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Passive plasticity and a sex difference in the predictability of mobility

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Abstract

7

8   Behavioural predictability (i.e. residual within-individual variation) 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: Anostostomatidae)

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

21

22   Individuals can differ in their behavioural predictability, defined as residual intra-individual

23   variation (i.e. rIIV), after controlling for individual variation in behavioural type (i.e. average

24   behaviour) and behavioural plasticity (i.e. context-dependent within-individual variation

25   represented as a reaction norm slope) (Stamps et al. 2012; Biro and Adriaenssens 2013; Cleasby

26   et al. 2015; Westneat et al. 2015). Unpredictable individuals exhibit high variability around their

27   behavioural type and reaction norm slope whereas predictable individuals do not (i.e. exhibit

28   little residual variance). Within-individual residual variance can arise from various non-

29   biological sources including sampling or measurement error and incompletely or inaccurately

30   parameterizing statistical models (i.e. terms are missing from the model that could explain or

31   account for residual heterogeneity) (Westneat et al. 2015). Conversely, greater behavioural

32   predictability (i.e. smaller rIIV) could be selected if consistent behaviour influences the future

33   responses of competitors in such a way that confers advantages upon the focal individual (Dall

34   et al. 2004) or if consistency indicates quality that can be used in mate choice by the choosy sex

35   (Schuett et al. 2010). Decreased behavioural predictability (i.e. larger rIIV) is also possible if

36   individual variation is a product of individual state or environmental differences (Briffa et al.

37   2013; Chang et al. 2017; Horváth et al. 2019; Gangloff et al. 2021).

38   Behavioural predictability could also be weakened by non-adaptive processes such as passive

39   plasticity whereby an environmental factor acts directly on the individual and creates non-

40   adaptive phenotypic variation (Scheiner 2006). For example, the time to find food could exhibit

41   unpredictable variance if the forager does not know the food's location when foraging

42   commences or if daily travel distance depends on the number and type of predators encountered,

43   which can be stochastic (Westneat et al. 2015). Therefore, individual animal phenotypes might

44 contain some stochastic variation that would be present as heterogeneous residual phenotypic

45 variance if left unaccounted (Westneat et al. 2015).

46 In this study, I field test the hypothesis that Cook Strait giant weta *Deinacrida rugosa*

47 (Orthoptera: Anostostomatidae) exhibit a sex difference in the predictability of their mobility

48 due to passive behavioural plasticity. *Deinacrida rugosa* is a sexually size dimorphic nocturnal

49 insect that is of high conservation importance (McIntyre 2001; White et al. 2017). It is endemic

50 to New Zealand where it inhabits old pastures, forests, and coastal scrub (McIntyre 2001; White

51 et al. 2017). Both sexes seek refuge from predators during the day by hiding under vegetation or

52 other objects on the ground (McIntyre 2001). *Deinacrida rugosa* exhibits a scramble

53 competitive mating system in which males search for receptive females as mates at night while

54 females are foraging (Kelly et al. 2008; Kelly and Gwynne 2023a). Males do not defend

55 resources required by sexually receptive females, nor do they guard harems of females, as do

56 other deinacridine weta (McIntyre 2001; Kelly 2006). Mate searching results in males travelling

57 considerably longer distances per night than females. In contrast, female nightly travel is

58 generally short because suitable forage is close by (Kelly et al. 2008; Kelly and Gwynne 2. Once

59 a male locates a receptive female, he uses his antennae and legs to remain in physical contact

60 with her and follows her until they pair up in a diurnal refuge (McIntyre 2001; Watts et al.

61 2012). The pair remains together at least until the following night and copulate repeatedly

62 throughout the day (McIntyre 2001; Kelly et al. 2008; Kelly et al. 2010; Kelly and Gwynne

63 2017; Kelly and Gwynne 2023b; Kelly and Gwynne 2023a).

64 I use radio telemetry to track the nightly distance travelled (i.e. mobility) by male and female *D.*

65 *rugosa* over several days to test the prediction that females exhibit more consistent mobility than

66 males because female travel distance is dictated largely by readily available food whereas male

67   mobility is dictated by females being stochastically dispersed throughout the environment. I will

68   also correlate individual average mating success with behavioural (un)predictability to test if

69   being more or less predictable confers a mating advantage.

70   **Methods**

71   This field study was conducted 5-18 March 2019 in an abandoned and regenerating pasture on

72   the southern side of Te Pākeka/Maud Island, New Zealand (41°02′S, 173°54′E), a 309-ha

73   scientific reserve free of alien predators (e.g., rodents Mus and Rattus spp. and stoats Mustela

74   erminea) (see Kelly and Gwynne 2023b; Kelly and Gwynne 2023a for details).

75   Adult giant weta were hand-collected by scanning the open ground and pastures at night. A 0.35

76   g radio transmitter (Pip Ag337; Lotek, Newmarket, Canada) was affixed to the pronotum with

77   cyanoacrylate glue while ensuring that the antenna pointed backwards (McIntyre 2001; Kelly et

78   al. 2008). Transmitters represent 3.83% and 1.74% of male and female body mass, respectively.

79   Weta were released at their point of capture. I used radio telemetry to locate radio-tagged weta

80   once each day while in their diurnal refuge. When located I noted whether the radio-tagged weta

81   was paired with an opposite-sex individual. I then placed a field flag at the location point and

82   measured the distance in meters between the current flag and the one from the previous day

83   using a 50-m fibreglass tape measure. This straight-line distance is assumed to be the distance

84   travelled by the tagged weta the previous night. The nightly travel distance was repeatedly

85   measured 7.44 ± 0.56 (n = 16) times, on average, for females and 5.76 ± 0.45 (n = 16) times for

86   males. Females and males were observed a total of 127 and 108 times, respectively (see

87   electronic supplementary material, figure S1).

88   I calculated mating success by dividing the total number of times that an individual was found

89   paired with an opposite-sex conspecific by the total number of times they were located.

90   **Statistical analysis**

91   Statistical analyses were performed within the R v. 4.2.1 statistical environment (R Core Team

92   2024). I used an inverse hyperbolic sine transformation in the R package *bestNormalize*

93   (Peterson 2021) to transform nightly travel distance (m) to approximate a Gaussian error

94   distribution. To aid model fitting and interpretation of parameter estimates, observation number

95   (1–8) was left-centred so that the first observation = 0, and transformed travel distance and sex

96   were scaled (mean = 0, SD = 1; female = -0.5, male = 0.5) before analysis. Scaling sex provided

97   variance estimates for the "average" weta irrespective of sex (Hertel et al. 2021).

98   I fitted a Bayesian double hierarchical generalized linear mixed-effects (DHGLM) multivariable

99   model to investigate sex differences in mean- and residual-level nightly travel distance using the

100   R package brms (Bürkner 2017). A DHGLM simultaneously estimates average-level

101   behavioural types (the mean part) and the residual variance (the dispersion part) as a function of

102   fixed effects. The dispersion part of a DHGLM estimates the residual intra-individual variation

103   (i.e., rIIV) around a behavioural type with larger values indicating less predictability (Hertel et

104   al. 2021). The mean model contained the fixed effects sex and observation number and their

105   interaction to explore whether the sexes differed in how they altered their travel distance over

106   time. Individual ID and observation number were included as random intercepts and slopes,

107   respectively. The residual model contained the fixed effect sex to test the prediction that females

108   and males differed in mobility predictability and individual ID and observation number as

109   random intercepts and slopes, respectively. This model included travel distance as the dependent

110   variable and was run on four chains using uninformative default priors for a total of 10000

111   iterations, with a warm-up of 6000, and a thinning interval of 4. Model convergence was

112   verified with sufficient mixing of trace plots, with all Rhat values = 1. I report posterior means

113   with 95% credible intervals (CrI), with inference based on CrIs not overlapping zero.

114   I extracted mobility behavioural type as the mean and credible interval of the posterior

115   distribution of each individual's random intercept. I then extracted the posterior distribution of

116   the rIIV for each level of the random intercept as an indicator of behavioural predictability. Each

117   of these measures of behavioural variation was then correlated with individual average mating

118   success using a Pearson product-moment correlation. Correlations were made for each sex

119   separately.

120   Data were visualized using the R package *ggplot2* (Wickham 2016). Unless otherwise noted,

121   means are given ± one standard error of the mean (SEM).

Results

123   A previous report on this population of animals (Kelly and Gwynne 2023a) showed that males

124   (18.77 ± 4.46 m/night, n = 17) travel significantly farther per night on average than females

125   (7.89 ± 1.26 m/night, n = 16) and that travel distance is significantly repeatable in both sexes

126   (males: R = 0.60 [0.33–0.77], n = 17; females: R = 0.30 [0.06–0.51], n = 16) with sex explaining

127   approximately 8% of the variation in travel distance (see supplemental material).

128   The population level mean residual standard deviation for nightly travel distance is 7.66 m

129   (back-transformed intercept of the dispersion model $\exp(y_0) = -0.47$; Table 1). As predicted,

130   females were more predictable in their nightly travel distance than males ($y_{sex} = 0.32$ [0.04,

131   0.57]; Figure 1). The predicted standard deviation from the mean residual standard deviation

132 (rIIV) for nightly travel distance varied across individuals (ω^2_{ID} = 0.12 [0.01, 0.32]), which

133 suggests that the predictability of nightly movement differs across individuals.

134 Behavioural type was not correlated with predictability (r = -0.12 [-0.87, 0.78]) nor was mating

135 success correlated with behavioural predictability (females: r = -0.122, df = 14, p=0.654; males:

136 r = 0.064, df = 15, p=0.807) or behavioural type (females: r = 0.10, df = 14, p=0.714; males: r =

137 -0.19, df = 15, p=0.453) in either sex.

138 **Discussion**

139 My field study found, as predicted, that adult male *D. rugosa* were less predictable in their

140 nightly travel distance than females but there was no correlation between behavioural type

141 (i.e. nightly travel distance) and predictability. Moreover, behavioural predictability did not

142 correlate with mating success. The observed sex difference in behavioural predictability is likely

143 caused by passive plasticity.

144 I hypothesize that the greater predictability of female nightly travel distance likely reflects

145 passive plasticity rather than adaptive residual within-individual variation (Westneat et al.

146 2015). Females travel significantly less per night, on average than males (Kelly et al. 2008;

147 Kelly and Gwynne 2023a), likely because adequate forage and diurnal refuges happen to be

148 nearby and do not require extensive travel. Short travel distances are likely also adaptive for

149 females because less travel means smaller energetic costs (Kelly and Gwynne 2016). In contrast,

150 male unpredictability also likely reflects passive plasticity as male travel distance is dictated by

151 female proximity (Kelly and Gwynne 2016; Kelly and Gwynne 2023a) meaning that the sooner

152 a mate is found, the less a male travels (Watts et al. 2011). Once a female is located, the male

153 follows her until she finds a suitable place to refuge for the day. The travel distance from the

154   point of mate location by the male to the daytime refugia is generally quite short (i.e. a few

155   metres). Since sexually receptive females are stochastically distributed across the landscape

156   male distance-to-location should vary across nights. Neither male nor female mating success

157   correlated with behavioural predictability. Females are likely predictable for non-reproductive

158   reasons therefore a lack of correlation with mating success is not surprising. On the other hand,

159   it is surprising that there appears to be little reproductive advantage to males in being

160   unpredictable further supporting the hypothesis that their plasticity is passive rather than

161   adaptive.

162   Hertel et al. (2020) also found that male African elephants (*Loxodonta africanus*) tend to be less

163   predictable than females in their daily travel distance, however, no biological explanation was

164   provided for this sex difference. Another study showed considerable variation among female

165   brown bears (*Ursus arctos*) in the predictability of their daily movement distances (Hertel et al.

166   2021). Unlike the current study, Hertel et al. (2021) showed that behavioural type correlates

167   with behavioural predictability as more predictable bears moved less per day on average and

168   were less diurnal than less predictable bears.

169   Although there is a paucity of studies examining sex differences in movement behaviour (see

170   Spiegel et al. 2017), a handful of studies have examined sex differences in the predictability of

171   other fitness-related behaviours (White and Briffa 2017; Horváth et al. 2019; McLean and

172   Morrell 2020; Brand et al. 2023). These studies suggest, however, that one sex is not more

173   consistently predictable than the other. For example, Brand et al. (2023) found that male

174   *Gambusia holbrooki* mosquitofish are more predictable than females in some behaviours but

175   less predictable in others. They suggest that the sexes might adjust their behavioural consistency

176   differently in response to subtle environmental changes.

177   Previous studies have shown that male *D. rugosa* move farther per night on average than

178   females on Maud Island (Kelly et al. 2008; Kelly and Gwynne 2023a) and Karori Sanctuary

179   (Watts et al. 2012) but not on Matiu-Somes Island (Watts et al. 2011). Population differences in

180   sex-specific travel distances might be related to the higher population density on Matiu-Somes

181   Island, making mate location easier for males (Watts et al. 2011). Kelly and Gwynne (2023a)

182   showed that both males and females exhibit significant repeatability in their nightly travel

183   distance suggesting that members of this species express behavioural types. I found, however,

184   that type-dependent movement patterns in *D. rugosa* were not related to mating success in either

185   sex. Perhaps behavioural types in this species confer survival advantages rather than

186   reproductive benefits. Future work should identify how male and female *D. rugosa* benefit from

187   adopting one behavioural type over another.

188   In conclusion, the sex difference in behavioural predictability exhibited by *D. rugosa* in the

189   current study appears to be driven by male responses to female dispersion across the landscape.

190   Confirmation of this hypothesis will require controlled laboratory tests wherein food, for

191   example, is not provided and travel distance is measured. I would expect no sex difference in

192   travel distance under this scenario because females will continue to walk in search of food and

193   males will walk as far in search of females. We need to redress the paucity of published studies

194   on sex differences in behavioural predictability, particularly regarding mobility (Spiegel et al.

195   2017), to elucidate if differences between males and females are the general pattern, and if so,

196   identify why.

Declarations

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

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

200 https://doi.org/10.17605/OSF.IO/T9CEH

References

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

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

206 Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel
207 analysis of plasticity, personality and predictability in hermit crabs. Anim Behav.
208 86(1):47–54.

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

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

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

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

218 Gangloff EJ, Leos-Barajas V, Demuth G, Zhang H, Kelly CD, Bronikowski AM. 2021.
219 Movement modeling and patterns of within- and among-individual behavioral variation
220 across time scales in neonate garter snakes (*T*hamnophis elegans). Behav Ecol Sociobiol.
221 75(12):162.

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

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

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

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

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

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

235   Kelly CD, Gwynne DT. 2016. The effect of condition on mate searching speed and
236   copulation frequency in the Cook Strait giant weta. Behav Ecol Sociobiol. 70(8):1403–
237   1409.

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

240   Kelly CD, Gwynne DT. 2023a. Effect of body condition on mobility and mating success in a
241   wild population of the scramble polygynous Cook Strait giant weta. Behav Ecol Sociobiol.
242   77:5.

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

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

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

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

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

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

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

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

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

262   Watts C, Empson R, Thornburrow D, Rohan M. 2012. Movements, behaviour and survival
263   of adult Cook Strait giant weta (*Deinacrida rugosa*; Anostostomatidae: Orthoptera)
264   immediately after translocation as revealed by radiotracking. J Insect Conserv. 16(5):763–
265   776.

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

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

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

275   White S, Briffa M. 2017. How do anthropogenic contaminants (ACs) affect behaviour?
276   Multi-level analysis of the effects of copper on boldness in hermit crabs. Oecologia.
277   183(2):391–400.

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

279

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	
$sd_{intercept}$	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]
$r_{intercept-\omega}$	-0.12 [-0.87, 0.78]
$r_{observation.n-\omega}$	-0.11 [-0.88, 0.83]

280

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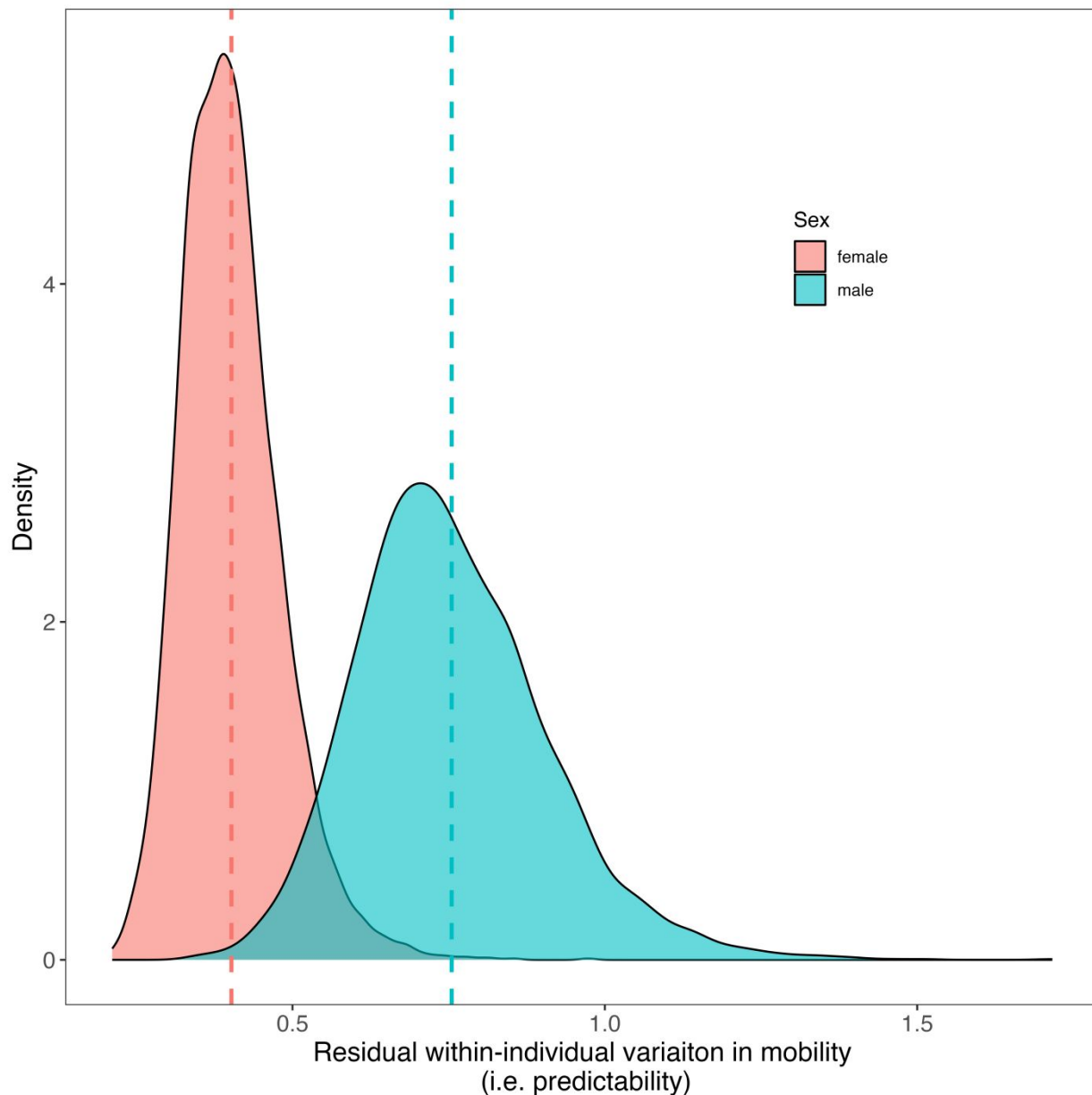
Figure 1: Sex difference in behavioural predictability in the Cook Strait giant weta (D. rugosa). Plots show the posterior probability distributions for residual within-individual variance (i.e., predictability) in nightly distance travelled extracted from a Bayesian double hierarchical linear mixed-effects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

282