



When righting is wrong: performance measures require rank repeatability for estimates of individual fitness



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Fitness proxies such as performance measures are used to quantify relative fitness in systems where direct measurements are unobtainable. To provide meaningful results at the individual level, fitness proxies must demonstrate not only repeatability, as measured by high intraclass correlation coefficients, but also rank repeatability. Here we illustrate the importance of rank repeatability in fitness proxies using a commonly employed example: righting time in hatchling turtles. Our results show that individual righting time varies strongly among trials and is not replicable enough to provide repeatable rankings of individuals or clutches. To illustrate the potential implications of this finding, we use our data to test the predication that larger turtles have faster righting times, using three consecutive trials of righting time. The resulting conclusions vary substantially among trials. Thus, we conclude that righting time does not meet the criterion of rank repeatability required for estimates of relative individual fitness, performance or phenotypic quality. Researchers employing similar proxies should assess the rank repeatability of a proxy before applying it to questions of relative individual fitness. If a measure shows satisfactory repeatability, the final test for a fitness proxy is to demonstrate a correlation with actual fitness, ideally in the organism's natural habitat.

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Performance measures and proxies of fitness or phenotypic quality are often used to study wild populations where a direct measure of fitness is not possible. Commonly used examples include body condition (Bradford et al., 2012), stress hormone concentrations (Bonier, Martin, Moore, & Wingfield, 2009), locomotor speed (Huey & Dunham, 1987; Langkilde, Lance, & Shine, 2005), symmetry (Alford, Bradfield, & Richards, 2007; Shine, Langkilde, Wall, & Mason, 2005), and most recently, personality (Ibáñez, Marzal, López, & Martín, 2013; Jandt et al., 2013; Menzies, Timonin, McGuire, & Willis, 2013; Seyfarth, Silk, & Cheney, 2012). Proxies of fitness or 'phenotypic quality' ideally meet several criteria. There must be significant among-individual variation for

the trait to be subject to selection, and of evolutionary importance (Wilson & Nussey, 2010). The trait should be relevant to the study species' ecology and should also be correlated with an individual's actual fitness (e.g. Isden, Panayi, Dingle, & Madden, 2013; Wikelski & Romero, 2003; Wilson & Nussey, 2010), although such correlations can be extremely difficult to demonstrate, especially in long-lived or rare species. Most importantly, the measured trait must provide a repeatable estimate of fitness or performance.

Repeatability is particularly critical with potentially plastic behavioural traits such as nesting phenology or locomotor performance. Repeatability of behaviour is typically measured using the intraclass correlation coefficient (ICC; Lessells & Boag, 1987), and many behaviours show high individual repeatability based on ICC (Bell, Hankison, & Lakowski, 2009; Briffa & Greenaway, 2011; Dingemanse, Kazem, Réale, & Wright, 2010; Huey & Dunham, 1987). But individual fitness is a relative quantity, not an absolute one. Therefore, for a fitness proxy or performance measure to be used to compare fitness among individuals with different traits (rather than among groups subjected to different treatments), these measures must also demonstrate rank repeatability: they must rank individuals in a consistent order when the

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measurement is repeated (Huey & Dunham, 1987; Laming, Jenkins, & McCarthy, 2013; Refsnider, 2013). Most studies assessing repeatability of a trait calculate the ICC, but there is a difference between high repeatability (high ICC) and rank repeatability (repeatable ranking of individuals). Rank correlation is often not assessed and its importance when considering questions related to relative individual fitness cannot be overstated.

The adaptive significance of various genetic or phenotypic traits at the individual level can be tested using fitness proxies that demonstrate rank repeatability. For example, male blue tits, *Cyanistes caeruleus*, that successfully sire offspring through extrapair copulations with a neighbouring female are typically larger than that female's social mate (Kempnaers, Verheyena, & Dhondia, 1997). Kempnaers et al. (1997) point out that this study relies on comparing the relative size and reproductive success of neighbouring males (the relative rank by size of individual males competing to fertilize a particular clutch), not on comparing size among all males within a population. In another study testing the effect of paternity on fitness, nestling bluethroats, *Luscinia svecica*, fathered by extrapair males displayed significantly higher immune responses than their half-siblings fathered by the mother's social mate (Johnsen, Andersen, Sunding, & Lifjeld, 2000). Comparison of sibling pairs within a clutch controls for maternal and nest effects and reveals effects of paternal variation that may not be detectable by comparing immune response of extrapair and within-pair offspring across an entire population.

In long-lived organisms where direct measures of fitness are challenging, repeatable performance measures or fitness proxies could also be used to test hypotheses about the relative fitness of half-siblings sired by different fathers, or the fitness of offspring produced by different pairs of mates (Banger, Blouin-Demers, Bulté, & Loughheed, 2013; Byrne & Roberts, 2000). However, the appropriate unit of measurement for such questions is the individual offspring, not the clutch. Therefore, this approach requires a measure of relative individual fitness that demonstrates rank repeatability. In this study we assess a commonly used performance measure in hatchling turtles to assess whether it demonstrates rank repeatability, and test potential effects of low rank repeatability in a performance measure on hypothesis testing.

Fitness, performance and phenotypic quality in hatchling turtles and squamates are often estimated using righting time: the time it takes an individual to right itself after being placed on its back (Burger, 1989; Freedberg, Stumpf, Ewert, & Nelson, 2004; Micheli-Campbell, Campbell, Cramp, Booth, & Franklin, 2011; Mullins & Janzen, 2006; Patterson & Blouin-Demers, 2008; Steyermark & Spotila, 2001). Righting time is considered an ecologically relevant parameter for all hatchling turtles because they risk overturning as they disperse from nests to aquatic environments, and because mortality from predators and desiccation during this dispersal is high (Burger, 1976; Finkler & Claussen, 1997). There is growing evidence that environmental conditions such as temperature and hydration during development affect righting response in hatchling turtles (Delmas, Baudry, Girondot, & Prevot-Juillard, 2007; Finkler, 1999; Freedberg et al., 2004; Micheli-Campbell et al., 2011; Mullins & Janzen, 2006; Refsnider, 2013). However, empirical evidence that righting time accurately predicts fitness is equivocal. Delmas et al. (2007) found that righting time was positively correlated with growth and survival rates in nests incubated at fluctuating temperatures, but not in a second, paired sample of nests incubated at constant temperatures. Further confounding the situation is the variation in crypsis among different species, which may also affect optimal righting strategy. Specifically, the coloration of the plastron may be cryptic enough that staying still provides a larger fitness advantage than righting and moving to safety. Finally, a clear link

between fitness and righting time (whether faster or slower) has not yet been established (Delmas et al., 2007; Refsnider, 2013).

Righting time is quantified in different ways among studies. Some studies quantify active righting time, or the time spent actively trying to turn onto the plastron (e.g. Ben-Ezra, Bulté, & Blouin-Demers, 2008; Freedberg et al., 2004; Micheli-Campbell et al., 2011). Others also measure latency time: the time the turtle spends lying passively on the carapace before attempting to right itself (e.g. Delmas et al., 2007; Rasmussen & Litzgus, 2010; Refsnider, 2013). Still others measure total righting time, the time from inverting the turtle until the turtle rights itself, equal to the sum of latency time and active righting time (Finkler, 1999; Mullins & Janzen, 2006; Steyermark & Spotila, 2001). Whichever measure is used, rank repeatability based on the results remains a key requirement for a proxy of individual fitness. To our knowledge, the repeatability of relative fitness estimates based on righting time (i.e. rank repeatability) has never been tested, as studies have either measured each turtle once (Finkler, 1999; Freedberg et al., 2004; Paitz, Clairardin, Griffin, Holgersson, & Bowden, 2009; Riley & Litzgus, 2013), measured each individual several times but selected the fastest time for analysis (Banger et al., 2013; Ben-Ezra et al., 2008; Mullins & Janzen, 2006), used the average of several trials (Maulany, Booth, & Baxter, 2012), or used the clutch as the unit of measurement (Refsnider, 2013).

Here, we investigate the hypothesis that righting response can be used as an indicator of relative fitness or phenotypic quality of individuals by testing the following predictions: (1) interindividual variation in righting response is higher than intraindividual variation; (2) individual repeatability of righting time (measured by the intraclass correlation coefficient) is high; and (3) individuals within a clutch rank in a similar order in repeated trials. We also test two competing hypotheses about individual response to multiple righting trials. If hatchlings learn to right themselves more quickly with experience (or right themselves more quickly because of handling stress), then individuals should right themselves more quickly in consecutive trials. Alternatively, if hatchlings tire with multiple trials, then individuals should right themselves more slowly in consecutive trials. Figure 1 shows two extreme examples of the expected results if righting time is a replicable measure of relative performance or fitness. In these examples, individual righting time changes among trials, but the rank of individuals within a clutch is stable. If individuals show a consistent response to multiple trials, we predicted three possible responses: (1) righting time of an individual could be stable among trials, (2) it could slow as hatchlings tire (righting time increases with progressive trials; Fig. 1a), or (3) hatchlings could learn to right themselves more quickly with experience (righting time decreases with progressive trials; Fig. 1b).

METHODS

Ethical Note

Animal care protocols were approved independently by the Animal Care Committee of the Royal Ontario Museum (ROM AUP number 2011-18) and the Wildlife Animal Care Committee of the Ontario Ministry of Natural Resources (OMNR) (WACC number 11-249). This research was also authorized under Wildlife Scientific Collector's Authorization 1062210 and permit AY-B-013-11 from the OMNR, and a research authorization from Ontario Parks.

Nest Collection and Care

We collected turtle nests in June and July 2011, during an ongoing conservation project in a wetland complex on Lake Erie,

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