BIOLOGY LETTERS

Passive plasticity and a sex difference in the predictability of mobility

Journal:	*Biology Letters*
Manuscript ID	Draft
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Kelly, Clint; Université du Québec à Montréal, Département des Sciences biologiques
Categories:	Animal Behaviour
Subject:	Behaviour < BIOLOGY
Keywords:	predictability, mobility, insect, radio telemetry, sex difference, behavioural variation

SCHOLARONE™ Manuscripts

Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
This research was approved by the Department of Conservation (New Zealand). All radio tags were removed from the animals at the time of study completion.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
Data are available on Open Science Framework: https://doi.org/10.17605/OSF.IO/T9CEH.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Use of AI

Please provide a statement of any use of AI technology in the preparation of the paper.

No, we have not used AI-assisted technologies in creating this article
CUST_IF_YES_DECLARATION_OF_AI_USE :No data available.

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

3   Clint D. Kelly[1,✉]

4   [1] Département des Sciences biologiques, Université du Québec à Montréal, Montréal, Canada

5   ✉ Correspondence: Clint D. Kelly <kelly.clint@uqam.ca>

6

Abstract

Residual within-individual variation (i.e. behavioural predictability) 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

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. within-individual variation) (Stamps et al. 2012; Biro

25 and Adriaenssens 2013; Cleasby et al. 2015; Westneat et al. 2015). Unpredictable individuals

26 exhibit high variability around their behavioural type and reaction norm slope whereas

27 predictable individuals do not (i.e. exhibit little residual variance). Within-individual residual

28 variance can arise from a variety of non-biological sources including sampling or measurement

29 error and incompletely or inaccurately parameterizing statistical models (i.e. terms are missing

30 from the model that could explain or account for residual heterogeneity) (Westneat et al. 2015).

31 Conversely, greater behavioural predictability (i.e. smaller rIIV) could be selected if it improves

32 success in agonistic encounters (e.g. Johnstone 2001) or mating competition (Schuett et al.

33 2010) or if decreased behavioural predictability (i.e. larger rIIV) improves survival (Briffa et al.

34 2013; Chang et al. 2017; Horváth et al. 2019; see also Brand et al. 2023).

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

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

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

38 unpredictable variance if food location is not known by the forager when foraging commences

39 or if daily travel distance is dependent on the number and type of predators encountered, which

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

41 some stochastic variation that would be present as heterogeneous residual phenotypic variance if

42 left unaccounted (Westneat et al. 2015).

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

44   (Orthoptera: Anostostomatidae) 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 (McIntyre 2001; White et al. 2017). It is endemic

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

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

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

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

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

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

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

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

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

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

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

58   2012). The pair remains together at least until the following night and copulate repeatedly

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

60   2017; Kelly and 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

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

66   being more or less predictable confers a mating advantage.

67   **Methods**

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

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

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

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

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

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

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

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

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

77   each day. When located I noted whether the radio-tagged weta was paired with an opposite-sex

78   individual. I then placed a field flag at the location point and measured the distance in meters

79   between the current flag and the one from the previous day using a 50-m fibreglass tape

80   measure. This straight-line distance is assumed to be the distance travelled by the tagged weta

81   the previous night. The nightly travel distance was repeatedly measured 7.44 ± 0.56 (n = 16)

82   times for females and 5.76 ± 0.45 (n = 16) times for males.

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

84   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 uninformative default priors for a total of 10000

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

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

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

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

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

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

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

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

114   separately.

115   Data were visualized using the R packages *ggplot2* (Wickham 2016). Means are given ± one

116   standard error of the mean (SEM) unless otherwise noted.

Results

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

119   (18.77 ± 4.46 m/night, n = 17) travel significantly farther per night on average than females

120   (7.89 ± 1.26 m/night, n = 16) and that travel distance is significantly repeatable in both sexes

121   (males: R = 0.60 [0.33–0.77], n = 17; females: R = 0.30 [0.06–0.51], n = 16).

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

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

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

125   0.57]; Figure 1). The predicted standard deviation from the mean residual standard deviation

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

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

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

129   behavioural predictability (females: r = -0.122, df = 14, p=0.654; males: r = 0.064, df = 15,

130   p=0.807) or behavioural type (females: r = 0.10, df = 14, p=0.714; males: r = -0.19, df = 15,

131   p=0.453) correlated with mating success in either sex.

132   **Discussion**

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

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

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

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

137   caused by passive plasticity.

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

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

140   2015). Females travel significantly less per night, on average than males (Kelly et al. 2008;

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

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

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

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

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

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

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

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

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

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

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

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

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

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

155   adaptive.

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

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

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

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

160   2021). Unlike the current study, Hertel et al. (2021) showed that behavioural type correlates

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

162   were less diurnal than less predictable bears.

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

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

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

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

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

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

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

170   differently in response to subtle environmental changes.

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

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

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

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

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

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

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

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

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

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

181   adopting one behavioural type over another.

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

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

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

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

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

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

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

189   2017), to elucidate if differences between males and females is the general pattern, and if so,

190   identify why.

Declarations

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

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

194   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.

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. Naturwissenschaften. 106(3-4):7.

Johnstone R. 2001. Eavesdropping and animal conflict. Proc Natl Acad Sci U S A. 98(16):9177–9180.

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.

230 Kelly CD, Gwynne DT. 2023a. Effect of body condition on mobility and mating success in a
231 wild population of the scramble polygynous Cook Strait giant weta. Behav Ecol Sociobiol.
232 77:5.

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

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

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

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

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

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

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

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

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

252 Watts C, Empson R, Thornburrow D, Rohan M. 2012. Movements, behaviour and survival
253 of adult Cook Strait giant weta (*Deinacrida rugosa*; Anostostomatidae: Orthoptera)
254 immediately after translocation as revealed by radiotracking. J Insect Conserv. 16(5):763–
255 776.

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

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

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

265   White S, Briffa M. 2017. How do anthropogenic contaminants (ACs) affect behaviour?
266   Multi-level analysis of the effects of copper on boldness in hermit crabs. Oecologia.
267   183(2):391–400.

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

269

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]

270

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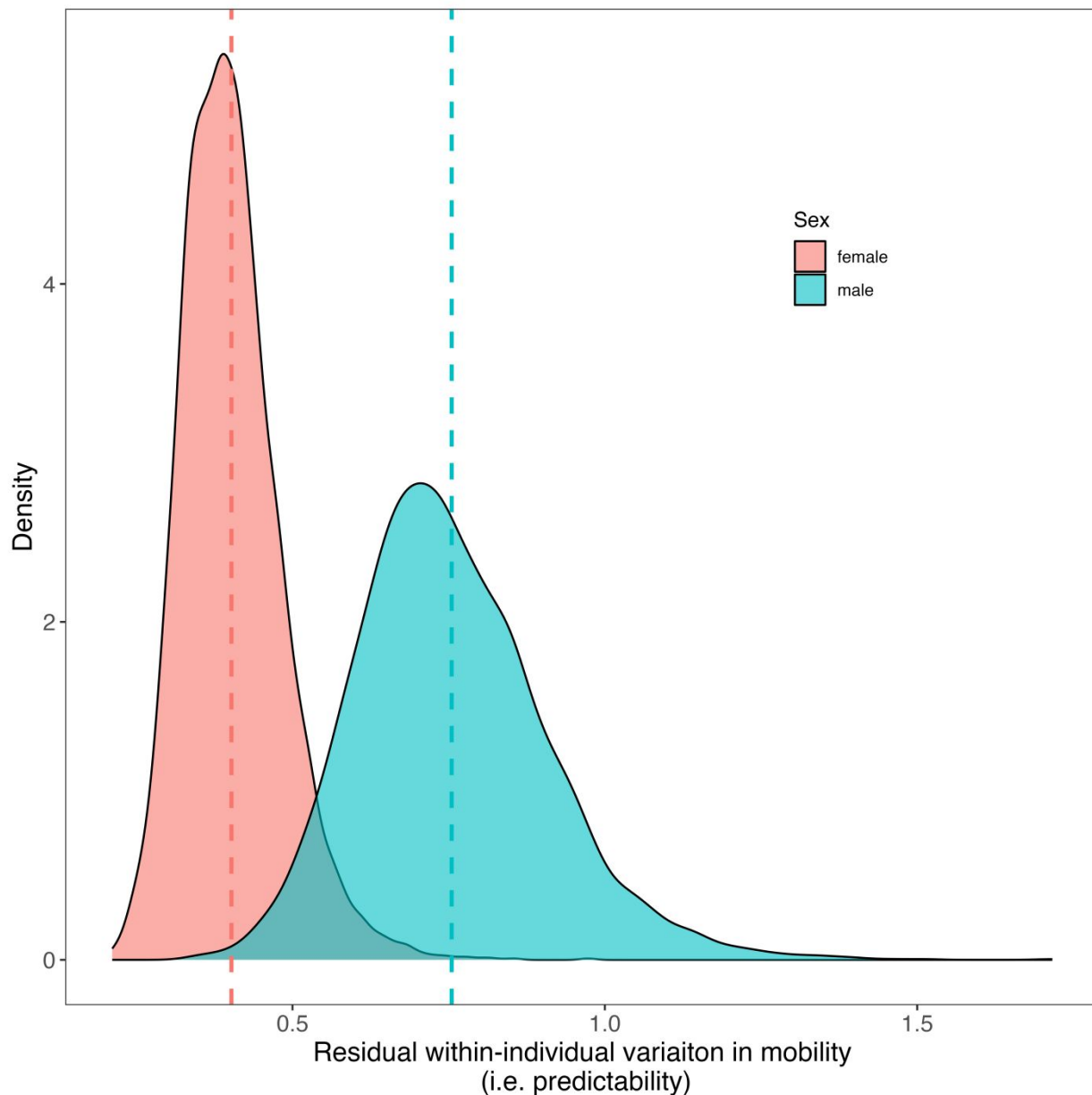
Figure 1: Sex difference in behavioural predictability in the Cook Strait giant weta (D. rugosa). Plots show the posterior probability distributions for residual within-individual variance (i.e., predictability) in nightly distance travelled extracted from a Bayesian double hierarchical linear mixed-effects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

272