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# **Passive plasticity and a sex difference in the predictability of mobility**

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For Review Only

## 7 **Abstract**

8 Behavioural predictability describes the behavioural variability of an individual.

9 Unpredictability can arise from many sources including non-adaptive passive plasticity in which

10 an environmental factor acts directly on the individual to create non-adaptive phenotypic

11 variation. In this study, I use radio telemetry to field test the hypothesis that Cook Strait giant

12 weta *Deinacrida rugosa* (Orthoptera: Anostomatidae) exhibit a sex difference in the

13 predictability of their nightly travel distance due to passive behavioural plasticity. As predicted,

14 I found that male mobility (i.e. nightly travel distance) was less predictable than female

15 mobility. Females travel short and predictable distances each night for food and refuges that are

16 close by and readily available. In contrast, male travel is less predictable because they search for

17 female mates that are stochastically dispersed across the landscape. Therefore, their travel

18 distance can vary considerably across nights.

19

## 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) [1–4]. 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) [2]. 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 [5] or if consistency indicates quality that can be used in mate choice by the choosy sex [6]. Decreased behavioural predictability (i.e. larger  $rIIV$ ) is also possible if individual variation is a product of individual state or environmental differences [7–10].

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 [11]. 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 [2]. Therefore, individual animal phenotypes might contain some stochastic variation that would be present as heterogeneous residual phenotypic variance if left unaccounted [2].

43 In this study, I field test the hypothesis that Cook Strait giant weta *Deinacrida rugosa*  
44 (Orthoptera: Anostomatidae) exhibit a sex difference in the predictability of their mobility  
45 due to passive behavioural plasticity. *Deinacrida rugosa* is a sexually size dimorphic nocturnal  
46 insect that is of high conservation importance [12,13]. It is endemic to New Zealand where it  
47 inhabits old pastures, forests, and coastal scrub [12,13]. Both sexes seek refuge from predators  
48 during the day by hiding under vegetation or other objects on the ground [12]. *Deinacrida*  
49 *rugosa* exhibits a scramble competitive mating system in which males search for receptive  
50 females as mates at night while females are foraging [14,15]. Males do not defend resources  
51 required by sexually receptive females, nor do they guard harems of females, as do other  
52 deinacridine weta [12,16]. Mate searching results in males travelling considerably longer  
53 distances per night than females. In contrast, female nightly travel is generally short because  
54 suitable forage is close by (Kelly et al. 2008; Kelly and Gwynne 2002). Once a male locates a  
55 receptive female, he uses his antennae and legs to remain in physical contact with her and  
56 follows her until they pair up in a diurnal refuge [12,17]. The pair remains together at least until  
57 the following night and copulate repeatedly throughout the day [12,14,15,18–20].

58 I use radio telemetry to track the nightly distance travelled (i.e. mobility) by male and female *D.*  
59 *rugosa* over several days to test the prediction that females exhibit more consistent mobility than  
60 males because female travel distance is dictated largely by readily available food whereas male  
61 mobility is dictated by females being stochastically dispersed throughout the environment. I will  
62 also correlate individual average mating success with behavioural (un)predictability to test if  
63 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*) [15 for details, see 18].

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 [12,14]. 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  $7.44 \pm 0.56$  (n = 16) times, on average, for females and  $5.76 \pm 0.45$  (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.

## 84 **Statistical analysis**

85 Statistical analyses were performed within the R v. 4.2.1 statistical environment [21]. I used an  
86 inverse hyperbolic sine transformation in the R package *bestNormalize* [22] to transform nightly  
87 travel distance (m) to approximate a Gaussian error distribution. To aid model fitting and  
88 interpretation of parameter estimates, observation number (1–8) was left-centred so that the first  
89 observation = 0, and transformed travel distance and sex were scaled (mean = 0, SD = 1; female  
90 = -0.5, male = 0.5) before analysis. Scaling sex provided variance estimates for the “average”  
91 weta irrespective of sex [23].

92 I fitted a Bayesian double hierarchical generalized linear mixed-effects (DHGLM) multivariable  
93 model to investigate sex differences in mean- and residual-level nightly travel distance using the  
94 R package *brms* [24]. A DHGLM simultaneously estimates average-level behavioural types (the  
95 mean part) and the residual variance (the dispersion part) as a function of fixed effects. The  
96 dispersion part of a DHGLM estimates the residual intra-individual variation (i.e., rIIV) around  
97 a behavioural type with larger values indicating less predictability [23]. The mean model  
98 contained the fixed effects sex and observation number and their interaction to explore whether  
99 the sexes differed in how they altered their travel distance over time. Individual ID and  
100 observation number were included as random intercepts and slopes, respectively. The residual  
101 model contained the fixed effect sex to test the prediction that females and males differed in  
102 mobility predictability and individual ID and observation number as random intercepts and  
103 slopes, respectively. This model included travel distance as the dependent variable and was run  
104 on four chains using uninformative default priors for a total of 10000 iterations, with a warm-up  
105 of 6000, and a thinning interval of 4. Model convergence was verified with sufficient mixing of



trace plots, with all  $R_{\text{hat}}$  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 packages *ggplot2* [25]. Unless otherwise noted, means are given  $\pm$  one standard error of the mean (SEM).

## Results

A previous report on this population of animals [15] showed that males ( $18.77 \pm 4.46$  m/night,  $n = 17$ ) travel significantly farther per night on average than females ( $7.89 \pm 1.26$  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  $\exp(y_0) = -0.47$ ; Table 1). As predicted, females were more predictable in their nightly travel distance than males ( $y_{\text{sex}} = 0.32$  [0.04, 0.57]; Figure 1). The predicted standard deviation from the mean residual standard deviation (rIIV) for nightly travel distance varied across individuals ( $\omega^2_{\text{ID}} = 0.12$  [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 [2]. Females travel significantly less per night, on average than males [14,15], 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 [26]. In contrast, male unpredictability also likely reflects passive plasticity as male travel distance is dictated by female proximity [15,26] meaning that the sooner a mate is found, the less a male travels [27]. 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. [28] 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 [23]. Unlike the current study, Hertel et al. [23] 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 29], a handful of studies have examined sex differences in the predictability of other fitness-related behaviours [9,30–32]. These studies suggest, however, that one sex is not more consistently predictable than the other. For example, Brand et al. [32] 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 [14,15] and Karori Sanctuary [17] but not on Matiu-Somes Island [27]. 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 [27]. Kelly and Gwynne [15] 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 [29], to elucidate if differences between males and females is the general pattern, and if so, identify why.

## Declarations

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**Availability of data and materials** The data are provided online at the Open Science Framework [33].

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- 274

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 (*r*<sub>IIV</sub>) 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	
sd <sub>intercept</sub>	0.72 [0.43, 1.09]
sd <sub>slope.observation.n</sub>	0.09 [0.01, 0.17]
r <sub>intercept-slope</sub>	-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	
ω <sup>2</sup>	0.12 [0.01, 0.32]
r <sub>intercept-ω</sub>	-0.12 [-0.87, 0.78]
r <sub>observation.n-ω</sub>	-0.11 [-0.88, 0.83]



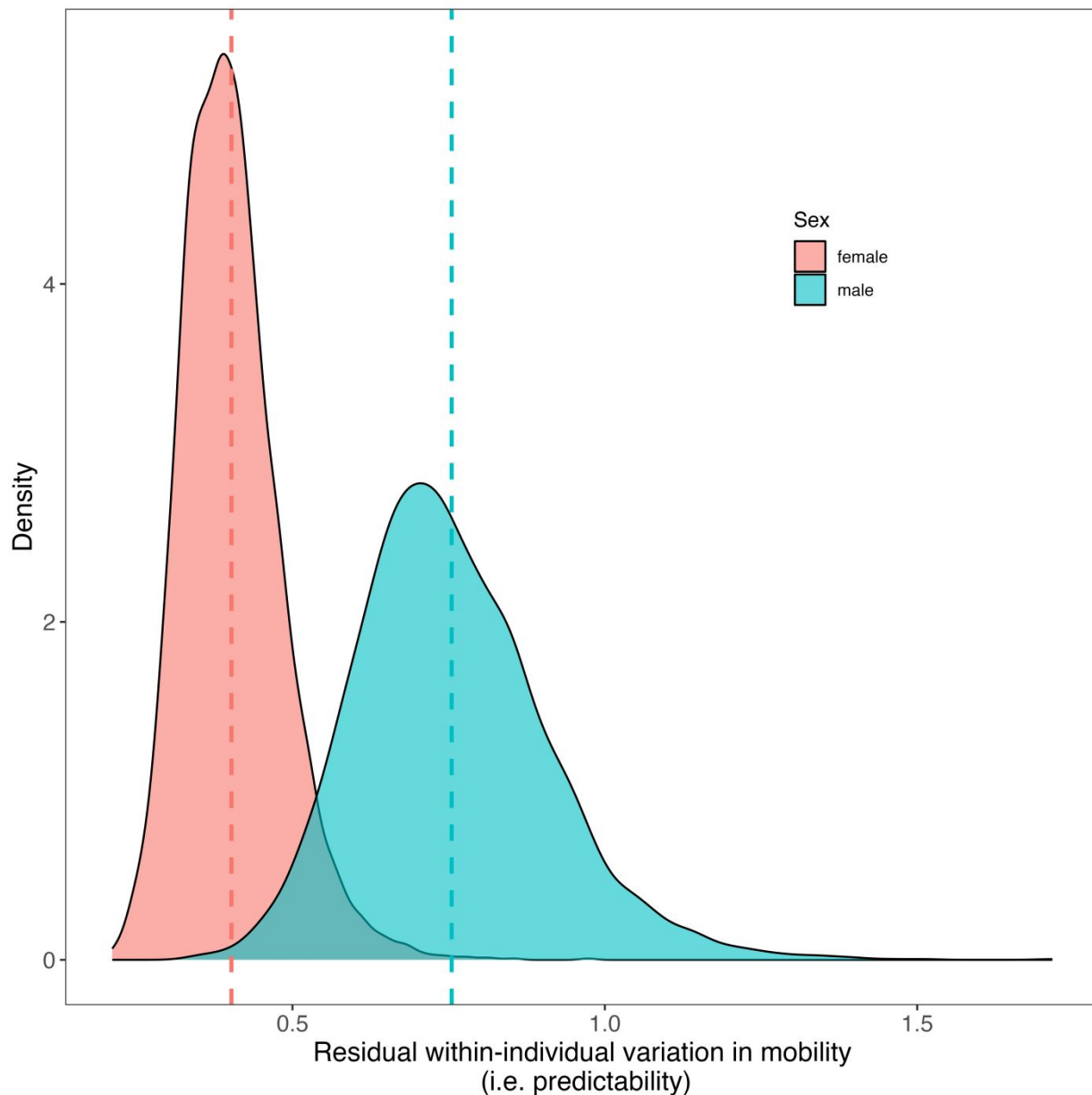
276 **Figure**

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.

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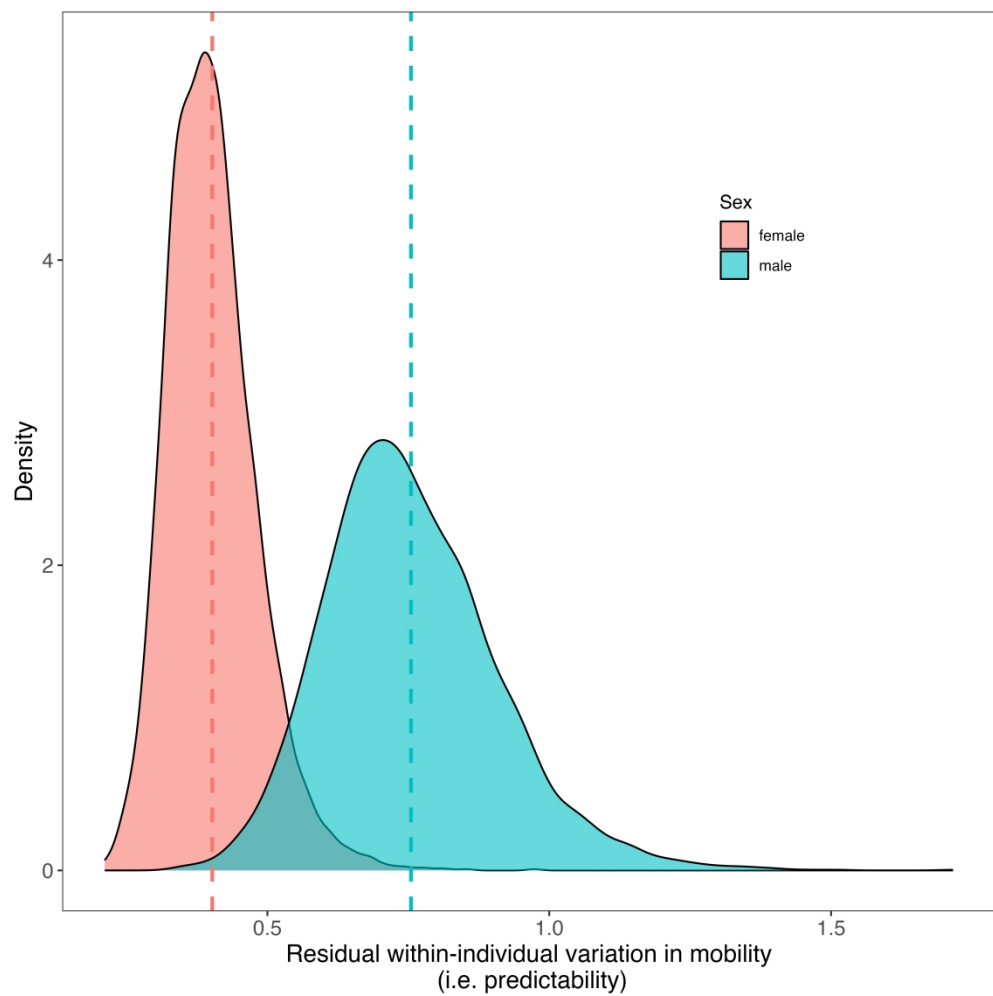


Figure 1: Sex difference in behavioural predictability in the Cook Strait giant weta (*D. rugosa*). Plots show the posterior probability distributions for residual within-individual variance (i.e., predictability) in nightly distance travelled extracted from a Bayesian double hierarchical linear mixed-effects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

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