



## Short- and long-term repeatability of docility in the roe deer: sex and age matter



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Behavioural consistency is a key assumption when evaluating how between-individual differences in behaviour influence life history tactics. Hence, understanding how and why variation in behavioural repeatability occurs is crucial. While analyses of behavioural repeatability are common, few studies of wild populations have investigated variation in repeatability in relation to individual status (e.g. sex, age, condition) and over different timescales. Here, we aimed to fill this gap by assessing within-population variation in the repeatability of docility, as assessed by the individual's response to human handling, in a free-ranging population of European roe deer, *Capreolus capreolus*. Docility was an equally repeatable behaviour at both short- and long-term timescales, suggesting that this behavioural trait is stable across time. Repeatability did not differ markedly between age and sex categories but tended to be higher in juvenile males than in juvenile females. Finally, contrary to expectation, individual variation in the repeatability of docility was not correlated with individual body mass. Further studies are required to assess the life history consequences of the individual variation in docility we report here.

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Interest in the study of behavioural differences between individuals has increased markedly over recent years (Bell, 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012) and consistent behavioural differences between individuals over time and/or across different ecological contexts have been documented within populations in a large variety of taxa (Bell, 2007; Bell, Hankison, & Laskowski, 2009). These consistent behavioural differences can indeed have profound effects on life histories (Bell, 2007; Biro & Stamps, 2008; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For instance,

annual adult survival is related to exploration behaviour in great tits, *Parus major* (Dingemanse, Both, Drent, & Tinbergen, 2004). In the common lizard, *Lacerta vivipara*, socially tolerant individuals grow faster and reproduce better than intolerant individuals (Cote, Dreiss, & Clobert, 2008). Similarly, boldness and docility are linked to survival and reproductive success in bighorn sheep rams, *Ovis canadensis* (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009), and to weaning success in bighorn sheep ewes (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000).

Behavioural consistency can be assessed by evaluating repeatability (Hayes & Jenkins, 1997), where repeatability is defined as the proportion of observed behavioural variation within a population that is accounted for by individual differences (Bell et al., 2009). This then requires that behavioural traits be assessed repeatedly in the same individuals. The vast majority of studies that have assessed behavioural repeatability have been conducted under

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somewhat unrealistic laboratory conditions (e.g. see Bell et al., 2009 for a review), whereas repeatability measures of behavioural traits in the wild are less common (e.g. Martin & Réale, 2008a in eastern chipmunks, *Tamias striatus*; Réale et al., 2000 in bighorn sheep; Montiglio, Garant, Thomas, & Réale, 2010 in house mice, *Mus musculus*, and eastern chipmunks; Garamszegi, Eens, & Janos, 2009 in collared flycatchers, *Ficedula albicollis*, Nakagawa, Gillespie, Hatchwell, & Burke, 2007 in house sparrows, *Passer domesticus*).

Despite the importance of individual behavioural differences for understanding the evolution of life history tactics (Sih et al., 2012), the individual characteristics that influence repeatability are still to be fully understood and require further investigation (Bell et al., 2009). Using a meta-analysis based on 114 studies (466 estimates assessed in the laboratory versus 293 in the field) investigating the repeatability of various behavioural traits, Bell et al. (2009) found that within-population variation in repeatability depends on the focal behavioural trait, as well as the species under study, and is affected by (1) time elapsed between measurements, (2) age, (3) sex and (4) ecological conditions.

Behavioural repeatability generally decreases as the time elapsed between successive measurements increases (Bell et al., 2009; David, Auclair, & Cezilly, 2012; Gifford, Clay, & Careau, 2014). This is probably because, with time, there is more opportunity for individuals to experience developmental modifications and fluctuating environments (Stamps & Groothuis, 2010), and also because their phenotype may be influenced by different genes at different ages (Charmantier, Perrins, McCleery, & Sheldon, 2006). Thus, experimental trials performed over short time intervals (i.e. short-term repeatability) generally yield higher estimates of repeatability than those carried out over longer time intervals (i.e. long-term repeatability) for a large range of traits, including docility (Bell et al., 2009; David et al., 2012; Gifford et al., 2014).

Repeatability also varies in relation to age, although predictions for age-dependent variations are not straightforward (Bell et al., 2009). Assuming that behavioural repeatability has an ontogenetic component (Stamps & Groothuis, 2010; i.e. it develops progressively over a lifetime), the behaviour of older individuals should be more repeatable than that of younger ones (De Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009). For instance, behavioural repeatability in humans increases with age up to 50 years old before reaching a plateau (Roberts & DelVecchio, 2000). Hence, higher repeatability of docility is expected among adults.

Behavioural repeatability may differ between the sexes under the action of sexual selection (Schuett, Tregenza, & Dall, 2010). Indeed, behaviours shaped by sexual selection should provide reliable, honest, and thus consistent, cues, so that they can reliably be interpreted by conspecifics (Bell et al., 2009; Schuett, Godin, & Dall, 2011). For instance, in two kangaroo rat species (*Dipodomys* spp.), food-hoarding behaviour, a behavioural trait that may partially underpin alternative mating tactics, has been reported to be more repeatable in males than in females (Jenkins, 2011). Surprisingly, however, based on the published literature, Bell et al. (2009) concluded that females generally tend to display more repeatable behaviours (except for mate choice-related behaviours) than males. Hence, between-sex differences in repeatability may depend on the behavioural trait under scrutiny, with males being more repeatable for behaviours linked to mate choice and subject to intrasexual competition (Schuett et al., 2010).

Repeatability may also vary among individuals within a given sex or age class. At the population level, a behavioural consistency estimate that is statistically different from 0 for a given trait in a given age and sex category does not mean that all individuals are equally consistent for that trait (Bell et al., 2009). Indeed, individual variation in predictability, or within-individual variability,

once variation due to sex and/or age differences has been accounted for, is widespread (Briffa, 2013; David et al., 2014; Stamps, Briffa, & Biro, 2012) and may have consequences for fitness-related traits. For instance, in hermit crabs *Pagurus bernhardus*, within-individual variation was higher in a risky situation, suggesting that animals benefit by behaving unpredictably under predation threat (Briffa, 2013). Such flexibility is assumed to be costly (DeWitt, Sih, & Wilson, 1998; Niemela, Vainikka, Forsman, Loukola, & Kortet, 2013) and should therefore vary as a function of individual body condition (David & Giraldeau, 2012; David et al., 2014). For example, zebra finches, *Taeniopygia guttata*, in higher body condition are less consistent in their producer tactic use in a producer–scrounger foraging game (David et al., 2014). A link between body condition and variation in docility may thus be expected.

The objective of this study was thus to test the effect of the above factors on the repeatability of docility in European roe deer, *Capreolus capreolus*. Docility is a commonly measured behavioural trait (Benhajali et al., 2010; Martin & Réale, 2008a; Réale et al., 2000) often associated with the shy–bold behavioural gradient (Réale et al., 2007). Indeed, docility has often been linked with other behavioural traits such as activity and exploration (Ferrari et al., 2013; Martin & Réale, 2008a) and with physiological parameters such as hypothalamo–pituitary–adrenal reactivity (Montiglio et al., 2010) or the level of cortisol (Martin & Réale, 2008b). Docility has been reported to be a repeatable behavioural trait in several studies, both in captivity (e.g. David et al., 2012; Mazurek et al., 2011) and in the field (Ferrari et al., 2013; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Réale et al., 2000, 2009). Moreover, docility is linked to fitness components in bighorn sheep (Réale et al., 2000, 2009), while it also influences the productivity of livestock farming enterprises (Norris, Ngambi, Mabelebele, Alabi, & Benyi, 2014). For instance, fearful cows produce lighter calves at birth that grow less well than those produced by nonfearful (i.e. docile) cows (Turner, Jack, & Lawrence, 2013). Because docility may be part of a behavioural syndrome (i.e. a suite of correlated behaviours reflecting between-individual consistency in behaviour across multiple situations; Sih, Bell, & Johnson, 2004), variation in docility may thus have important consequences for life history traits. Information about which factors influence the repeatability of docility remains scarce, however. In yellow-bellied marmots, *Marmota flaviventris*, Petelle et al. (2013) reported that boldness was repeatable only in yearlings, whereas docility was repeatable in all age classes. Repeatability of docility was also shown to be higher when measured over the short term than over the long term (Bell et al., 2009; David et al., 2012).

In this study, we investigated the repeatability of docility taken as the behavioural responses to human manipulation at capture in a free-ranging, wild population of European roe deer in central Sweden. The response of roe deer to human handling during capture is assumed to reliably reflect docility (Le Neindre et al., 1995; Réale et al., 2000). The roe deer is a medium-sized (20–30 kg), slightly dimorphic and weakly polygynous ungulate in which adults of both sexes are highly sedentary (Andersen, Duncan, & Linnell, 1998). Roe deer life expectancy in the wild at 1 year of age is around 10–12 years in the absence of hunting, but varies among populations (Veiberg et al., 2007). Despite being primarily a forest-dwelling species, roe deer have colonized almost all types of habitats since the early 1980s, including human-modified landscapes (Andersen et al., 1998; Hewison et al., 2001), and express a high degree of behavioural plasticity (Jepsen & Topping, 2004). Here, we investigated whether the repeatability of docility varies in relation to the time elapsed between successive measurements, age, sex and body mass. We expected (1) short-term repeatability estimates to be higher than long-term ones, (2) repeatability to be

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