

PAPER NAME AUTHOR

WORD COUNT CHARACTER COUNT

3397 Words 19548 Characters

PAGE COUNT FILE SIZE

15 Pages 509.7KB

SUBMISSION DATE REPORT DATE

Aug 7, 2024 6:33 PM GMT+1 Aug 7, 2024 6:35 PM GMT+1

#### 34% Overall Similarity

The combined total of all matches, including overlapping sources, for each database.

• 25% Internet database

• 33% Publications database

Crossref database

Crossref Posted Content database

• 0% Submitted Works database

### Excluded from Similarity Report

• Bibliographic material

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

- 3 Clint D. Kelly $^{1, ext{□}}$
- 4 Département des Sciences biologiques, Université du Québec à Montréal, Montréal, Canada
- 5 <sup>™</sup>Correspondence: Clint D. Kelly <kelly.clint@uqam.ca>

#### **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

Individuals can differ in their behavioural predictability, defined as residual intra-individual 22 variation (i.e. rIIV), after controlling for individual variation in behavioural type 1.e. average 23 behaviour) and behavioural plasticity (i.e. within-individual variation) (Stamps et al. 2012; Biro 24 25 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 26 predictable individuals do not (i.e. exhibit little residual variance). Within-individual residual 27 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. 2010) or if decreased behavioural predictability (i.e. larger rIIV) improves survival Briffa et al. 33 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 prey could exhibit unpredictable variance if the location of prey is not known by the forager when foraging 38 39 commences or if daily travel distance is dependent on the number and type of predators 40 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 41 42 be present as heterogeneous residual phenotypic variance (Westneat et al. 2015).

in this study, I field test the hypothesis that Cook Strait giant weta Deinacrida rugosa 43 44 (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 45 insect that is endemic to New Zealand and of high conservation importance (McIntyre 2001; 46 47 White et al. 2017). It inhabits old pastures, forests, and coastal scrub, and seeks refuge from predators in the daytime by hiding under vegetation or other objects on the ground (McIntyre 48 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, as do other deinacridine weta (McIntyre 2001; Kelly 2006). Rather, male D. rugosa seek 51 52 receptive females as mates at night while females are foraging (McIntyre 2001). Mate searching results in males travelling considerably longer distances per night than females kelly et al. 53 54 2008; Kelly and Gwynne 2023a). In contrast, female nightly travel is generally short because suitable forage is close by Kelly et al. 2008; Kelly and Gwynne 2023a). Once a male locates a 55 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 day (McIntyre 2001; Kelly et al. 2008; Kelly et al. 2010; Kelly and Gwynne 2017; Kelly and 59 Gwynne 2023b; Kelly and Gwynne 2023a). 60 Puse radio telemetry to track the nightly distance travelled (i.e. mobility) by male and female D. 61 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

66

67

- This field study was conducted 5-18 March 2019 in an abandoned and regenerating pasture on 68 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). Adult giant weta were hand-collected by scanning the open ground and pastures at night. A 3.35 72 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. Weta were released at their point of capture. I used radio telemetry to locate radio-tagged weta 76 each day. When located I noted whether the radio-tagged weta was paired with an opposite-sex 77 individual. Then placed a field flag at the location point and measured the distance in meters 78 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 the previous night. The nightly travel distance was repeatedly measured 7.44  $\pm$  0.56 (n = 16) 81 82 times for females and  $5.76 \pm 0.45$  (n = 16) times for males. 83 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

85

Statistical analyses were performed within the R v. 4.2.1 statistical environment (R Core Team 86 87 2024). I used an inverse hyperbolic sine transformation in the R package bestNormalize (Peterson 2021) to transform nightly travel distance (m) approximate a Gaussian error 88 distribution. To aid model fitting and interpretation of parameter estimates, observation number 89 90 (1-8) was left-centred so that the first observation = 0, and transformed travel distance and sex were scaled  $\frac{2}{1}$  mean = 0, SD = 1; female = -0.5, male = 0.5) before analysis. Scaling sex provided 91 variance estimates for the "average" weta irrespective of sex (Hertel et al. 2021). 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 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 11xed effects. The dispersion part of a DHGLM estimates the residual intra-individual variation 97 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 time. Individual ID and observation number were included as random intercepts and slopes, 101 102 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 103 104 random intercepts and slopes, respectively. This model included travel distance as the dependent variable and was run on four chains using relatively uninformative, default priors for a total of 105 106 10000 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. I extracted mobility behavioural type as the mean and credible interval of the posterior 109 distribution of each individual's random intercept. I then extracted the posterior distribution of 110 111 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.

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**

115

116

- 118 A previous report on this population of animals (Kelly and Gwynne 2023a) showed that males
- 119 (18.77  $\pm$  4.46 m/night, n = 17) travel significantly farther per night on average man females
- 120  $(7.89 \pm 1.26 \text{ m/night}, n = 16)$  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 coack-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,
- 125 0.57]; Figure 3). The predicted standard deviation from the mean residual standard deviation
- 126 (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

128

129

130

131

132

133

134

135

136

137

138

139

140

141

142

143

144

145

146

147

148

149

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 Spieger 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 Relly et al. 2008; Kelly and Gwynne 2023a) and Karori Sanctuary

150

151

152

153

154

155

156

157

158

159

160

161

162

163

164

165

166

167

168

169

170

171

(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**

173

174

175

176

177

178

179

180

181

182

183

184

185

186

187

188

189

190

191

- Funding Natural Sciences and Engineering Research Council of Canada (NSERC).
- 193 **Availability of data and materials** Data are available on Open Science Framework:
- 194 DOI 10.17605/OSF.IO/T9CEH.

#### 195 **References**

- Biro P, Adriaenssens B. 2013. Predictability as a personality trait: Consistent differences in
- intraindividual behavioral variation. Am Nat. 182(5):621–629.
- 198 Brand J, Henry J, Melo G, Wlodkowic D, Wong B, Martin J. 2023. Sex differences in the
- 199 predictability of risk-taking behavior. Behav Ecol. 34(1):108–116.
- 200 Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel
- analysis of plasticity, personality and predictability in hermit crabs. Anim Behav.
- 202 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.
- 205 Chang C, Teo H, Norma-Rashid Y, Li D. 2017. Predator personality and prey behavioural
- predictability jointly determine foraging performance. Sci Rep. 7:40734.
- 207 Cleasby IR, Nakagawa S, Schielzeth H. 2015. Quantifying the predictability of behaviour:
- 208 Statistical approaches for the study of between-individual variation in the within-
- individual variance. Hadfield J, editor. Methods Ecol Evol. 6(1):27–37.
- 210 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
- 215 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.
- 218 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
- 222 (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–
- 227 1409.
- 228 Kelly CD, Gwynne DT. 2017. Do male Cook Strait giant weta prudently allocate sperm. J
- 229 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.
- 232 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.
- 235 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
- 237 Publishing. p. 225–242.
- 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.
- Scheiner SM. 2006. Genotype-environment interactions and evolution. In: Fox C, Wolf J,
- editors. Evolutionary genetics: Concepts and case studies. Oxford, UK: Oxford ÉUniversity
- 245 Press. p. 326–338.
- Schuett W, Tregenza T, Dall S. 2010. Sexual selection and animal personality. Biol Rev
- 247 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.
- 250 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. I Insect Conserv. 16(5):763–
- 255 776.
- 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.
- 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?
- Multi-level analysis of the effects of copper on boldness in hermit crabs. Oecologia.
- 267 183(2):391-400.

269

Wickham H. 2016. ggplot2: Elegant graphics for data analysis. 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]

	Estimate [95 /0 C11]		
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]		
$r_{ m intercept-slope}$	-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			
$\omega^2$	0.12 [0.01, 0.32]		
$r_{ m intercept-\omega}$	-0.12 [-0.87, 0.78]		
robservation.n-ω	-0.11 [-0.88, 0.83]		

#### Figure Figure

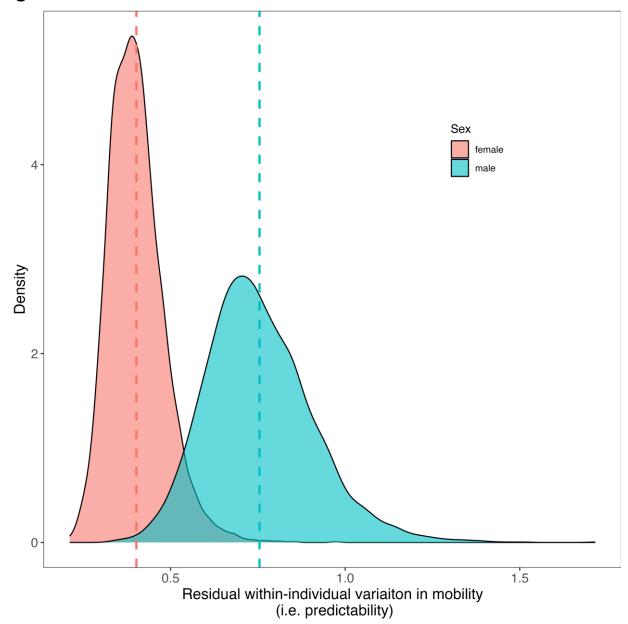


Figure 1. Sex difference in behavioural predictability in the Cook Strait giant weta (D. rugosa). Plots represent the posterior probability distributions for residual within-individual variance (i.e., predictability) in nightly distance travelled extracted from a Bayesian double hierarchical linear mixed-effects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



#### 34% Overall Similarity

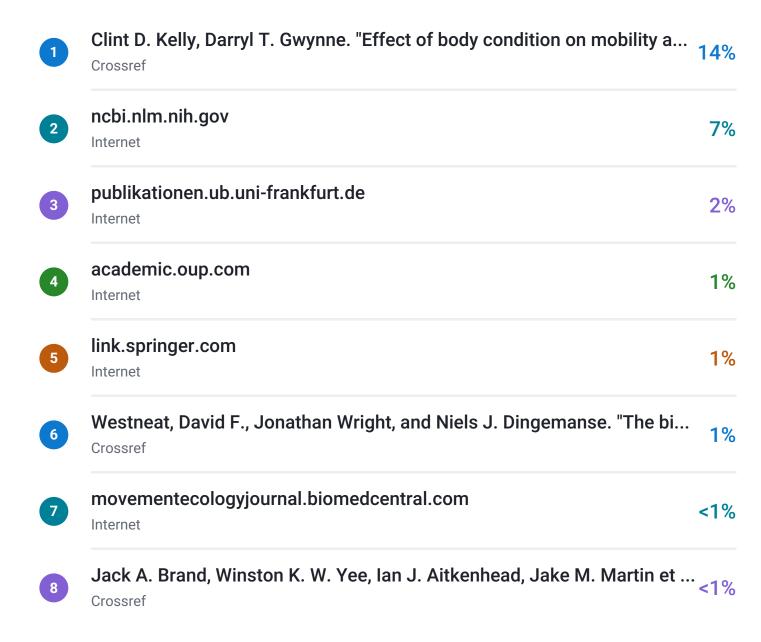
Top sources found in the following databases:

- 25% Internet database
- Crossref database
- 0% Submitted Works database

- 33% Publications database
- · Crossref Posted Content database

#### **TOP SOURCES**

The sources with the highest number of matches within the submission. Overlapping sources will not be displayed.





researchgate.net Internet		
<b>Gergely Horváth, T</b> Crossref	ibor Sos, Gábor Bóné, Csanád Endre Lőrincz	z, Péter L
Clint D. Kelly. " Sex	rually dimorphic effect of mating on the mel	anotic e
<b>microbiomejourna</b> l Internet	l.biomedcentral.com	
Peter A. Biro, Theo Crossref	odore Garland, Christa Beckmann, Beata Ujv	ari, Frede
<b>Anne G. Hertel, Ra</b> Crossref	phaël Royauté, Andreas Zedrosser, Thomas	Mueller
assets.researchsq Internet	uare.com	
Clint D. Kelly. "Alte Crossref	ernative mating strategies in the Wellington	tree weta
dx.doi.org		
Internet		



21	Kasper, Julia C "Mate Choice and Sexual Conflict in a Livebearing Fis Publication
22	Clint D Kelly, Darryl T Gwynne. "Mating assortment and the strength of <19
23	Kasja Malkoc, Lucia Mentesana, Stefania Casagrande, Michaela Hau. " <19 Crossref
24	eprints.nottingham.ac.uk Internet
25	Clint D. Kelly. " Effect of nutritional stress and sex on melanotic encaps <19
26	lago Sanmartín-Villar, Raphaël Jeanson. "Early social context does not <19