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Passive plasticity and a sex difference in the predictability of mobility

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7 **Abstract**

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

20

Introduction

Individuals can differ in their behavioural predictability, defined as residual intra-individual variation (i.e. r_{IIV}), after controlling for individual variation in behavioural type (i.e. average behaviour) and behavioural plasticity (i.e. within-individual variation) (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 a variety of 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 r_{IIV}) could be selected if it improves success in agonistic encounters (e.g. Johnstone 2001) or mating competition (Schuett et al. 2010) or if decreased behavioural predictability (i.e. larger r_{IIV}) improves survival (Briffa et al. 2013; Chang et al. 2017; Horváth et al. 2019; see also Brand et al. 2023).

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 prey could exhibit unpredictable variance if the location of prey is not known by the forager when foraging commences or if daily travel distance is dependent 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, if not otherwise accounted for, would be present as heterogeneous residual phenotypic variance (Westneat et al. 2015).

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 endemic to New Zealand and of high conservation importance (McIntyre 2001;
47 White et al. 2017). It inhabits old pastures, forests, and coastal scrub, and seeks refuge from
48 predators in the daytime by hiding under vegetation or other objects on the ground (McIntyre
49 2001). *Deinacrida rugosa* exhibits a scramble competitive mating system wherein males do not
50 defend resources required by sexually receptive females, nor do they guard harems of females,
51 as do other deinacridine weta (McIntyre 2001; Kelly 2006). Rather, male *D. rugosa* seek
52 receptive females as mates at night while females are foraging (McIntyre 2001). Mate searching
53 results in males travelling considerably longer distances per night than females (Kelly et al.
54 2008; Kelly and Gwynne 2023a). In contrast, female nightly travel is generally short because
55 suitable forage is close by (Kelly et al. 2008; Kelly and Gwynne 2023a). Once a male locates a
56 receptive female, he remains in physical contact with her by using either his antennae or his legs
57 and follows her until they pair up in a diurnal refuge (McIntyre 2001; Watts et al. 2012). The
58 pair remains together at least until the following night and copulate repeatedly throughout the
59 day (McIntyre 2001; Kelly et al. 2008; Kelly et al. 2010; Kelly and Gwynne 2017; Kelly and
60 Gwynne 2023b; Kelly and Gwynne 2023a).

61 I use radio telemetry to track the nightly distance travelled (i.e. mobility) by male and female *D.*
62 *rugosa* over several days to test the prediction that females exhibit more consistent mobility than
63 males because female travel distance is dictated largely by readily available food whereas male
64 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 each day. 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 for females and 5.76 ± 0.45 (n = 16) times for males.

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.

85 **Statistical analysis**

86 Statistical analyses were performed within the R v. 4.2.1 statistical environment (R Core Team
87 2024). I used an inverse hyperbolic sine transformation in the R package *bestNormalize*
88 (Peterson 2021) to transform nightly travel distance (m) to approximate a Gaussian error
89 distribution. To aid model fitting and interpretation of parameter estimates, observation number
90 (1–8) was left-centred so that the first observation = 0, and transformed travel distance and sex
91 were scaled (mean = 0, SD = 1; female = -0.5, male = 0.5) before analysis. Scaling sex provided
92 variance estimates for the “average” weta irrespective of sex (Hertel et al. 2021).

93 I fitted a Bayesian double hierarchical generalized linear mixed-effects (DHGLM) multivariable
94 model to investigate sex differences in mean- and residual-level nightly travel distance using the
95 R package *brms* (Bürkner 2017). A DHGLM simultaneously estimates average-level
96 behavioural types (the mean part) and the residual variance (the dispersion part) as a function of
97 fixed effects. The dispersion part of a DHGLM estimates the residual intra-individual variation
98 (i.e., rIIV) around a behavioural type with larger values indicating less predictability (Hertel et
99 al. 2021). The mean model contained the fixed effects sex and observation number and their
100 interaction to explore whether the sexes differed in how they altered their travel distance over
101 time. Individual ID and observation number were included as random intercepts and slopes,
102 respectively. The residual model contained the fixed effect sex to test the prediction that females
103 and males differed in mobility predictability and individual ID and observation number as
104 random intercepts and slopes, respectively. This model included travel distance as the dependent
105 variable and was run on four chains using relatively uninformative, default priors for a total of
106 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 R_{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* (Wickham 2016). Means are given \pm one standard error of the mean (SEM) unless otherwise noted.

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], $n = 16$).

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 ($y_{sex} = 0.32$ [0.04, 0.57]; Figure 1). The predicted standard deviation from the mean residual standard deviation (rIIV) for nightly travel distance varied across individuals ($\omega^2_{ID} = 0.12$ [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 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: $r = -0.19$, $df = 15$, $p = 0.453$) correlated with mating success 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 is the general pattern, and if so, identify why.

Declarations

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Availability of data and materials Data are available on Open Science Framework:

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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*_{IIV}) 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 _{intercept}	0.72 [0.43, 1.09]
sd _{slope.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	
ω ²	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]

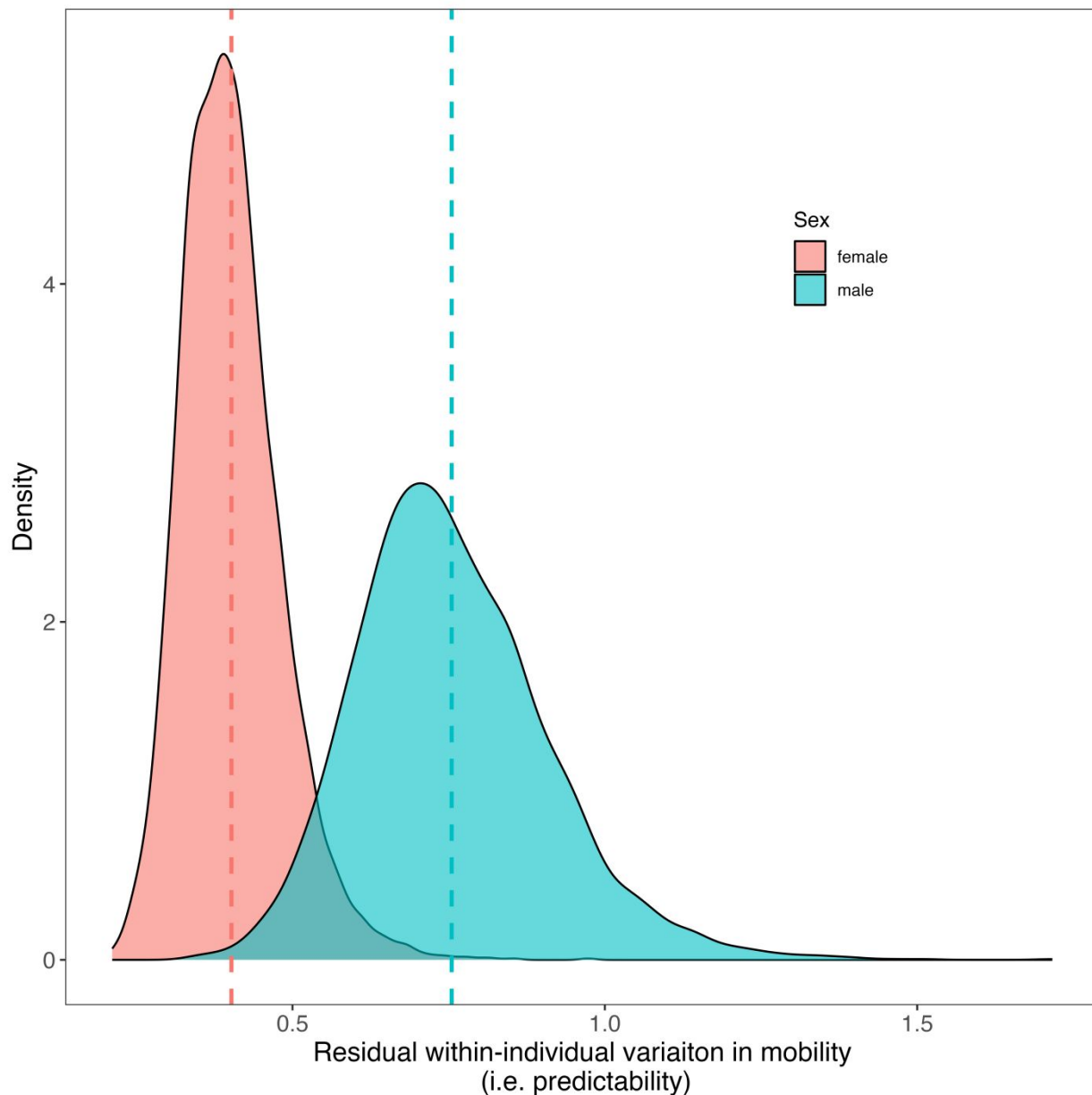
271 **Figure**

Figure 1: Sex difference in behavioural predictability in the Cook Strait giant weta (*D. rugosa*). Plots represent 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 posterior means for each sex, respectively.

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