis within the confines of the project. Practically this would also require a much larger scale project to ensure the recapture of related individuals. Although this is an important point of reintroductions, this study was focused on initial response to release and success in the short term. Presumably by the time animals are ready to mate within a release environment it is not considered novel and so potentially patterns of personality and breeding success would be the same as shown in previous studies of wild living animals, as long as the release population has a representative range of personality types.

Following on from the discussion by Cote *et al.* (2010) of different stages of the invasion process, the data collected here would concur with their conclusions. Bolder, more active individuals seemed more willing to leave a site and travel between locations and more shyer asocial individuals more likely to leave a location when population densities were high. This study did not necessarily model these different stages as discrete steps as animals tended to move and settle fairly rapidly, but had data been collected on a more fine scale and in greater quantities, particularly with more location fixes taken from individuals, it may potentially have been possible to identify different stages of departing, travelling and settling. With the decreasing cost and weight of GPS collars, future studies may be able to use this technology to obtain detailed information of post release movements which could significantly contribute to knowledge of post release behaviour.

As a practical recommendation to translocation studies, activity scores potentially gave a better indicator of behaviour after release than boldness scores. Translocation projects may therefore benefit from monitoring activity in a simulated open field test, defined as an individual's response to being in a novel environment, which could potentially be an empty cage for larger species or a dedicated arena for smaller species. If this is not possible then taking a subjective handling score during routine handling would provide some information on the variety of personality scores within a population. Here activity was relatively reliably estimated using a simple handling test which could be easily adapted for use with most species. This study suggests these simple measures could reasonably predict how animals will respond, with more active individuals ranging further, having greater mortality rates and potentially being less likely to disperse immediately after release but more likely disperse once settled in a release site.

6.4.1 Group Composition

Another key aim of this study was to examine if group composition had any effect on individual and group survival in a reintroduction. A single individual is usually not able to express the full range of behaviours exhibited by the population (Watters and Meehan, 2007), therefore variation in personality traits within populations naturally exist in the wild (Dingemanse *et al.,* 2004; Reale *et al.,* 2000). It is unlikely that this consistent variation is due to chance alone and may have important fitness consequences (McDougall *et al.,* 2006). Populations composed of multiple personality types are likely to be more resilient to varied selection pressures than those only containing one or a limited number of personality types (Watters and Meehan, 2007). Previous studies have therefore suggested that releasing a mix of personality types into a novel environment may provide the greatest probability of success (Watters and Meehan, 2007).

This study represents one of the first empirical tests of this theory. By working with a non-endangered species it was possible to manipulate release group composition based on personality scores to observe what effect this had on dispersal and mortality in the critical period shortly after release. The results found were complex and difficult to interpret, but do show support for the suggestion by previous studies that releasing a mix of individuals may increase survival and reduce competition, lowering both dispersal rates from the release site and mortality.

Due to setbacks and restrictions during the project answering this question was only achieved to a limited extent, as only one repeat of each release group composition was possible. However even with this limited data there were some suggestions that group composition had an impact. The release group containing all shy individuals initially showed an inflated level of dispersal that was not explained by individual personality score, but could have been due to the high composition of shy individuals in the group. Shy individuals tend to be more asocial (Myers and Krebs, 1971) and potentially this high concentration of asocial individuals may have caused excessive dispersal. Second, the mixed release group showed the lowest rates of mortality in the radio tracked individuals as none of the 5 radio collared individuals in this group died. Although these sample sizes are small and therefore may be strongly affected by stochastic elements, this may still represent a group effect. When incorporating the trapping data the mixed group also had the lowest rate of losses from the release site, either due to dispersion or mortality, and more individuals remained at the release site for the duration of the study. Little group level effect was seen of placing all bold individuals together unlike previous studies (Sih and Watters, 2005).

Unfortunately in this study confounding factors of habitat differences between release sites and other environmental factors which were not able to be controlled for provokes caution in the interpretation of the patterns seen here. However, this may reflect ‘real life’ situations where even a prepared release site is unlikely to contain a homogenous habitat and external variables are often outside of the manager’s control. Numbers of mice able to be trapped and released in a time scale appropriate for welfare reasons prevented more simultaneous repeats being carried out and delays in the project prevented an additional release being carried out later as initially proposed. These would have provided additional evidence that environmental factors were not the cause of the apparent additional success of the mixed group. Another potential confounding factor of the data collected at this group level was the existence of resident mice at the release site. Due to ethical and licensing restrictions it was not possible to remove these resident mice before releasing the mice from captivity. Differing numbers of resident mice at the three sites may have caused different patterns of dispersal through competition or differing population densities. Measuring the density of resident populations may also have provided an indication of habitat quality at the release sites. Unfortunately due to limited time and manpower there was not time to carry out a comprehensive trapping at the release sites before the release which would have provided important information on these potentially confounding factors. However, this does provide indicators of the effect of resident animals in a reinforcement translocation.

There are a number of theoretical studies that have suggested that a mix of personality types may aid in colonization and reduce within group competition. For example Trillmich and Hudson (2011) discuss how niche specialization, a potential effect of differing personality types, may be selected for within populations. The authors suggest that even small differences in how individuals use the environment will reduce competitive and potentially agonistic interactions between individuals (Trillmich and Hudson, 2011). This may relate to different feeding patterns, large scale habitat use or small scale habitat use as identified in this study through the use of more or less open habitats. This is important within a population as if different niches are being utilised then if the environment shifts so one niche becomes unavailable only part of the population will be affected (Watters, Lema and Nevitt, 2003). A series of models discussing the evolution and development of different personality traits discuss how the benefits of different personality types may be frequency dependant (Sih and Watters, 2005; Wilson *et al.,* 1994), therefore introducing a variety of individuals may increase the mean fitness of the group. Michelena *et al.* (2010) also suggest that having a variety of personality types, particularly in group living species will help optimize the exploitation of environmental resources. For example, Hessing *et al.,* (1994) showed that pigs from groups containing a mixture of personality types have higher weight gain than those from groups containing a single personality type.

As discussed above this may indicate that retaining a variety of personality typed individuals in captivity may be doubly important, both at the individual level and the population level. To promote a variety of personality types within a captive population (Watters and Meehan, 2007) recommend raising individuals under differing environmental conditions. Previous research suggests that individuals have a behavioural reaction norm based on their genetic background, but that their developmental environment causes them to select different personality types from within this reaction norm (Stamps, 2003). Within the same environment different personality types will still arise if there are individuals with different genetic backgrounds, but within different environments there may develop different personality types from individuals with a similar genetic background. However rearing conditions need to remain ecologically relevant to not develop aberrant personality types (Watters and Meehan, 2007). Even with the same parentage and rearing environment variation in behaviour between young may exist (McPhee, 2004), but if it is not reinforced or has no selective advantage it may be selected against in adulthood (Bremner-Harrison and Cypher, 2011). Watters and Meehan (2007) suggest that competition can be a main driver of different behavioural tactics, but that the relaxed competition seen in most captive situations may prevent this from occurring. Reducing this kind of selective pressure may allow the development of behaviours that would not naturally develop in the wild (McPhee and Silverman, 2004).

Historically, translocation studies have rarely kept track of whether the population is displaying an adequate range of behaviours (Box, 1991), however this practise is improving (Soorae (ed.), 2013). This study would encourage as a minimum for managers during translocation projects to attempt to record personality traits in source populations and captive populations and attempt to select varied individuals for release. Continued monitoring of the success of individuals with different personality traits in real reintroductions should allow the identification of general trends in how individuals with different personality types respond to different stimuli encountered in a reintroduction. Alongside this, studies using model species such as this one can apply manipulations to group compositions not possible or practical in conservation studies to examine their effect. Different personality types do better under different conditions which can fluctuate from year to year (Dingemanse *et al.,* 2004). Generating a body of evidence from multiple empirical studies should aid in identifying which environmental factors are of key importance and what effect they may have. This study does not recommend replacing any techniques currently employed to advance post release success. On the contrary personality monitoring may enhance the success of some techniques. For example previous studies have identified that personality type may affect learning ability (Sneddon, 2003), therefore the knowledge of personality types may be utilized to aid in pre-release training, by identifying which individuals may respond to different training techniques.

6.5 Future Research

6.5.1 Tailoring Releases

This study has supported evidence that personality measured in a standardised test can predict the behaviour of individual animals once they are released into the wild. It has also provided some evidence that group composition may have an additional effect on individual survival. However there is potential to take this work a step further and investigate how individuals with different personality scores may react under different stimuli. Watters, Lema and Nevitt (2003) initially suggested releasing a variety of individuals as this may allow managers to ‘hedge their bets’ in an unpredictable environment. However some aspects of an environment are predictable. Certain areas of a release site may provide more cover or have higher chances of predation or are closer to risk (e.g. human habitation) or provide more resources. Previous studies of personality provide evidence that an individual’s personality may affect how it responds to these different stimuli and its chance of surviving under different conditions (Dochtermann *et al.,* 2012; Dingemanse and Reale, 2005). For example, bolder individuals are often suggested to do better than shy individuals under minimal risk or when competing with conspecifics (Ward *et al.,* 2004; Westerberg, Staffan and Magnhagen, 2004). There is therefore the potential to tailor which individuals are released in areas with high risk or based on conspecific density. For practical reasons managers may not be able to select the population of animals that they have ready for release, however they may be able to improve the success of those individuals by tailoring their release strategy to suit their individual personality traits. A direction for future research in this area would be to identify how different environmental gradients commonly found across release sites (e.g. predation level, resource abundance, vegetation cover) differentially affect individuals with easily identifiable personality types. This is not just restricted to spatial environmental variability but also temporal. As discussed previously different stages of a reintroduction or invasion front may favour different personality types (Bremner-Harrison *et al.,* 2013; Cote *et al.,* 2010; Duckworth and Badyaev, 2007b). For example it has been suggested that bolder individuals may be better at coping with novel habitats or more asocial individuals may do better under low population densities commonly found immediately after release (Cote *et al.,* 2010; Clobert *et al.,* 2009). Under these situations it may be advisable to release bolder or more asocial individuals first, releasing either shyer individuals who may cope better knowing there are conspecifics in the local habitat or more social individuals who may do better at higher population densities later on to bolster numbers and increase population growth. In an ideal world it would be possible to predict how any individual would react to any stimuli and adjust release strategies accordingly. The probability of achieving this level of details is minimal, but by identifying general trends it may be possible to produce easily applicable recommendations which may work to improve success.

6.5.2 Individual responses to stress

One other suggestion to come from this study is the importance of individual responses to stress (coping styles) on how animals behave in a reintroduction. The patterns seen in this study through the different responses of individuals and groups with different personality compositions may have been caused by differing stress responses, mapped on a proactive-reactive continuum. Translocations include numerous causes of stress at various stages, from trapping through transport to release (Teixeira *et al.,* 2007). How an individual responds to each of these stressors may affect how successful it is upon release (Mathews *et al.,* 2005). Individuals can respond differently to different stressors, and individuals with different personality types may react more or less negatively to different stimuli (Carlstead *et al.,* 1999). Stress can play a large role in success in a reintroduction, not only from clinical stress which can reduce immune function and life expectancy but from subclinical stress which can affect learning and memory (Teixeira *et al.,* 2007). Surviving after release into a novel environment relies on an individual being able to find food and shelter and remember their location (Box, 1991). Individuals which face stressors can have impaired cognitive ability including memory retention for a significant length of time after the stressor has been removed. For example when stressful stimuli were applied to tree shrews it affected their memory for up to ten weeks (Ohl and Fuchs, 1998). The behavioural scores measured here appeared to indicate that mice fell along a proactive-reactive axis. Generally it is more reactive individuals who respond more negatively to stressful events such as handling. An interesting future avenue would be to examine how individuals with differing personality types respond to a variety of common stressors within a reintroduction context. This data could then be used to identify which individuals are more negatively impacted by certain parts of the translocation procedure, and potentially inform ways to reduce the negative impacts of these stressors. For example individuals may respond more or less favourably to hard or soft releases (Sinn *et al.,* 2014). Soft release protocols require a significant input of resources, which means the majority of releases are hard releases. However if a subset of the population were identified to significantly benefit from a soft release then it may be advantageous to provide some post release help to this subset of the population. Different stress responses between individuals can be affected by their life history and previous experience (Wingfield and Sapolsky, 2003; Wingfield, 2013). If it was identified, for example, that more social individuals are more stressed by parts of a reintroduction that necessitate isolation, then they could be appropriately prepared during captivity.

A review by Mason *et al.* (2013) suggested that how individuals respond to being taken into captivity may be a good model for how individuals respond to Human Induced Rapid Environmental change (HIREC). They suggest that by observing how different individuals cope with captivity we may be able to model how individuals or species will cope with environmental change. If this is true it seems plausible that by observing how individuals cope with being taken into captivity may also provide a model for how they may cope with being released into a novel habitat. Those individuals who cope better with captivity, finding food, shelter and potentially dealing with conspecifics may also be those who cope better with release into a novel habitat where these same challenges are faced. However there are some obvious differences, such as the lack of predation risk within a captive environment. This study identified some traits which seemed to indicate an individual’s response to captivity, such as the differing change in activity levels or the lab boldness score identified in Chapter Five. These scores differed from the general activity and boldness scores used, but could be used as an estimate of how well individuals coped with captivity. These scores were only taken after individuals were in captivity for 24 hours, monitoring this change in behaviour over a longer period, potentially in more naturalistic caged environments, could provide an interesting model for coping with a release environment.

6.6 Recommendations

Table 6.1. Recommendations for the application of personality research to improve reintroduction success, with suggestions for practical application.

Recommendation	Application
Captive populations destined for release back into the wild should be monitored for both mean and variance of behavioural change compared to a relevant wild population.	Collect simple behavioural scores for animals using handling or distance moved in an open arena as a proxy for activity. Compare distribution with target wild population. If there is significant deviation attempts should be made to discover why this is (e.g. inadvertent selective breeding in captivity, unenriched rearing environment, stress related to captivity) and correct for it.
Future conservation translocations should use simple behavioural techniques to identify personality traits in individuals before release, this data can then be used to build up a body of evidence on what affect this has post release.	Calculate simple behavioural scores as above. Look for correlations with data collected from post release monitoring for relevant factors i.e. mortality rates, dispersal distance and reproductive rates.
If no other data are available ensuring individuals showing a natural range of personality types should be released.	Calculate simple behavioural scores as above. Ensure release groups include

	individuals from across the spectrum of scores collected.
Identifying how individuals with different personalities or coping styles respond to different potentially stressful aspects of the translocation process could provide key insights into how to reduce stress and improve survival.	After calculating simple behavioural scores, observe for relationships with individuals which seem to react most strongly to different stressors e.g. sickness or weight-loss in captivity, injury during capture and handling etc. Alternatively scores could be related to physiological measures of stress taken at different stages such as cortisol levels. Management practices should then focus on alleviating stress to these individuals under identified situations
Further empirical or modelling studies should be carried out to identify the effect personality plays at different stages of the translocation process	Once a body of evidence has been collected on some of the above a meta-analysis can be used to look for constant patterns. Further empirical studies potential using other model species may help highlight important factors which may not be possible in conservation releases such as release placement or further work on group composition.

6.7 Conclusions

To conclude, this study has provided evidence that wood mice can act as a model species to investigate the effects of personality on translocation success. The study has found that personality affects a number of behavioural factors displayed in an individual's natural environment such as habitat use and risk taking. Results have shown that personality is heritable in this species and joins with a number of studies showing that breeding in captivity can severely bias the personality of populations (Archard and Braithwaite, 2010; Niemelae and Dingemanse, 2014). Data also warns against the assumptions made when carrying out personality tests under different conditions, particularly captivity, as individuals may express different behaviours when tested under different conditions. Finally the study has shown that personality plays a key role in how an individual responds to being released into a novel environment, both at the individual and the group level. Practical recommendations to come from this study suggest that during translocation studies the personality of individuals should be assessed and behaviour monitored. Whenever trapping takes place it should occur over a suitable length of time and in different habitats to prevent bias in the captured population. If captive bred animals are planned on being rereleased into the wild then captive populations should be monitored to ensure a variety of personality traits are maintained. Finally, results from this empirical study support theories that releasing individuals with a variety of personality types increases the probability of reintroduction project success. However it also urges that more research may provide additional information regarding patterns of how individuals with different personality types or stress responses may respond to the proposed release methods or release environment, and that this information could be used to further inform release strategy.

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8 Appendix – Site Maps

Figure A1. "UK Map" Identifying locations of field sites. EDINA Digimap Ordnance Survey Service.

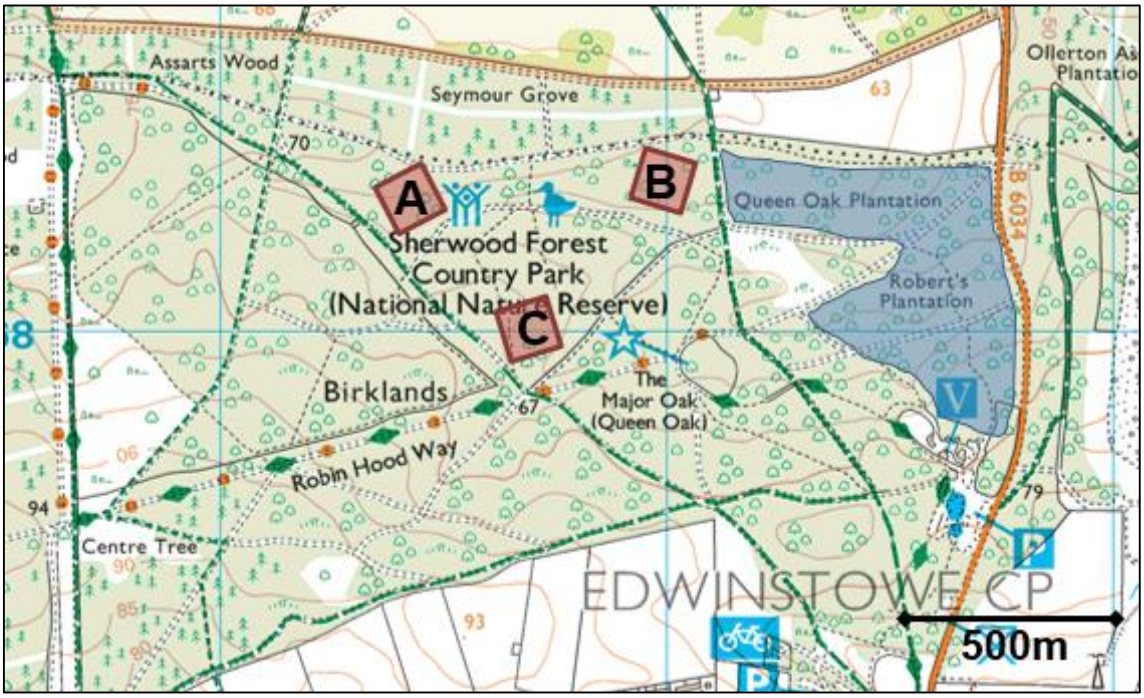

Figure A2. "Sherwood Forest National Nature Reserve Map". Indicates area used for trapping and testing of mice in Chapters 2 and 3 which was also the area used for trapping mice for removal into captivity in chapter 5 (Blue). Release sites and trapping grid locations used in chapter 5 are shown in red, A = Bold, B = Shy, C = Mixed. EDINA Digimap Ordnance Survey Service.

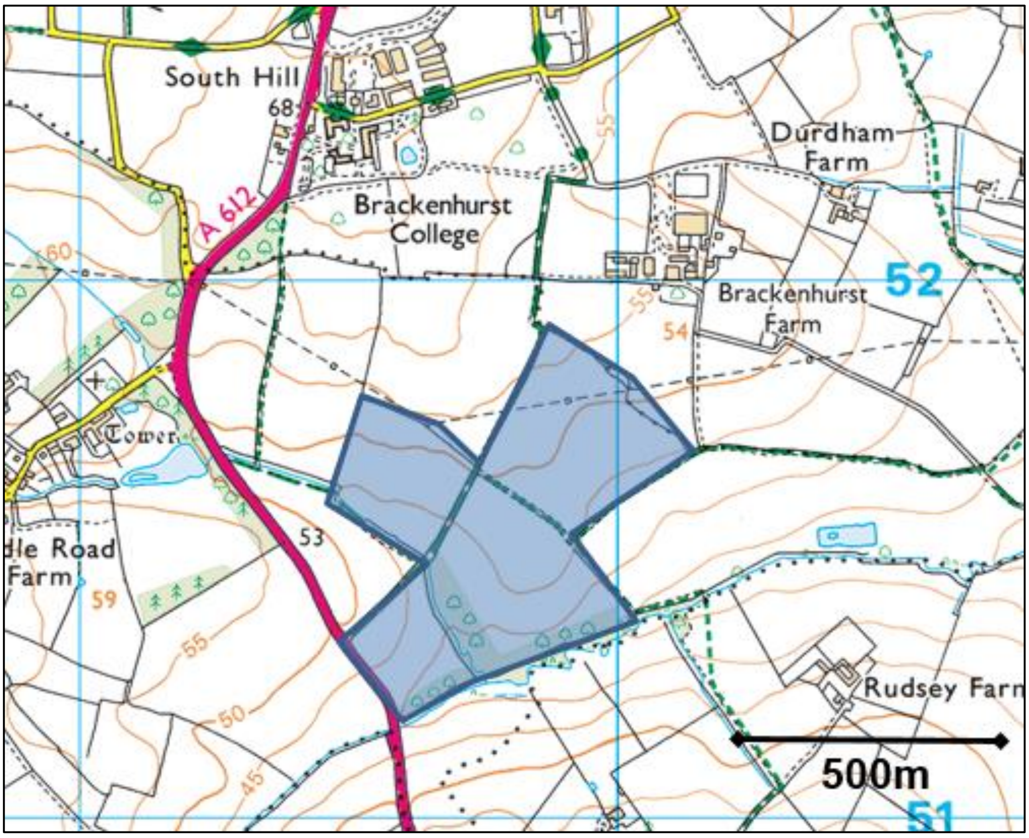

Figure A3. "Brackenhurst Campus map". Area used for trapping and testing mice in chapters 2 and 3 indicated in blue. EDINA Digimap Ordnance Survey Service.

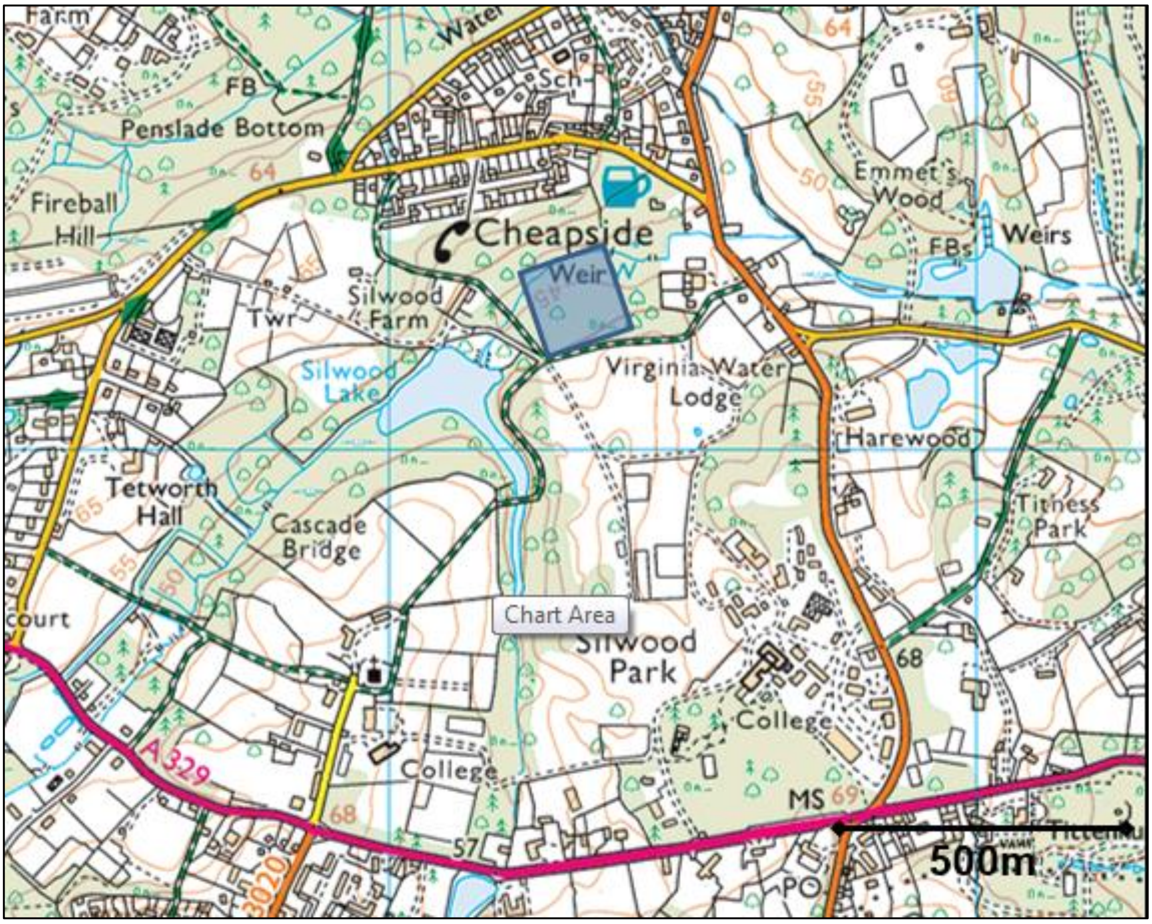

Figure A4. "Silwood park map". Area used for trapping and testing of mice in chapters 2 and 3 shown in blue. EDINA Digimap Ordnance Survey Service.