Passive plasticity and a sex difference in the predictability of mobility

Clint D. Kelly1,✉

1 Département des Sciences biologiques, Université du Québec à Montréal, Montréal, Canada

✉ Correspondence: [Clint D. Kelly <kelly.clint@uqam.ca>](mailto:kelly.clint@uqam.ca)

# Abstract

Behavioural predictability (i.e. residual within-individual variation) represents the unexplained variance of repeated behavioural measures after controlling for individual variation in behavioural type and plasticity. Unpredictability can arise from many sources including non-adaptive passive plasticity in which an environmental factor acts directly on the individual to create non-adaptive phenotypic variation. In this study, I use radio telemetry to field test the hypothesis that Cook Strait giant weta *Deinacrida rugosa* (Orthoptera: Anostostomatidae) exhibit a sex difference in the predictability of their nightly travel distance due to passive behavioural plasticity. As predicted, I found that male mobility (i.e. nightly travel distance) was less predictable than female mobility. Females travel short and predictable distances each night for food and refuges that are close by and readily available. In contrast, male travel is less predictable because they search for female mates that are stochastically dispersed across the landscape. Therefore, their travel distance can vary considerably across nights.

# Introduction

Individuals can differ in their behavioural predictability, defined as residual intra-individual variation (i.e. rIIV), after controlling for individual variation in behavioural type (i.e. average behaviour) and behavioural plasticity (i.e. context-dependent within-individual variation represented as a reaction norm slope) (Stamps et al. 2012; Biro and Adriaenssens 2013; Cleasby et al. 2015; Westneat et al. 2015). Unpredictable individuals exhibit high variability around their behavioural type and reaction norm slope whereas predictable individuals do not (i.e. exhibit little residual variance). Within-individual residual variance can arise from various non-biological sources including sampling or measurement error and incompletely or inaccurately parameterizing statistical models (i.e. terms are missing from the model that could explain or account for residual heterogeneity) (Westneat et al. 2015). Conversely, greater behavioural predictability (i.e. smaller rIIV) could be selected if consistent behaviour influences the future responses of competitors in such a way that confers advantages upon the focal individual (Dall et al. 2004) or if consistency indicates quality that can be used in mate choice by the choosy sex (Schuett et al. 2010). Decreased behavioural predictability (i.e. larger rIIV) is also possible if individual variation is a product of individual state or environmental differences (Briffa et al. 2013; Chang et al. 2017; Horváth et al. 2019; Gangloff et al. 2021).

Behavioural predictability could also be weakened by non-adaptive processes such as passive plasticity whereby an environmental factor acts directly on the individual and creates non-adaptive phenotypic variation (Scheiner 2006). For example, the time to find food could exhibit unpredictable variance if the forager does not know the food’s location when foraging commences or if daily travel distance depends on the number and type of predators encountered, which can be stochastic (Westneat et al. 2015). Therefore, individual animal phenotypes might contain some stochastic variation that would be present as heterogeneous residual phenotypic variance if left unaccounted (Westneat et al. 2015).

In this study, I field test the hypothesis that Cook Strait giant weta *Deinacrida rugosa* (Orthoptera: Anostostomatidae) exhibit a sex difference in the predictability of their mobility due to passive behavioural plasticity. *Deinacrida rugosa* is a sexually size dimorphic nocturnal insect that is of high conservation importance (McIntyre 2001; White et al. 2017). It is endemic to New Zealand where it inhabits old pastures, forests, and coastal scrub (McIntyre 2001; White et al. 2017). Both sexes seek refuge from predators during the day by hiding under vegetation or other objects on the ground (McIntyre 2001). *Deinacrida rugosa* exhibits a scramble competitive mating system in which males search for receptive females as mates at night while females are foraging (Kelly et al. 2008; Kelly and Gwynne 2023a). Males do not defend resources required by sexually receptive females, nor do they guard harems of females, as do other deinacridine weta (McIntyre 2001; Kelly 2006). Mate searching results in males travelling considerably longer distances per night than females. In contrast, female nightly travel is generally short because suitable forage is close by (Kelly et al. 2008; Kelly and Gwynne 2. Once a male locates a receptive female, he uses his antennae and legs to remain in physical contact with her and follows her until they pair up in a diurnal refuge (McIntyre 2001; Watts et al. 2012). The pair remains together at least until the following night and copulate repeatedly throughout the day (McIntyre 2001; Kelly et al. 2008; Kelly et al. 2010; Kelly and Gwynne 2017; Kelly and Gwynne 2023b; Kelly and Gwynne 2023a).

I use radio telemetry to track the nightly distance travelled (i.e. mobility) by male and female *D. rugosa* over several days to test the prediction that females exhibit more consistent mobility than males because female travel distance is dictated largely by readily available food whereas male mobility is dictated by females being stochastically dispersed throughout the environment. I will also correlate individual average mating success with behavioural (un)predictability to test if being more or less predictable confers a mating advantage.

# Methods

This field study was conducted 5-18 March 2019 in an abandoned and regenerating pasture on the southern side of Te Pākeka/Maud Island, New Zealand (41°02′S, 173°54′E), a 309-ha scientific reserve free of alien predators (e.g., rodents Mus and Rattus spp. and stoats Mustela erminea) (see Kelly and Gwynne 2023b; Kelly and Gwynne 2023a for details).

Adult giant weta were hand-collected by scanning the open ground and pastures at night. A 0.35 g radio transmitter (Pip Ag337; Lotek, Newmarket, Canada) was affixed to the pronotum with cyanoacrylate glue while ensuring that the antenna pointed backwards (McIntyre 2001; Kelly et al. 2008). Transmitters represent 3.83% and 1.74% of male and female body mass, respectively. Weta were released at their point of capture. I used radio telemetry to locate radio-tagged weta once each day while in their diurnal refuge. When located I noted whether the radio-tagged weta was paired with an opposite-sex individual. I then placed a field flag at the location point and measured the distance in meters between the current flag and the one from the previous day using a 50-m fibreglass tape measure. This straight-line distance is assumed to be the distance travelled by the tagged weta the previous night. The nightly travel distance was repeatedly measured 7.44 ± 0.56 (n = 16) times, on average, for females and 5.76 ± 0.45 (n = 16) times for males. Females and males were observed a total of 127 and 108 times, respectively (see electronic supplementary material, figure S1).

I calculated mating success by dividing the total number of times that an individual was found paired with an opposite-sex conspecific by the total number of times they were located.

### Statistical analysis

Statistical analyses were performed within the R v. 4.2.1 statistical environment (R Core Team 2024). I used an inverse hyperbolic sine transformation in the R package *bestNormalize* (Peterson 2021) to transform nightly travel distance (m) to approximate a Gaussian error distribution. To aid model fitting and interpretation of parameter estimates, observation number (1–8) was left-centred so that the first observation = 0, and transformed travel distance and sex were scaled (mean = 0, SD = 1; female = -0.5, male = 0.5) before analysis. Scaling sex provided variance estimates for the “average” weta irrespective of sex (Hertel et al. 2021).

I fitted a Bayesian double hierarchical generalized linear mixed-effects (DHGLM) multivariable model to investigate sex differences in mean- and residual-level nightly travel distance using the R package brms (Bürkner 2017). A DHGLM simultaneously estimates average-level behavioural types (the mean part) and the residual variance (the dispersion part) as a function of fixed effects. The dispersion part of a DHGLM estimates the residual intra-individual variation (i.e., rIIV) around a behavioural type with larger values indicating less predictability (Hertel et al. 2021). The mean model contained the fixed effects sex and observation number and their interaction to explore whether the sexes differed in how they altered their travel distance over time. Individual ID and observation number were included as random intercepts and slopes, respectively. The residual model contained the fixed effect sex to test the prediction that females and males differed in mobility predictability and individual ID and observation number as random intercepts and slopes, respectively. This model included travel distance as the dependent variable and was run on four chains using uninformative default priors for a total of 10000 iterations, with a warm-up of 6000, and a thinning interval of 4. Model convergence was verified with sufficient mixing of trace plots, with all Rhat values = 1. I report posterior means with 95% credible intervals (CrI), with inference based on CrIs not overlapping zero.

I extracted mobility behavioural type as the mean and credible interval of the posterior distribution of each individual’s random intercept. I then extracted the posterior distribution of the rIIV for each level of the random intercept as an indicator of behavioural predictability. Each of these measures of behavioural variation was then correlated with individual average mating success using a Pearson product-moment correlation. Correlations were made for each sex separately.

Data were visualized using the R package *ggplot2* (Wickham 2016). Unless otherwise noted, means are given ± one standard error of the mean (SEM).

# Results

A previous report on this population of animals (Kelly and Gwynne 2023a) showed that males (18.77 ± 4.46 m/night, n = 17) travel significantly farther per night on average than females (7.89 ± 1.26 m/night, n = 16) and that travel distance is significantly repeatable in both sexes (males: R = 0.60 [0.33–0.77], n = 17; females: R = 0.30 [0.06–0.51], n = 16) with sex explaining approximately 8% of the variation in travel distance (see supplemental material).

The population level mean residual standard deviation for nightly travel distance is 7.66 m (back-transformed intercept of the dispersion model exp(y0) = -0.47; [Table 1](#tbl-one)). As predicted, females were more predictable in their nightly travel distance than males (ysex = 0.32 [0.04, 0.57]; [Figure 1](#fig-one)). The predicted standard deviation from the mean residual standard deviation (rIIV) for nightly travel distance varied across individuals (2ID = 0.12 [0.01, 0.32]), which suggests that the predictability of nightly movement differs across individuals.

Behavioural type was not correlated with predictability (*r* = -0.12 [-0.87, 0.78]) nor was mating success correlated with behavioural predictability (females: *r* = -0.122, df = 14, p=0.654; males: *r* = 0.064, df = 15, p=0.807) or behavioural type (females: *r* = 0.10, df = 14, p=0.714; males: *r* = -0.19, df = 15, p=0.453) in either sex.

# Discussion

My field study found, as predicted, that adult male *D. rugosa* were less predictable in their nightly travel distance than females but there was no correlation between behavioural type (i.e. nightly travel distance) and predictability. Moreover, behavioural predictability did not correlate with mating success. The observed sex difference in behavioural predictability is likely caused by passive plasticity.

I hypothesize that the greater predictability of female nightly travel distance likely reflects passive plasticity rather than adaptive residual within-individual variation (Westneat et al. 2015). Females travel significantly less per night, on average than males (Kelly et al. 2008; Kelly and Gwynne 2023a), likely because adequate forage and diurnal refuges happen to be nearby and do not require extensive travel. Short travel distances are likely also adaptive for females because less travel means smaller energetic costs (Kelly and Gwynne 2016). In contrast, male unpredictability also likely reflects passive plasticity as male travel distance is dictated by female proximity (Kelly and Gwynne 2016; Kelly and Gwynne 2023a) meaning that the sooner a mate is found, the less a male travels (Watts et al. 2011). Once a female is located, the male follows her until she finds a suitable place to refuge for the day. The travel distance from the point of mate location by the male to the daytime refugia is generally quite short (i.e. a few metres). Since sexually receptive females are stochastically distributed across the landscape male distance-to-location should vary across nights. Neither male nor female mating success correlated with behavioural predictability. Females are likely predictable for non-reproductive reasons therefore a lack of correlation with mating success is not surprising. On the other hand, it is surprising that there appears to be little reproductive advantage to males in being unpredictable further supporting the hypothesis that their plasticity is passive rather than adaptive.

Hertel et al. (2020) also found that male African elephants (*Loxodonta africanus*) tend to be less predictable than females in their daily travel distance, however, no biological explanation was provided for this sex difference. Another study showed considerable variation among female brown bears (*Ursus arctos*) in the predictability of their daily movement distances (Hertel et al. 2021). Unlike the current study, Hertel et al. (2021) showed that behavioural type correlates with behavioural predictability as more predictable bears moved less per day on average and were less diurnal than less predictable bears.

Although there is a paucity of studies examining sex differences in movement behaviour (see Spiegel et al. 2017), a handful of studies have examined sex differences in the predictability of other fitness-related behaviours (White and Briffa 2017; Horváth et al. 2019; McLean and Morrell 2020; Brand et al. 2023). These studies suggest, however, that one sex is not more consistently predictable than the other. For example, Brand et al. (2023) found that male *Gambusia holbrooki* mosquitofish are more predictable than females in some behaviours but less predictable in others. They suggest that the sexes might adjust their behavioural consistency differently in response to subtle environmental changes.

Previous studies have shown that male *D. rugosa* move farther per night on average than females on Maud Island (Kelly et al. 2008; Kelly and Gwynne 2023a) and Karori Sanctuary (Watts et al. 2012) but not on Matiu-Somes Island (Watts et al. 2011). Population differences in sex-specific travel distances might be related to the higher population density on Matiu-Somes Island, making mate location easier for males (Watts et al. 2011). Kelly and Gwynne (2023a) showed that both males and females exhibit significant repeatability in their nightly travel distance suggesting that members of this species express behavioural types. I found, however, that type-dependent movement patterns in *D. rugosa* were not related to mating success in either sex. Perhaps behavioural types in this species confer survival advantages rather than reproductive benefits. Future work should identify how male and female *D. rugosa* benefit from adopting one behavioural type over another.

In conclusion, the sex difference in behavioural predictability exhibited by *D. rugosa* in the current study appears to be driven by male responses to female dispersion across the landscape. Confirmation of this hypothesis will require controlled laboratory tests wherein food, for example, is not provided and travel distance is measured. I would expect no sex difference in travel distance under this scenario because females will continue to walk in search of food and males will walk as far in search of females. We need to redress the paucity of published studies on sex differences in behavioural predictability, particularly regarding mobility (Spiegel et al. 2017), to elucidate if differences between males and females are the general pattern, and if so, identify why.

# Declarations

**Funding** Natural Sciences and Engineering Research Council of Canada (NSERC).

**Availability of data and materials** Data are available on Open Science Framework: https://doi.org/10.17605/OSF.IO/T9CEH

# References

Biro P, Adriaenssens B. 2013. Predictability as a personality trait: Consistent differences in intraindividual behavioral variation. Am Nat. 182(5):621–629.

Brand J, Henry J, Melo G, Wlodkowic D, Wong B, Martin J. 2023. Sex differences in the predictability of risk-taking behavior. Behav Ecol. 34(1):108–116.

Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. Anim Behav. 86(1):47–54.

Bürkner P-C. 2017. brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software. 80(1):4308.

Chang C, Teo H, Norma-Rashid Y, Li D. 2017. Predator personality and prey behavioural predictability jointly determine foraging performance. Sci Rep. 7:40734.

Cleasby IR, Nakagawa S, Schielzeth H. 2015. Quantifying the predictability of behaviour: Statistical approaches for the study of between‐individual variation in the within‐individual variance. Hadfield J, editor. Methods Ecol Evol. 6(1):27–37.

Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. Ecol Lett. 7(8):734–739.

Gangloff EJ, Leos-Barajas V, Demuth G, Zhang H, Kelly CD, Bronikowski AM. 2021. Movement modeling and patterns of within- and among-individual behavioral variation across time scales in neonate garter snakes (*T*hamnophis elegans). Behav Ecol Sociobiol. 75(12):162.

Hertel A, Niemelä P, Dingemanse N, Mueller T. 2020. A guide for studying among-individual behavioral variation from movement data in the wild. Mov Ecol. 8:30.

Hertel A, Royauté R, Zedrosser A, Mueller T. 2021. Biologging reveals individual variation in behavioural predictability in the wild. J Anim Ecol. 90(3):723–737.

Horváth G, Garamszegi L, Bereczki J, Urszán T, Balázs G, Herczeg G. 2019. Roll with the fear: Environment and state dependence of pill bug (armadillidium vulgare) personalities. The Science of Nature. 106(3-4):7.

Kelly CD. 2006. The relationship between resource control, association with females and male weapon size in a male dominance insect. Ethology. 112(4):362–369.

Kelly CD, Bussiere LF, Gwynne DT. 2010. Pairing and insemination patterns in a giant weta (*Deinacrida rugosa*: Orthoptera; Anostostomatidae). J Ethol. 28(3):483–489.

Kelly CD, Bussière LF, Gwynne DT. 2008. Sexual selection for male mobility in a giant insect with female-biased size dimorphism. Am Nat. 172(3):417–423.

Kelly CD, Gwynne DT. 2016. The effect of condition on mate searching speed and copulation frequency in the Cook Strait giant weta. Behav Ecol Sociobiol. 70(8):1403–1409.

Kelly CD, Gwynne DT. 2017. Do male Cook Strait giant weta prudently allocate sperm. J Insect Behav. 30(3):308–317.

Kelly CD, Gwynne DT. 2023a. Effect of body condition on mobility and mating success in a wild population of the scramble polygynous Cook Strait giant weta. Behav Ecol Sociobiol. 77:5.

Kelly CD, Gwynne DT. 2023b. Mating assortment and the strength of sexual selection in a polyandrous population of cook strait giant weta. Behav Ecol. 34:506–513.

McIntyre M. 2001. The ecology of some large weta species in New Zealand. In: Field LH, editor. The biology of wetas, king crickets and their allies. Wallingford, UK: CABI Publishing. p. 225–242.

McLean S, Morrell L. 2020. Consistency in the strength of laterality in male, but not female, guppies across different behavioural contexts. Biol Lett. 16(5):20190870.

Peterson RA. 2021. Finding optimal normalizing transformations via best normalize. R Journal. 13(1):2312–2327.

R Core Team. 2024. R: A language and environment for statistical computing.

Scheiner SM. 2006. Genotype-environment interactions and evolution. In: Fox C, Wolf J, editors. Evolutionary genetics: Concepts and case studies. Oxford, UK: Oxford ÉUniversity Press. p. 326–338.

Schuett W, Tregenza T, Dall S. 2010. Sexual selection and animal personality. Biol Rev Camb Philos Soc. 85(2):217–246.

Spiegel O, Leu S, Bull C, Sih A. 2017. What’s your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol Lett. 20(1):3–18.

Stamps JA, Briffa M, Biro PA. 2012. Unpredictable animals: Individual differences in intraindividual variability (IIV). Anim Behav. 83(6):1325–1334.

Watts C, Empson R, Thornburrow D, Rohan M. 2012. Movements, behaviour and survival of adult Cook Strait giant weta (*Deinacrida rugosa*; Anostostomatidae: Orthoptera) immediately after translocation as revealed by radiotracking. J Insect Conserv. 16(5):763–776.

Watts C, Stringer I, Thornburrow D, MacKenzie D. 2011. Are footprint tracking tunnels suitable for monitoring giant weta (Orthoptera: Anostostomatidae)? Abundance, distribution and movement in relation to tracking rates. J Insect Conserv. 15(3):433–443.

Westneat D, Wright J, Dingemanse N. 2015. The biology hidden inside residual within-individual phenotypic variation. Biological Reviews. 90(3):729–743.

White DJ, Watts C, Allwood J, Prada D, Stringer I, Thornburrow D, Buckley TR. 2017. Population history and genetic bottlenecks in translocated Cook Strait giant weta, *Deinacrida rugosa*: Recommendations for future conservation management. Conservation Genetics. 18(2):411–422.

White S, Briffa M. 2017. How do anthropogenic contaminants (ACs) affect behaviour? Multi-level analysis of the effects of copper on boldness in hermit crabs. Oecologia. 183(2):391–400.

Wickham H. 2016. ggplot2: Elegant graphics for data analysis. New York: Springer.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Table 1: Estimates [95% credible intervals, CrI] of fixed and random effects on nightly travel distance (mean model) and residual standard deviation of nightly travel distance (dispersion model) in Cook Strait giant weta (D. rugosa). Variation in mean behaviour and residual standard deviation of behaviour (rIIV) was estimated among individual weta of both sexes. Estimates are based on double hierarchical mixed models.   |  |  | | --- | --- | |  | **Estimate [95% CrI]** | | **Mean model** |  | | **Fixed effects** |  | | Intercept | 0.28 [-0.07, 0.63] | | Sex | 0.85 [0.13, 1.57] | | Observation.n | -0.07 [-0.15, 0.01] | | Sex x observation.n | -0.08 [-0.24, 0.08] | | **Random effects** |  | | sdintercept | 0.72 [0.43, 1.09] | | sdslope.observation.n | 0.09 [0.01, 0.17] | | *r*intercept-slope | -0.51 [-0.88, 0.50] | | **Dispersion model** |  | | **Fixed effects** |  | | Intercept | -0.47 [-0.65, -0.27] | | Sex | 0.32 [0.04, 0.57] | | **Random effects** |  | | ω2 | 0.12 [0.01, 0.32] | | *r*intercept-ω | -0.12 [-0.87, 0.78] | | *r*observation.n-ω | -0.11 [-0.88, 0.83] | |

# Figure

|  |
| --- |
| Figure 1: Sex difference in behavioural predictability in the Cook Strait giant weta (D. rugosa). Plots show the posterior probability distributions for residual within-individual variance (i.e., predictability) in nightly distance travelled extracted from a Bayesian double hierarchical linear mixed-effects model. Distributions are shown for females (red) and males (blue) with vertical dotted lines representing the posterior mean for each sex. |