

Static allometry suggests female ornaments in the long-tailed dance fly (*Rhamphomyia longicauda*) are not deceptive

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1 **Static allometry suggests female ornaments in the long-tailed dance fly**
2 **(*Rhamphomyia longicauda*) are not deceptive**

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11 **Running head:** Honest female ornaments in *Rhamphomyia longicauda*

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26 Despite their prevalence in nature, the evolution of sex-specific female ornaments is still
27 not well understood. Although in some cases (often carotenoid-based ornaments) they appear to
28 honestly signal quality, such as fecundity, it has been suggested that some female ornaments
29 have evolved to deceptively to obtain matings. We address these two hypotheses in the long-
30 tailed dance fly (*Rhamphomyia longicauda*) where females possess two sex-specific ornaments:
31 pinnate scales on the hind femur and tibia and abdominal sacs that are inflated in female-biased
32 “display” swarms. Although several studies have suggested that female ornaments in this species
33 are deceptive, evidence is mixed and requires further investigation. Here, we use static allometry
34 (with body size as a proxy for condition) of both ornamental and non-ornamental traits in
35 females (and homologous non-ornamental traits in males) in order to determine whether they are
36 honest or deceptive signals of quality. Most male traits scaled isometrically with body size,
37 however male leg hairs showed positive static allometry, probably because they are involved in
38 nuptial-prey capture or in grasping mates. Ornamental traits in females (abdomen area and tibia
39 scale length) showed significant positive allometry and had steep slopes relative to non-
40 ornamental traits. As larger females invest more in ornamentation relative to smaller females,
41 this suggests that these traits are likely honest, condition-dependent signals of quality. We note
42 that honesty and deception are not mutually exclusive hypotheses. Individuals may vary in their
43 signalling strategy, resulting in, for example, deception from some low condition individuals but
44 honesty overall. Although our finding of positive allometry makes it unlikely this occurs in long
45 tailed dance flies, simultaneous honesty and deception should be considered in future studies of
46 female ornamentation.

48 **Introduction**

49 Although it is typically males that possess elaborate or showy traits used to increase
50 mating success, there are an increasing number of species known where females possess
51 ornamental traits resulting from strong sexual selection (Darwin 1871; Trivers 1972; Amunsten
52 2000; Tobias et al 2012; Nordeide et al 2013; Hare and Simmons 2020). Strong sexual selection
53 and female-specific ornamentation are typically found in systems where males make large
54 investments in offspring such as nuptial feeding or paternal care and thus females are highly
55 motivated to mate, often relying on these direct benefits for offspring development (Trivers,
56 1972; Gwynne 1981; Gwynne 1991; Gwynne 1993; Gwynne and Simmons 1990; Jones 2001).
57 On the other hand, potential male mating rate is more limited in such paternally investing
58 species, leading males to discriminate among potential mates, especially when females vary in
59 quality (Trivers, 1972; Gwynne 1991; Jones 2001; Bonduriansky 2001).

60 Because male fitness is typically limited by the number of offspring sired, the highest
61 quality females are those that provide the greatest opportunity for fertilization success
62 (Fitzpatrick et al 1995; Bonduriansky 2001; Herridge et al 2016). For many organisms, female
63 quality is fecundity but may also include egg maturity or mating status as, for example, immature
64 eggs mean an increased likelihood that the female will re-mate prior to oviposition (thus
65 compromising paternity) (Bonduriansky 2001). Thus, it is reasonable to predict that female
66 ornaments evolved to signal fecundity or reproductive status to males (Andersson 1994). When
67 investment in ornamentation is condition-dependant (costly), however, females that produce
68 these elaborate structures may reduce the resources available for egg production, thus reducing
69 fecundity (or egg size) relative to females that do not invest in these traits (Fitzpatrick et al.
70 1995). Such trade-offs are expected to constrain the evolution of ornamental traits in females as

71 males would be unlikely to favor traits that reduce fitness, even if they honestly signal fecundity
72 (Fitzpatrick et al. 1995).

73 Chenoweth et al (2006) suggest that female ornaments may be adaptive even with costs
74 to fecundity, if they function as valuable signals when direct assessment of female quality is
75 difficult (e.g. body size does not scale predictably with fecundity, or if visual signaling occurs in
76 poor light conditions). In this case, ornaments still provide males with some cue of quality, but
77 with females overinvesting in ornamentation (possibly due to stochastic environmental variation)
78 suffering costs to fecundity relative to females of similar condition that invest less in ornaments
79 (Chenoweth et al. 2006). Thus, Chenoweth et al. (2006) predict that males are expected to avoid
80 the most elaborately ornamented females, leading to stabilizing selection for intermediate-sized
81 ornaments. This hypothesis may help explain female ornamentation in empid dance flies,
82 *Rhamphomyia longicauda* (Wheeler et al. 2012), where female ornaments are sex-specific
83 pinnate leg scales and inflatable abdominal sacs. Prior to entering their lek-like mating swarms
84 (which occur at dusk and dawn when there is less light), females inflate their abdominal sacs by
85 swallowing air and pull their legs up alongside the abdomen, increasing their apparent size to
86 males entering from below (Funk and Tallamy 2000). Males arrive to female-biased swarms
87 carrying nutritious prey-items (usually small flies, mayflies, or caddisflies) that they exchange
88 with females for mating (Funk and Tallamy 2000). Because female empids do not hunt for prey,
89 they rely on these mating gifts for egg development (Downes 1970; Funk and Tallamy 2000) and
90 thus mate frequently (Herridge PhD thesis 2016; Browne and Gwynne unpublished).

91 Experimental manipulations of female trait size in display swarms in the field (using
92 plastic models) have shown that males are most attracted to females with large ornaments (Funk
93 and Tallamy 2000), with abdomen area being the most important (Murray et al. 2018). However,

94 when comparing mated and unmated females, Wheeler et al. (2012) found that female ornaments
95 are under stabilizing sexual selection, supporting the Chenoweth et al. (2006) overinvestment
96 prediction (Wheeler et al. 2012). Given that males are attracted to highly ornamented females
97 more often (Funk and Tallamy 2000; Murry et al. 2018), males may be able to assess weight
98 after pairing (Murray et al. 2018) (males carry females from swarms; Funk and Tallamy 2000;
99 personal observation) and reject females that are light relative to their degree of ornamentation,
100 both maximizing mate quality and potentially reinforcing the honesty of female signals.

101 Female ornaments in *R. longicauda* as honest indicators of quality, however, has been
102 questioned (Funk and Tallamy 2000; Hockham and Ritchie 2000; Murray et al. 2018) as one of
103 the female ornaments, abdomen size (inflated), explained quite a low proportion of variance in
104 egg size (likelihood that a female will re-mate prior to oviposition: $r^2=0.23$) relative to a non-
105 inflatable related species, *Rhamphomyia sociabilis* ($r^2=0.72$) (Funk and Tallamy 2000). This
106 study suggested that female inflatable abdomens in *R. longicauda* may have evolved via sexual
107 conflict as they deceive males by masking quality in order to avoid rejection. Since then, two
108 other studies of this species have found slightly higher relationships between inflated abdomen
109 size and fecundity or egg size: r^2 respectively; = 0.49, and 0.33, (Bussière et al. 2008) and 0.06,
110 $r^2= 0.49$; Wheeler 2008). Although the correlation between ornament expression and measures of
111 female quality appears to be weaker in *R. longicudia*, this relationship does not deviate from
112 trends expected for honest female signals (Andersson 1994; Berglund 1997; Nordeide et al.
113 2013; Barry 2015). Not only was this relationship consistently positive and significant (Funk and
114 Tallamy 2000; Bussiere et al. 2008; Wheeler et al. 2012), but the strength of the relationship is
115 not unlike many other species where female traits are considered honest signals of quality (e.g.
116 $r^2=0.35$ in barn swallows; Møller 1993, $r^2=0.32-0.40$ in Inca terns; Velando et al. 2001, $r^2= 0.439$

117 in scissor tail fly catchers; Regosin and Pruett-Jones 2001, $r^2=0.11$ in penguins; Massaro et al.
118 2003, $r^2= 0.34-0.35$ in dance fly *Rhamphomyia tarsata*; LeBas et al. 2003, and $r^2=0.68$ in
119 mantids; Barry 2015). The low explanatory power of abdomen size in *R. longicauda* relative to a
120 related species may be a result of our ability to accurately measure inflated abdomen size. Not
121 only is it unknown whether *R. longicauda* females vary temporally in the amount they inflate
122 pleural sacs (Murry et al. 2018), but collection of females sometimes results in damage to the
123 abdomen (Bussière et al. 2008) or triggers females to deflate (personal observation), potentially
124 causing variation in abdomen measures relative to species with no inflation. Further, if females
125 are prone to erroneous over-investments in ornamental traits at the cost of their fecundity as
126 Chenoweth et al. (2006) suggest, this may result in weaker correlations between egg size/number
127 and abdomen size relative to *R. sociabilis* (where females lack inflatable pleural sacs) while still
128 maintaining some level of reliability in signalling quality to males.

129 Despite this, additional support for the sexual conflict (deception) hypothesis comes from
130 the existence of two different female ornaments in *R. longicauda*. Murray et al. (2018) suggest
131 these are a result of cyclic bouts of antagonistic co-evolution in which deceptive ornaments
132 function in acquiring necessary nutrition (nuptial prey), and males evolve to resist deception by
133 more closely assessing mates. Because the second female ornament, pinnate leg scales, do not
134 accurately predict egg number or egg size (Wheeler 2008) and males only show a preference for
135 larger leg scales when abdomens are small, Murray et al. (2018) suggested that pinnate leg scales
136 may represent a more ancestral form of ornamentation that is no longer the primary signal used
137 to assess females. As expected with deceptive female ornaments, male *R. longicauda* possess
138 enlarged dorsal ommatidia, which may indicate that they closely inspect females when entering
139 swarms from below (Downes 1970), however, this does not exclude the possibility that males

140 also assess female ornaments as honest signals. Thus, despite *R. longicauda* being cited as an
141 example of female deception (Hockham and Ritchie 2000; Barry 2015), more work is necessary
142 to address honest versus dishonest hypotheses for female abdominal ornaments in this species.

143 One way that we can differentiate between these hypotheses is by examining the
144 investment females make in ornaments relative to their condition. If female ornaments are honest
145 signals of quality, higher condition females (who presumably are of higher quality) are expected
146 to produce larger ornaments than those of poor condition. Further, if these traits are costly for
147 females to produce (i.e. condition-dependant), we would expect low condition females to invest
148 minimally in exaggerated traits, while higher condition females are able to invest in larger
149 ornaments without suffering large fecundity costs (high quality), thus maintaining the overall
150 honesty of these traits (Andersson 1994; Fitzpatrick et al. 1995). On the other hand, if female
151 ornaments are deceptive, those in the lowest condition are expected to invest relatively more in
152 these traits in order to compete with high condition females and thus avoid being rejected (Funk
153 and Tallamy 2000). With condition-dependence, poor condition females are expected to
154 experience a greater decrease in fecundity when investing in ornamentation, however, this is
155 adaptive because they have the most to gain from deceiving males (Barry 2015). This appears to
156 be the case in the sexually cannibalistic preying mantid species, *Pseudomantis albofimbriata*,
157 where females attract males using airborne sex-pheromones (Barry 2015). In this species, poorly
158 fed females that are in the lowest condition have the most to gain from attracting and
159 cannibalizing males, and thus do not signal honestly. Although sex-pheromones are costly to
160 produce (condition-dependent), females in the poorest condition maximize their investment in
161 these signals and thus lure mate-seeking males for easy-access to nutrition and delay egg
162 production until after they have eaten a mate (Barry 2015).

163 In the current study, we measure static allometry of inflated abdomen area and pinnate-
164 scale ornaments as well as several non-ornamental female traits to determine how smaller
165 females invest in ornamental traits relative to larger ones. Although body size is not a direct
166 indicator of female condition, it is closely related and has been used to estimate condition in
167 other species (e.g. Emlen 1997; Johnstone et al. 2009). If female ornaments honestly signal
168 quality, we expect abdomens and leg scales to show positive static allometry (i.e. larger sized
169 females invest more in ornamentation relative to smaller ones- indicative of condition-
170 dependence) or to scale isometrically with body size (in which female invest equally relative to
171 their body size – no apparent condition dependence). In either case, ornamental traits are also
172 expected to have greater allometric slopes relative to non-ornamental traits (Bonduriansky 2007;
173 Eberhard et al., 2009; Rodríguez et al. 2015). In contrast, if female ornaments are deceptive, we
174 predict negative static allometry on deceptive ornamental traits (or shallow allometric slopes
175 relative to non-ornamental traits) in which lower condition females (who have more to gain from
176 deception; Barry 2015) invest more in ornamentation relative to those of higher condition
177 (Bonduriansky 2007; Eberhard et al., 2009; Rodríguez et al. 2015).

178 We can gain further insight into the evolution of female ornaments by comparing their
179 investment in traits relative to males. In *R. longicauda*, males do not possess the abdominal and
180 leg-scale ornaments but have the likely ancestral state of the traits: non-inflatable abdomens and
181 leg hairs instead of scales on the tibiae and femora. A previous study (Bussière et al. 2008)
182 compared the nature of sexual selection on males and females in *R. longicauda*, but this did not
183 include any ornamental traits. Here, we measure allometric patterns on female ornaments and
184 homologous male traits with the prediction that allometric slopes will be steeper for females, as
185 is often observed when sexual selection has led to an exaggerated trait in one sex (Petrie 1988;

186 Green 1992). Given the divergent feeding ecologies of male and female dance flies however,
187 selection may be expected to act on male traits as well, which may cause allometric patterns to
188 deviate from expectation. In particular, male leg hairs may be selected for capturing nuptial prey
189 (Svensson and Petersson 1987; Svensson 1997) and in other insects, smaller bodies have been
190 associated with greater maneuverability (Kelly et al. 2008).

191

192 **Methods**

193 **Dance Fly biology**

194 Empid dance flies include many species where males provide their mates with nuptial
195 gifts (Cumming 1994). In our study species, *R. longicauda*, females gather in large swarms
196 during dusk or dawn and males enter the swarm with nutritious prey-items which they exchange
197 with females for mating (Funk and Tallamy 2000). These food gifts are valuable to females as
198 they are their only source of protein, which is necessary for egg development (Downes 1970;
199 Funk and Tallamy 2000). It is thought that females' reliance on mating for nutrition (Downes,
200 1970) drives sexual competition among females and has led to the evolution of two female-
201 specific ornaments used to attract males- large inflatable abdominal sacs and pinnate scales on
202 each leg. When in the lek-like mating swarms, females inflate their abdominal sacs and pull up
203 their legs alongside the abdomen, which increases their apparent size (Funk and Tallamy 2000).

204

205 **Specimen Collection and Measurement**

206 We collected 224 female and 113 male *R. longicauda* from mating swarms in the Credit
207 river valley, near Glen Williams, Ontario (43.6865660, -79.9260960) from mid-June to early
208 July of 2017 and 2018. Males were caught individually and transferred to vials where they were

209 frozen and then stored in >70% ethanol. Females were collected using a sweep net and flash
210 frozen with liquid nitrogen in order to preserve the inflated abdominal sacs. Once frozen, females
211 were stored in ethanol. We took images of male and females, using a camera fitted to a
212 dissecting microscope and measured male and female traits using ImageJ. Measurements
213 included thorax scutum length as an estimate of body size, ornamental traits: inflated abdomen
214 area (as an estimate of pleural sac size), and the length of the longest scale (hairs in males) on the
215 femur and tibia (Figure 1) as well as non-ornamental traits: wing length, hind femur length, and
216 hind tibia length. We did not include measures of tibial or femoral scale area (as in LeBas et al.
217 2003; Herridge 2016; Wheeler et al. 2012), as these traits were highly correlated with the length
218 of the leg segment in both sexes (tibia length: females $R=0.92$, males $R=0.80$; femur length:
219 females $R=0.84$, males $R=0.85$), thus likely are not independent measurements.

220

221 **Statistical Analysis**

222 We square root-transformed abdomen area to ensure that all measurements were in the
223 same units (mm) and confirmed that all traits were normally distributed using a Shapiro-Wilk
224 test of normality. We then calculated the average trait size (\pm SD) for both males and females
225 and used a Student's T-test to test for significant differences. Next, we determined the allometric
226 relationship using model II major axis regression (MA; see Green 2000; Simmons and Tomkins
227 1996; Kelly 2014) of the log transformed traits (wing length, femur length, tibia length,
228 $\sqrt{\text{abdomen area}}$, femur scale length, and tibia scale length) on log thorax length for both males
229 and females. We determined whether traits deviated significantly from isometry using the 95%
230 Confidence intervals of the MA slope.

231

232 **Results**

233 While females had significantly larger abdomens, legs, and leg scales (hairs in males)
234 than males, there was no significant difference (with Bonferroni correction) in male and female
235 thorax or wing size (Table 1). We found evidence of positive allometry for several male and
236 female traits as slopes were significantly higher than one. In females, both abdominal area and
237 tibia scale length scaled positively with body size with slopes significantly greater than those for
238 non-ornamental traits (Table 2). Although femur scale length did not differ significantly from
239 isometry, this trait also had a steep (but not significantly greater) slope relative to non-
240 ornamental traits. Female femur and tibia length did not differ significantly from isometry, while
241 wing length showed significant negative allometry. In males, three traits including wing length,
242 femur length, and tibia length all scaled negatively with body size. Interestingly, male leg hairs
243 on both the tibia and femur scaled positively with body size. Although the allometric intercept
244 was higher in females across both these traits, males showed a steeper allometric slope for hairs
245 compared to female scales (Table 2; Fig. 2-4).

246

247 **Discussion**

248 In the dance fly *R. longicauda*, we found evidence of positive allometry on two female
249 ornaments: abdomen area and tibia scale length. Both these traits had allometric slopes greater
250 than one and were steep relative to non-ornamental traits, including tibia and femur length. The
251 relationship between body size and femur scale length did not differ significantly from isometry,
252 however as predicted, the slope still tended to be steeper than that of non-ornamental traits. In the
253 context of female ornament evolution, this finding suggests that the ornaments are honest signals
254 of quality in *R. longicauda*. Not only does it appear that larger and thus higher condition females

255 produce larger ornaments, but in most cases (abdomens and tibial scales) larger females are
256 investing more in ornamentation relative to smaller ones. This suggests that female ornaments
257 are probably condition dependant (Rodriguez et al. 2015) which may help to maintain the
258 honesty of these traits (Andersson 1994; Fitzpatrick et al. 1995).

259 Despite this, honesty and deception are not necessarily mutually exclusive hypotheses, as
260 variation in signalling strategies between individuals has been shown to result in a combination
261 of deception (“cheats”) and honesty (Johnstone 1993; Barry 2015). Indeed, while *P.*
262 *albofimbriata* mantid females in the poorest condition signal deceptively to cannibalize mate-
263 seeking males, female pheromones are overall honest signals of female quality – both fecundity
264 and the risk of the attracted male being cannibalized (Barry 2010; 2015). While Barry (2015)
265 found that fecundity and female condition decreased non-significantly with pheromone
266 attractiveness, both relationships became positive and significant when the lowest condition
267 females were removed from the analysis (Barry 2015). The observation of partial deception (i.e.
268 among just the lowest condition females; Barry 2015) in mantids is likely a result of the
269 condition-dependence of the pheromone signal. Because investment in secondary sexual traits is
270 expected to trade off with fecundity (Fitzpatrick et al. 1995), it is only adaptive for the poorest
271 condition females to produce over-exaggerated (deceptive) traits to avoid rejection and acquire
272 nuptial gifts. In contrast, higher condition females are at a low risk of being rejected and thus
273 their trait expression reflects their condition. In cases where secondary sexual traits are not
274 dependent on female condition, we may expect all females to maximize their investment in
275 ornamentation, however this is likely constrained in larger female *R. longicauda* by natural
276 selection (risk of getting caught in spider webs; Gwynne and Bussière 2002; Gwynne et al.
277 2007).

278 Another factor that may influence the perceived honesty of a trait, is the difficulty of
279 determining female quality, especially in systems where egg development is dependent on the
280 male-supplied nutrition received over the course of the mating period (Bussière et al. 2008;
281 Wheeler et al. 2012). While fecundity is undoubtedly important to choosy males (Bonduriansky
282 2001), it can be difficult to measure accurately given that females may acquire additional
283 nutrition in future mating bouts or may have already laid a proportion of their eggs (in the lab,
284 females oviposit eggs in 1-3 bouts; J. B., personal observation). The other measure of female
285 quality used for *R. longicauda* is egg size, which is representative of the degree of egg
286 development, and thus a reduced likelihood that a female will mate with a rival male prior to
287 oviposition (Funk and Tallamy 2000; Murray et al. 2018). This estimate of quality assumes that
288 there is last male sperm precedence when fertilizing eggs, and while this is a common pattern in
289 many insects (Simmons 2001), there is little evidence that this is the case in *R. longicauda*.
290 Although females possess a single sclerotized spermatheca, creating high potential for sperm
291 displacement and thus biased paternity in favor of the last male (Simmons 2001), preliminary
292 work shows that last males father few offspring relative to a female's other mates (Browne and
293 Gwynne unpublished). Note, however, we cannot rule out that this finding was influenced by our
294 sampling methods, which may have disrupted the last mating male's copulation prior to
295 insemination (Browne and Gwynne unpublished). Additional research regarding sperm
296 competition and egg development, specifically whether nuptial gifts directly increase a female's
297 fecundity, will help to clarify the factors determining female quality in this species.

298 Surprisingly, we also found that two male traits – tibia hair length and femur hair length-
299 scaled positively with body size (thorax length), while male hind tibia and femur length showed
300 negative allometric slopes. Although females had higher allometric intercepts for both tibia and

301 femur scales, consistent with female-biased sexual dimorphism, males showed much steeper
302 allometric slopes for homologous (almost certainly non-ornamental) leg hairs. Despite positive
303 allometry often being associated with strong sexual selection (Petrie 1988; Green 1992), it seems
304 unlikely that male traits are a product of sexual selection to attract mates (although they are
305 potentially involved in grasping females) due to their lack of exaggeration, and the fact that
306 males probably do not need to invest in attractive signals when females are eager to mate.
307 Indeed, naturally selected traits can also result in positive allometric slopes when the benefit of
308 expressing the trait is greater for larger males relative to small ones (Bonduriansky and Day
309 2003, van Lieshout et al. 2013). Given the divergent feeding ecologies of males and female
310 dance flies, differences in selection pressures are expected. Because males are the only sex that
311 hunt prey, they are likely subject to natural (or sexual, given prey are used in obtaining mates)
312 selection for hunting efficiency (Svensson and Petersson 1987; Svensson 1997). In other dance
313 fly species, it has been suggested that leg adaptations, including fore-femur length and leg hairs
314 (*Empis borealis*; Svensson and Petersson 1987, *R. marginata*; Svensson 1997) are related to prey
315 capture and thus may serve a similar function in *R. longicauda*. We may expect such selection to
316 result in positive allometry if males benefit from longer leg hairs while experiencing reduced
317 maneuverability or flying ability if they are small (Karlsson and Wickman 1990; van Lieshout et
318 al. 2013).

319 Based on the finding of positive static allometry on secondary sexual traits, we suggest
320 that female ornaments in *R. longicauda* likely serve as overall honest signals of quality.
321 Although this is consistent with predictions about female ornamentation (Nordeide et al. 2013)
322 the evolution of secondary sexual traits is particularly complicated in nuptial gift systems
323 because of the conflicting interests of males and females. While females are highly motivated to

324 mate and suffer fitness losses if they do not, males are under strong selection to mate with the
325 highest quality females so that their investment is not wasted. Given that the fitness stakes are
326 extremely high for both males and females, we might expect selection to act differently in these
327 unusual systems, resulting in variation from typical models of honesty and deception.

328

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333

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341 Availability of data and material: Data are available to be posted to Dryad

342 Code availability (software application or custom code): R script available to be posted to Dryad

343 Authors' contributions: JHB – concept and design, specimen/data collection, data analysis,
344 primary author, DTG – contributions to concept and design, specimen collection, substantial
345 editing and revisions

346

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497 **Tables and Figures**
498

499 **Table 1.** Comparison of male and female trait sizes for *R. longicauda*

	Females			Males			
Traits	n	mean	SD	n	mean	SD	p
Thorax length (mm)	224	1.50	0.13	113	1.53	0.11	0.0598
Wing length (mm)	222	5.95	0.43	113	5.86	0.34	0.0295
Femur length (mm)	221	3.00	0.24	113	2.79	0.16	<0.0001 *
Tibia length (mm)	202	2.78	0.22	113	2.56	0.15	<0.0001 *
Abdomen area (mm²)	202	6.31	1.56	109	1.76	0.28	<0.0001 *
Femur scale length (mm)	218	0.39	0.04	112	0.18	0.03	<0.0001 *
Tibia scale length (mm)	205	0.38	0.04	113	0.24	0.04	<0.0001 *

509 * Denotes significance with Bonferroni corrected $\alpha=0.0055$

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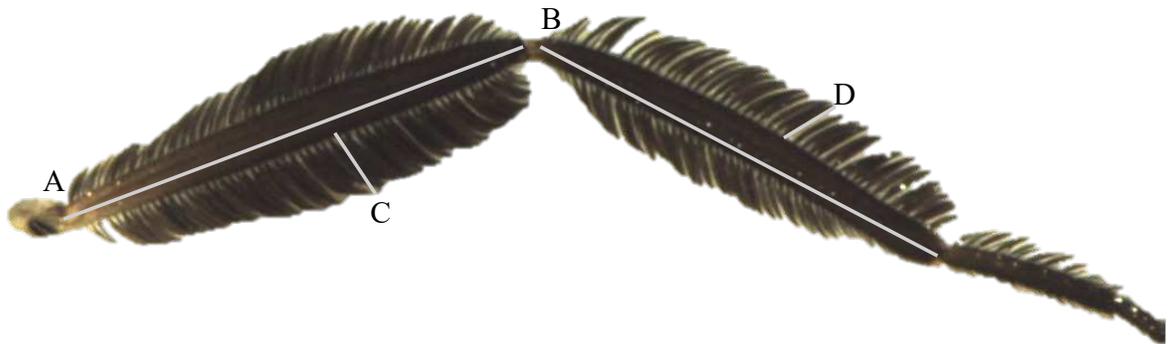
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521 **Table 2.** Static allometry of *R. longicauda* traits in both sexes using major axis regression

522		log y	Intercept	Slope	95% CI	r
523	Females	Wing length	0.634	0.796 *	0.740, 0.857	0.875
524		Femur length	0.321	0.89	0.764, 1.040	0.661
525		Tibia length	0.282	0.923	0.814, 1.046	0.744
526		Abdomen area	0.068	1.844 *	1.523, 2.281	0.572
527		Femur scale length	-0.575	1.052	0.886, 1.251	0.616
528		Tibia scale length	-0.646	1.275 *	1.117, 1.461	0.719
529						
530	Males	Wing length	0.269	0.746 *	0.641, 0.864	0.784
531		Femur length	0.316	0.734 *	0.626, 0.855	0.772
532		Tibia length	0.269	0.756 *	0.655, 0.893	0.802
533		Abdomen area	-0.097	1.172	0.944, 1.466	0.66
534		Femur hair length	-1.484	4.000 *	2.761, 6.955	0.399
535		Tibia hair length	-1.389	4.170 *	3.150, 6.050	0.512

536 * Indicates static allometric slopes deviate significantly from 1 as determined by the 95%
 537 confidence intervals (CI) from major axis regression.

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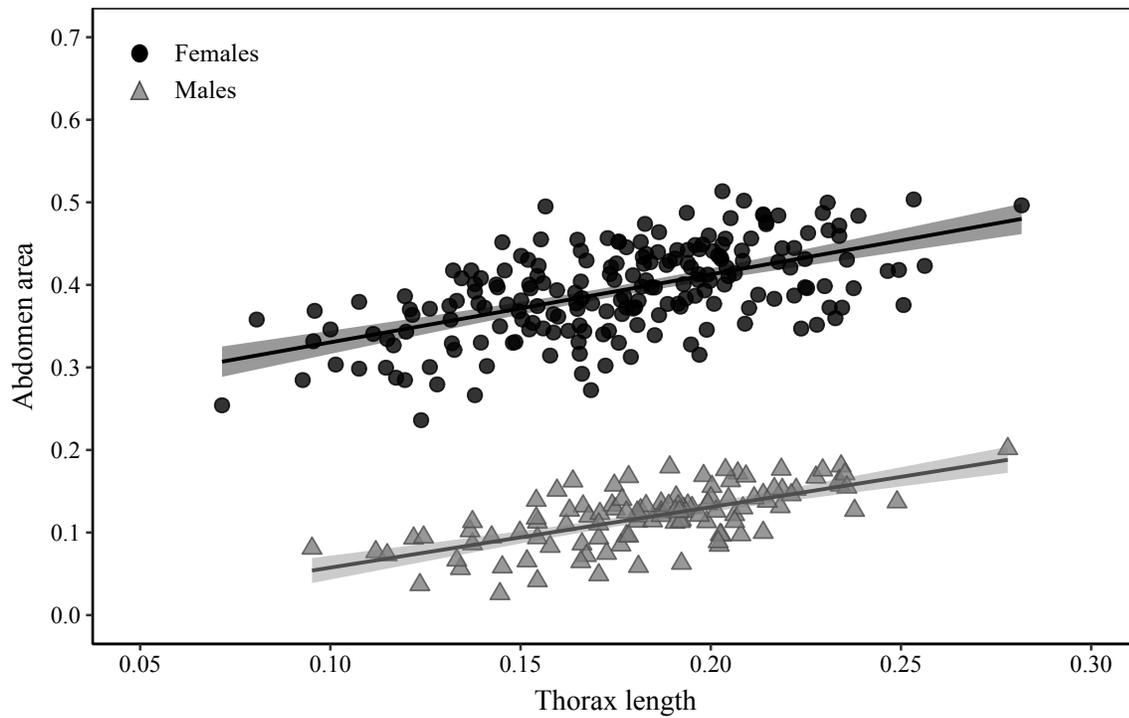
539 **Figure 1.** Leg measurements for females and homologous male structures in *R. longicauda*. **A:**
540 Femur length. **B:** Tibia length. **C:** Femur scale (male hair) length (longest scale on posterior side
541 of femur). **D:** Tibia scale (male hair) length (longest scale on anterior side of tibia).

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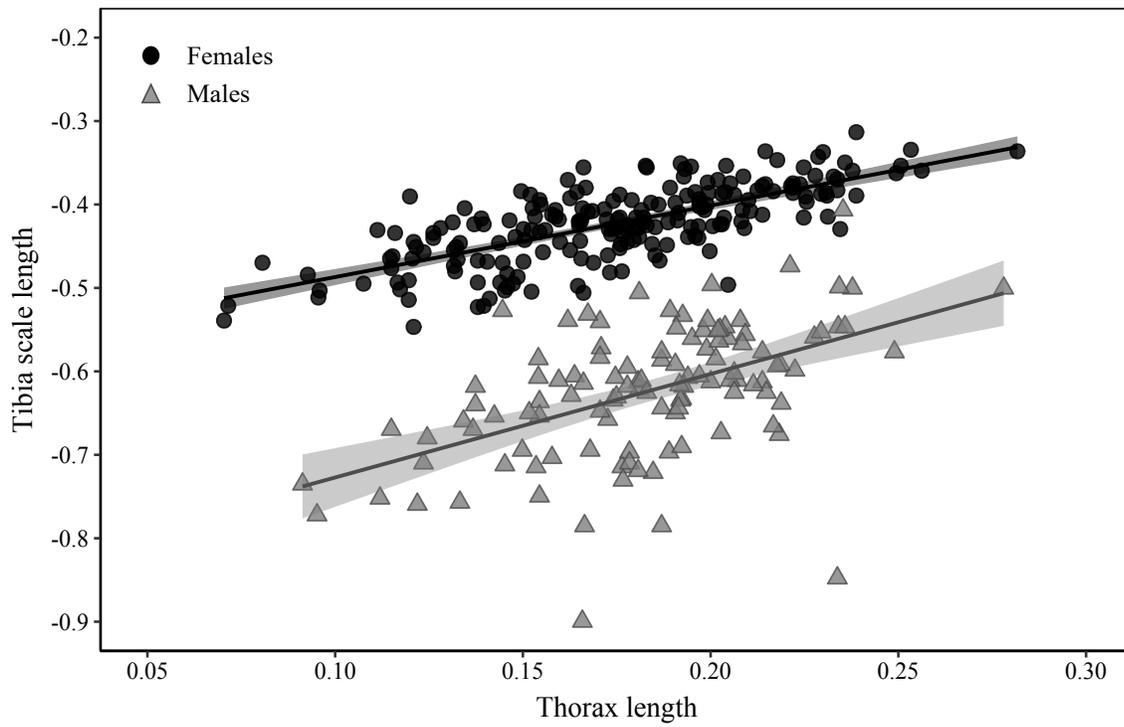
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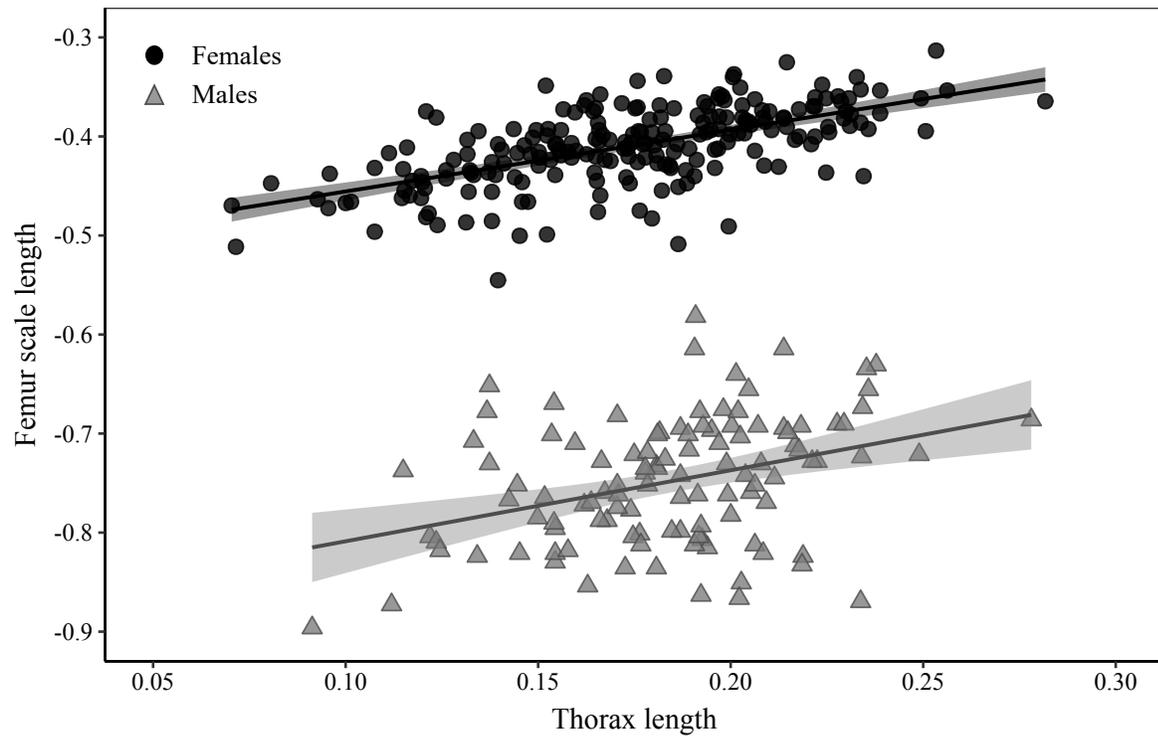


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548 **Figure 2.** Allometric relationships between log thorax length (body size) and log
549 $\sqrt{\text{abdomen area}}$ in (inflated abdomen) female and male *R. longicauda*. Best fit lines are from an
550 ordinary least squares (OLS) regression.



551

552 **Figure 3.** Allometric relationships between log thorax length (body size) and log tibia scale/hair
553 length in female and male *R. longicauda*. Best fit lines are from an ordinary least squares (OLS)
554 regression.



555

556 **Figure 4.** Allometric relationships between log thorax length (body size) and log femur scale or
557 hair length in female and male *R. longicauda*. Best fit lines are from a linear regression.

558

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [female.data.csv](#)
- [male.data.csv](#)