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Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality

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Behavioural tendencies vary consistently among individuals and this variation is known as personality. Previous studies have found that personality traits measured through standardized behavioural tests predict trappability (i.e. 'trap happy' versus 'trap shy'). However, the nature of this relationship is unclear since it has been explored only within single species and never across environments. This is problematic because trappability is a labile characteristic that can vary between seasons, environments and years. It is essential to understand this link because there is great potential for the use of trappability as a proxy for personality. For example, if trappability reflects personality, this would allow researchers to extract personality data from long-term capture–mark–recapture data sets. To clarify this relationship, we designed a large-scale field experiment to measure personality and trappability in five small mammal species and across four distinct forest types. With an open field test, we quantified behaviour in 189 deer mice, *Peromyscus maniculatus*, 170 southern red-backed voles, *Myodes gapperi*, 42 American red squirrels, *Tamiasciurus hudsonicus*, 58 woodland jumping mice, *Napaeozapus insignis*, and 87 northern short-tailed shrews, *Blarina brevicauda*. We identified personality in all five of our target species, and through mixed-effects modelling we found that personality traits did not predict different aspects of trappability. Furthermore, trappability was not a repeatable measure (i.e. animals that were trap happy in one session were not necessarily trap happy throughout the trapping season). Our results suggest that trappability cannot be used as a proxy for personality.

Behavioural tendencies often vary consistently among individuals and this variation is known as personality (Carere & Maestripieri, 2013; Sih, Bell, Johnson, & Ziemba, 2004). Personalities have been observed in multiple species and across taxa: from insects (Pruitt & Modlmeier, 2015), fish (Wilson, Binder, McGrath, Cooke, & Godin, 2011; Wilson, Coleman, Clark, & Biederman, 1993) and reptiles (Carter, Heinsohn, Goldizen, & Biro, 2012) to birds (Dingemanse, Both, Van Noordwijk, Rutten, & Drent, 2003; Garamszegi, Eens, & Török, 2009) and mammals (Blumstein, Petelle, & Wey, 2013; Boon, Réale, & Boutin, 2007; Montiglio, Garant, Pelletier, & Réale, 2012; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000), and can have important implications for the fitness of the individual (Dingemanse & Réale, 2005; Smith & Blumstein, 2008). Because individuals vary in both personality type and their ability to exhibit behavioural plasticity (Dingemanse, Kazem, Réale, & Wright, 2010), there are important links between an individual's personality and its response to a changing environment (Sih, Ferrari, & Harris, 2011). This has resulted in an increasing focus on the study of animal personalities in the field of behavioural ecology and, more recently, conservation biology (Candolin & Wong, 2012).

Personality has been measured in several ways and in both field and laboratory settings (for summaries of existing methods using standardized tests, see Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Gosling et al., 2001; for an example using behavioural observations of noncaptured animals, see Dammhahn & Almeling, 2012). Although these methods are often quite inexpensive in terms of the materials and equipment required, tests like open field (Archer, 1973; Walsh & Cummins, 1976), hole board (Careau et al., 2011; Martin & Réale, 2008; Menzies, Timonin, McGuire, & Willis, 2013) and mirror image stimulation (Boon, Réale, & Boutin, 2008; Svendsen & Armitage, 1973) are time consuming to perform and require additional time in the laboratory to quantify the behaviours observed, making them expensive in terms of labour costs.

More recently, correlations between an individual's personality and other measurable aspects of behaviour have been identified,

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including dispersal distance and exploration of the environment (Dingemanse et al., 2003; Wilson, 1998), extraterritorial behaviours (Boon et al., 2008) and, commonly, trappability (Krebs & Boonstra, 1984). Trappability encompasses measures such as the propensity (or latency) to enter a trap, the probability of being captured and trap response (a systematic trapping bias in which certain individuals become either more or less likely to be trapped after the initial capture; Nichols, Hines, & Pollock, 1984). Trappability can also encompass characteristics such as the number of different traps utilized and can give insight into aspects of an individual's territory size or space use (Boon et al., 2008; Kanda & Hatzel, 2015). Differing individual responses to trapping are common and have resulted in terms such as 'trap happy' and 'trap shy' becoming widespread descriptors to explain the reaction of different animals to trapping methods (Nichols & Pollock, 1983).

In some studies, trappability has been shown to be consistent within individuals, and this consistency has been quantified using repeatability (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; La Coeur et al., 2015; Réale et al., 2000). Statistically, repeatability can be defined as the proportion of total phenotypic variation accounted for by individual differences after controlling for the potential impacts of fixed effects (Dingemanse & Dochtermann, 2013; Dingemanse et al., 2010; Nakagawa & Schielzeth, 2010). When the proportion of the total variance accounted for by differences within individuals is small in relation to the variance attributed to differences between individuals, this is evidence for personality. Trappability has also been shown to correlate significantly with other aspects of personality such as boldness or risk taking in bighorn ewes, *Ovis canadensis* (Réale et al., 2000), Namibian rock agamas, *Agama planiceps* (Carter et al., 2012), and bluegill sunfish, *Lepomis macrochirus* (Wilson et al., 2011); activity levels in American red squirrels *Tamiasciurus hudsonicus* (Boon et al., 2008) and Siberian chipmunks, *Tamias sibiricus* (Boyer et al., 2010); exploratory behaviours in collared flycatchers, *Ficedula albicollis* (Garamszegi et al., 2009); and reduced fear response in Japanese quail, *Coturnix japonica* (Mills & Faure, 2000) (for more thorough reviews, see Biro, 2013; Biro & Dingemanse, 2008; Merrick & Koprowski, 2017; Stuber et al., 2013).

Although these relationships have been observed in a number of species, these findings have encouraged some studies to use trappability directly as an index of other personality traits. For example, this has been done either by relying on the consistency of trappability in only a subsample of individuals (Boyer et al., 2010), supposing that trappability is consistent within individuals (Montiglio et al., 2012), or assuming a relationship between trappability and repeatable behaviours based on the findings of others (La Coeur et al., 2015; Patterson & Schulte-Hostedde, 2011).

There is an issue with these above scenarios, because the relationships between trappability and personality observed in previous studies are context and species specific, meaning they lack a sound basis for generalization. Furthermore, not all have calculated the repeatability of trappability, which is concerning because trappability has been shown to vary with changes in resource abundance and availability (Adler & Lambert, 1997) as well as species abundance (Royle & Nichols, 2003). In fact, trappability has also been shown to vary among and between sexes, age classes, study areas, seasons and years (Adler & Lambert, 1997; Byrne et al., 2012; Silver et al., 2004; Tuyttens et al., 1999), which may complicate the calculation of repeatability. This lack of repeatability estimates means also that there can be no direct comparison between studies. For trappability to be considered personality, it must be repeatable (e.g. a trap-shy individual should consistently behave in a trap-shy manner) (Bell, Hankison, & Laskowski, 2009; Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Additionally, to consider trappability a proxy for a specific personality trait such as boldness, activity or exploration, the trait should have been quantified independently of the trapping itself, and trappability must be found to correlate significantly with that trait.

Furthermore, as several studies have suggested (Biro, 2013; Biro & Dingemanse, 2008; Carter et al., 2012; Stuber et al., 2013), if certain individuals are consistently trapped more often than others (i.e. trap-happy individuals), this will result in sampling methods representing a disproportionate number of individuals with a certain personality type; resulting in nonrandom and potentially behaviourally biased samples. This would be troublesome for studies utilizing behavioural observations or life-history information from captured individuals. However, if trappability is not a repeatable measure, it is likely that the trappability of individuals is contingent upon many factors and may be changing constantly, reducing the negative effects of trap response on the validity of data.

It is critical to resolve this ambiguity and extend our understanding of the relationship between trappability and personality. Confirming, as previous studies have suggested, that trappability is a measure of personality and is highly correlated with other personality traits would support the use of trappability as a proxy for traits that are usually expensive and time exhaustive to measure. Ultimately, it may also be possible to use existing data sets, such as long-time series of capture–mark–recapture data, to explore questions relating to personality and population dynamics (Ogawa, Mortelliti, Witham, & Hunter, 2017). Finally, this might indicate the need for a shift in the way animals are captured for behavioural studies; perhaps requiring the use of multiple different trapping approaches to limit the inherent behavioural bias caused by passive trapping methods (Biro, 2013).

To fill this knowledge gap, we developed a large-scale field experiment involving multiple species (5 small mammal species belonging to 2 orders and 4 families) living in contrasting environments (i.e. forestry treatments). To the best of our knowledge, we are among the first to compare the relationship between personality and trappability simultaneously in multiple species and to concurrently investigate how these relationships might vary across environments.

The main objective of our study was to determine whether trappability reflects personality in five small mammal species and whether it can be used as a proxy for these traits (see Fig. 1 for a conceptual diagram). We hypothesized that individuals who show increased activity/locomotion and exploratory behaviours in an open field test would also show increased trappability (Boon et al., 2008; Boyer et al., 2010; Dingemanse et al., 2003; Garamszegi et al., 2009). Particularly, we predicted that behaviours related to activity in the open field test would be positively correlated with an increased number of captures and with captures occurring earlier in the trapping session. We also predicted that behaviours related to exploration would correlate positively with the number of different traps that an animal used. Furthermore, since previous studies have found evidence for a relationship between personality traits and trappability among multiple taxa, we predicted that we would see similar results across all five study species, confirming that trappability can be used as a proxy for correlated personality traits.

METHODS

Study Site

This study was conducted in the Penobscot Experimental Forest (PEF, 44°51′N, 68°37′W). This is a 1578 ha Forest Service experimental forest located in the towns of Bradley and Eddington,