Relationship between weapon size and six key behavioural and physiological traits in males of the European earwig

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SUMMARY

In many animals, male weapons are large and extravagant morphological structures that typically enhance fighting ability and reproductive success. It is generally assumed that growing and carrying large weapons is costly, thus only males in the best condition can afford it. In the European earwig, males carry weapons in the form of forceps-like cerci, which can vary widely in size within populations. While long forceps appear to increase male's access to females, it is surprisingly unknown whether it also correlates with other important life-history traits. However, this information is important for determining the potential reliability of forceps length as an indicator of male quality and the stability of this signalling system. Here, we tested whether forceps length of earwig males is associated with six important behavioural and physiological traits. We sampled hundreds of males from two populations, selected the 120 males with the longest and shortest forceps and then measured their locomotor performance, boldness, aggregation behaviour, survival under harsh conditions, sperm quantity, and survival after pathogen exposure. Contrary to our predictions, we found no association between forceps length and any of the traits measured. This lack of association was consistent between the two populations, although there were population-specific levels of boldness and survival in harsh conditions. Overall, these results challenge our current understanding of the function and quality signal of forceps length in this species and raise questions about the evolutionary drivers that could explain the maintenance of weapon size diversity within and between populations.

Keywords: Weapons; Forceps; Ornament; Sexual selection; Insect; Behaviour

INTRODUCTION

Animal reproduction often requires males to engage in physical competition and courtship to attract females in search of mates (Davies et al., 2012). From vertebrates to arthropods, these two needs have often led to the evolution of male weapons and ornaments through sexual selection (Emlen, 2008; Goldberg et al., 2019; McCullough et al., 2016). These weapons and ornaments are typically large and extravagant morphological structures that can grow on different parts of the male's body, take a variety of forms such as antlers, horns, spurs, fangs and tusks, and work to enhance the male's fighting ability and/or attractiveness to females (Emlen, 2008). Textbook examples of this enhancement can be found in the white-tailed deer *Odocoileus virginianus*, where males growing the largest antlers are more likely to win fights with other males and have higher annual breeding success (Newbolt et al., 2017), and in the stalk-eyed flies *Cyrtodiopsis whitei* and *C. dahnanni*, where females prefer to mate with males exhibiting the longest eye stalks (Wilkinson et al., 1998).

Despite these benefits, not all males engage in displaying extravagant weapons or ornaments (Emlen, 2008; Goldberg et al., 2019; McCullough et al., 2016). This is because the development and maintenance of these sexually selected traits often comes at a cost to males. This cost can arise from the fact that carrying heavy, bulky weapons (or ornaments) makes males less mobile and more visible to both predators and preys (Oufiero & Garland, 2007). This has been reported in the rubyspot damselfly *Hetaerina americana*, where males with experimentally-enlarged wing spots have lower survival rates due to increased conspicuity to both visually orienting predators and visually orienting prey (Grether, 1997). This cost can also arise because carrying large morphological structures may impose investment trade-offs with physiological

55 functions ranging from metabolism to muscle development and spermatogenesis, which can be
56 crucial for male fitness and survival (Emlen, 2001). For example, males with the largest hind leg
57 weapon pay the highest resting metabolic rate and energy costs in the Hemiptera *Leptoscelis*
58 *tricolor* (Somjee et al., 2018). Similarly, growing large mandibles come with low flight-muscle mass
59 in the stag beetle *Cyclommatus metallifer* (Mills et al., 2016), and males who invest in extravagant
60 sexual displays show a more rapid decline in spermatogenesis than males who invest less in these
61 displays in the houbara bustard *Chlamydotis undulata* (Preston et al., 2011). As a result, only the
62 males in the very best condition are expected to possibly afford the development and
63 maintenance of extravagant weapons and ornaments (Otte & Stayman, 1979; Emlen & Nijhout,
64 2000). Determining the reliability of these morphological structures as indicators of the male
65 quality is therefore crucial to understanding the stability of these signalling systems (Berglund et
66 al., 1996).

67 Earwigs (Dermaptera) are textbook examples of insects with males displaying a sexually
68 selected weapon. In this taxonomical group, females have relatively short, straight and hardened
69 forceps-like cerci typically used to defend the clutch against predators (Meunier, 2024), whereas
70 males display elongated, curved and hardened forceps-like cerci (hereafter referred to as forceps)
71 involved in mating courtship and fights against other males (Briceño & Eberhard, 1995; Kamimura,
72 2014; Walker & Fell, 2001). There are several lines of evidence to suggest that long forceps provide
73 males with benefits in terms of mating success (Eberhard & Gutierrez, 1991; Kamimura, 2014;
74 Tomkins & Brown, 2004). For example, males with long forceps are more likely to win fights with
75 other males by squeezing them between their cerci, and thus gain better access to females in the
76 toothed earwig *Vostox apicedentatus* (Moore & Wilson, 1993). In the European earwig *Forficula*

77 *auricularia,* male forceps are also used in male-male contests as a weapon to deter competitors
78 prior to mating (Styrsky & Rhein, 1999) or to interrupt mating by non-copulating males (Forslund,
79 2000, 2003; Walker & Fell, 2001). Long-forceps males are also generally more aggressive, more
80 readily accepted by females for mating and copulate longer compared to short-forceps males
81 (reviewed in Kamimura, 2014). Although forceps are involved in male courtship (Walker & Fell,
82 2001), females do not seem to select their mate on the basis of forceps length (Forslund, 2000,
83 2003; Radesäter & Halldórsdóttir, 1993; Walker & Fell, 2001).

84 While the relationship between male forceps length and mating success has been well
85 documented in earwigs (reviewed in Kamimura, 2014), it remains unclear whether having long or
86 short forceps is associated with other important life-history traits in these males. However, this is
87 important information to determine the potential reliability of forceps length as an indicator of
88 male quality and the stability of this possible signalling system. The very few studies that have
89 addressed this question focused on male immunity in the European earwig *F. auricularia* (Körner
90 et al., 2017; Rantala et al., 2007). On the one hand, they show that males with long forceps have
91 lower basal levels of certain components of the immune system, such as lysozyme activity and
92 hemocyte concentrations. This suggests that having long forceps comes with an immune cost for
93 males. On the other hand, they show no association between forceps length and other
94 components of the immune response, such as encapsulation rate and phenoloxidase activity.
95 Taken together, these findings suggest that the immune costs of having long forceps may be
96 relatively limited and raise the question of whether other important life-history traits can be
97 associated with forceps length.

98 Here, we investigated whether long and short forceps are associated with six important
99 behavioural and physiological traits in males of the European earwig. We sampled hundreds of
100 males in two natural populations of earwigs separated by 400 km and in each population, we
101 selected the 30 males with the longest and the 30 males with the shortest forceps. We then
102 performed standard measurements on each male to assess their locomotor performance,
103 likelihood to flee after a physical disturbance (i.e., boldness), their propensity to aggregate with
104 conspecifics, as well as their survival rate under harsh environmental conditions (i.e., isolated with
105 no access to a food source for 31 days), the number of sperm in their seminal vesicles and their
106 survival rate after exposure to the common entomopathogenic fungus *Metarhizium brunneum*. If
107 forceps length is a reliable signal of good quality, we predict that long forceps males would 1) have
108 higher locomotor performance, 2) be bolder and thus less likely to flee after a simulated attack, 3)
109 be more social and thus more likely to aggregate with conspecifics, 4) be more resilient to harsh
110 environmental conditions and thus have a higher survival rate after 31 days of starvation, and/or
111 would 5) have higher immune defences and thus survive better after a pathogen infection than
112 short-forceps males. We also predict that 6) long-forceps males would produce more sperm and
113 contain more sperm in their seminal vesicles than short forceps males, which would be consistent
114 with the longer duration of copulation reported for the former (Kamimura, 2014).

115

116 MATERIAL AND METHODS

117 Animal rearing and selection

118 In July 2022, we field sampled 3000 males and females in a cultivated peach orchard near Valence,
119 France (Lat 44.9772790, Long 4.9286990) and 400 males and females in a non-cultivated area at
120 the edge of a forest near Cinais, France (Lat 47.1606970, Long 0.1763663). All these individuals
121 belong to *F. auricularia* sp. A (González-Miguéns et al., 2020). Immediately after field sampling, we
122 distributed them by population of origin into 50 plastic terrariums (37 × 22 × 25 cm, balanced sex
123 ratio) to homogenize nutrition, habitation, and access to mates for the males (Körner et al., 2017).
124 Three months later (i.e., at the end of the reproductive season), we removed the males from all
125 the terrariums and, for each population, we visually selected the 30 males exhibiting the longest
126 forceps and the 30 males exhibiting the shortest forceps (Körner et al., 2017). We then isolated
127 each male in Petri dishes (diameter 5 cm) to later use them for behavioural and physiological
128 measurements. Two days after isolation, we confirmed the robustness of our two forceps
129 categories by measuring the mean of the left and right outer forceps of the 120 males. These
130 measurements were done to the nearest 0.001 mm using the Leica Application Suite 4.5 software
131 (Leica Microsystems, Wetzlar, Germany) on pictures taken under a binocular scope (Leica, MZ
132 12.5). These measurements confirmed that there was no overlap between the two male
133 categories (Figure 1). All the remaining males and females that were not used in this experiment
134 were involved in other experiments that are not presented here.

135 From field sampling to isolation, we fed animals with artificial food containing mostly
136 pollen, carrots, and cat food (see details in Kramer et al. 2015). During these three months, we
137 offered this food *ad libitum* to homogenise the nutritional condition of the males when we started
138 our measurements. We then kept the isolated males without access to food (except during the
139 measurement of survival to pathogen infection) to determine their survival rate in harsh

140 environmental conditions. We kept all animals on a 12h:12h light:dark schedule at 18°C, and both
141 the terrarium and Petri dishes contained a layer of moist sand.

142

143 Behavioural measurements

144 From the 5th to the 24th day after isolation, we measured three behaviours in the 120 isolated
145 males: the locomotor performance, the likelihood of fleeing after a physical disturbance, and the
146 level of aggregation. All these measurements followed standard protocols for earwigs (Honorio et
147 al., 2023; Merleau et al., 2022).

148 First, we measured male's locomotor performance 5 days after isolation. On that day, we
149 transferred each male to a 3D-printed circular arena (Open field; diameter = 8 cm, height 0.4 cm)
150 with a cover made of glass, placed on an infrared table and kept in complete darkness. We then
151 video recorded males' locomotion for 20 minutes (Camera: BASLER BCA 1300, Germany; Media
152 Recorder v4.0, Noldus Information Systems, Netherland) and subsequently analyzed the resulting
153 videos with the software Ethovision XT 16 (Noldus Information Systems, Netherland). We defined
154 the locomotor performance of each male as the total distance he walked (in cm) during the entire
155 recording (Honorio et al., 2023; Merleau et al., 2022).

156 Second, we measured the likelihood of fleeing after a physical disturbance 10 days after
157 isolation. On that day, we carefully opened each Petri dish, pricked the male on the pronotum with
158 a glass capillary and then recorded whether or not the male's first reaction was to move more
159 than one body length away from its initial position (i.e., flee).

160 Finally, we measured the level of aggregation of each male 24 days after isolation. We
161 placed each male in a 3D-printed arena used in Van Meyel & Meunier, 2022, consisting of four
162 linearly aligned circular chambers (diameter 4 cm). Three of the chambers were connected by 0.5
163 cm wide corridors allowing earwigs to move between chambers. The width of the corridor
164 connecting to the fourth (outer) chamber was reduced to 0.15 cm, which prevented earwig
165 movement while allowing the circulation of odours and antennal contacts between individuals on
166 both sides (Van Meyel & Meunier, 2022). We started the experiment by placing two naive males
167 and one female from the same population (but not involved in any other experiment or
168 measurement) in this isolation chamber, and the tested male in one of the connected chambers.
169 We then started to record whether the tested male was in the chamber next to the group of
170 conspecifics (yes or no) and repeated this measurement by taking pictures every hour for 48 hours
171 using infrared cameras and the software Pylon Viewer v5.1.0 (Basler©, Ahrensburg, Germany).
172 For each tested male, we thus obtained an aggregation score ranging from 0 to 48, which was
173 defined as the total number of pictures in which a male was in the chamber next to the group of
174 conspecifics. After the 48h of aggregation test, we returned each male to its Petri dish until its use
175 for subsequent measurements (see below). For ease of handling, all manipulated earwigs were
176 anaesthetised with CO_2 during the set-up of this last measurement. Overall, the number of males
177 still alive at the beginning of each of the three measurement (which reflects their survival rate
178 under harsh environmental conditions) is detailed in Table 1.

179

180 Physiological measurements

181 Of the 91 males still alive on day 31 after isolation (Table 1), we used a random subset of 39 to
182 count the number of sperm present in their seminal vesicles and the remaining 52 to measure
183 their survival after pathogen exposure. We counted sperm numbers in 19 males from Cinais (10
184 short forceps and 9 long forceps) and 20 males from Valence (10 short forceps and 10 long forceps)
185 following the protocol detailed in Damiens et al. (2002). In brief, we dissected each male under a
186 binocular, placed their seminal vesicles on a slide with 15 µL of 1x Phosphate Buffered Saline and
187 then pierced it to release all the sperm. We subsequently dried the plate on a heating block, after
188 which the smear of sperm was sealed with a 70% ethanol solution and allowed to dry again at
189 ambient temperature. The slides were then stored at 3°C. Two days later, we deposited 20µL of
190 DAPI dye (concentration = 10 µmol/L) on the smear, covered it with a small piece of plastic wrap
191 to allow the dye to infiltrate the cells while not drying out, and 10 minutes later, we replaced the
192 plastic wrap with a glass slide cover. The slide was then viewed under the microscope at 20x
193 magnification, and we took pictures of 5 different fields of the smear. Using an Olympus
194 micrometre calibration slide and the software Image J (Schneider et al., 2012), we then counted
195 the number of spermatozoa in all 5 fields for each mal. Finally, we used all these numbers to
196 calculate the number of spermatozoa per millimetre square and multiplied this number by the
197 total area of the smear to obtain the total number of sperm per male.

198 We measured the survival rate of males after a pathogen infection by exposing the
199 remaining 20 males from Cinais (8 long forceps and 12 short forceps) and 32 males from Valence
200 (18 long forceps and 14 short forceps) to spores of the entomopathogenic fungus *Metharizium*
201 *brunneum*. *M. brunneum* (formerly *M. anisopliae*) is a natural and lethal pathogen of *F. auricularia*
202 (Arcila & Meunier, 2020; Coulm & Meunier, 2021; Günther & Herter, 1974). The infection followed

203 a standard protocol detailed in Kohlmeier et al. (2016). In brief, we immersed each male in an
204 Eppendorf tube containing 1.5 mL of a conidiospore suspension of *M. brunneum* diluted in 0.05%
205 Tween 20 (Sigma P-1379) at a concentration of 10^6 spores/mL. We then gently swirled the tube
206 from side to side for 4 seconds, removed the male and placed it back in its original Petri dish with
207 standard food (see above) that was changed twice a week. We then kept the infected males at
208 20°C on a 12:12 light:dark schedule. We checked them daily for mortality over the course of 45
209 days.

210

211 Statistical analyses

212 We conducted all statistical analyses using the software R v4.3.2 (https://www.r-project.org/)
213 loaded with the packages *DHARMa* (Hartig, 2020), *car* (Fox & Weisberg, 2019), *survival* (Therneau,
214 2020) and *emmeans* (Lenth, 2022). We analysed locomotor performance, sperm count and
215 aggregation score using three general linear models (*lm* in R), while we analysed the likelihood to
216 flee (yes or no) and whether males were dead 31 days after isolation (yes or no) using two
217 generalized linear model (*glm* in R) with binomial error distributions. Finally, we analysed the
218 survival rate of the pathogen-exposed males using a Cox proportional hazard regression model
219 allowing for censored data (*Coxph* in R), i.e., males still alive 45 days after exposure to the
220 pathogen. In these six models, we entered the type of forceps length (long or short), the
221 population of origin of the males (Cinais or Valence) and the interaction between these two
222 variables as explanatory factors. Overall, we checked that all model assumptions were met (e.g.,
223 homoscedasticity and normality of residuals) using the *DHARMa* package. To this end, we log-
224 transformed male locomotor performance and log+1-transformed the aggregation scores. In the

225 model where we found a significant interaction, we conducted pairwise comparisons using the
226 estimated marginal means of the models and we corrected P values for multiple testing using the
227 Tukey method, as implemented in the *emmeans* R package.

228

229 ## RESULTS

230 Overall, there was no association between forceps length and the six traits measured. This applied
231 to male locomotor performance, likelihood of fleeing after a physical disturbance, aggregation
232 score, sperm count and survival after pathogen infection (Figure 2; Table 2). There was also no
233 difference between males with short and long forceps in terms of survival under harsh
234 environmental conditions, although males with long (not short) forceps survived better when they
235 came from Cinais compared to Valence (Figure 2; interaction in Table 2; pairwise comparisons:
236 Long forceps Cinais vs Valence: Z = -3.311; P = 0.005; Short forceps Cinais vs Valence: Z = -0.611;
237 P = 0.929). Regardless of forceps length, males from Cinais were less likely to flee after a physical
238 disturbance than males from Valence (Table 2). This difference between the two populations was
239 absent for all other traits measured (Table 2). There was no interaction between the population
240 of origin and forceps length for any of the traits measured, except for survival under harsh
241 environmental conditions (Table 2).

242

243 ## DISCUSSION

244 The display of large, extravagant weapons often comes at a cost to the males (Emlen, 2008;
245 Goldberg et al., 2019; McCullough et al., 2016). It is therefore expected that only males in the best

246 condition can afford them and thus that these large weapons signal good male quality (Otte &
247 Stayman, 1979; Emlen & Nijhout, 2000). Here, we tested this prediction in the European earwig
248 by investigating whether male forceps length is associated with six important behavioural and
249 physiological traits. Contrary to our predictions, we found no association between forceps length
250 and any of the traits measured. Having long or short forceps was not linked to any difference in
251 terms of locomotor performance, boldness (i.e., likelihood to flee after a physical disturbance) or
252 aggregation behaviour. It also had no effect on male survival rate under harsh environmental
253 conditions (i.e., isolated without access to a food source for 31 days), the amount of sperm present
254 in their seminal vesicles, or their survival after pathogen infection. These findings were consistent
255 between the two populations, although some of the traits measured were population specific:
256 males were overall bolder when they came from Cinais, and males with long (not short) forceps
257 survived better in harsh conditions when they also came from Cinais.

258 Our results contrast with much of the literature reporting associations between sexually
259 selected male attributes and physiological, behavioural or immunological traits in arthropods
260 (Emlen, 2008; Goldberg et al., 2019; McCullough et al., 2016). However, the European earwig is
261 not the only case where such associations appear to be lacking (Emlen, 2008; Swallow & Husak,
262 2011). For example, carrying giant claw is not associated with the efficiency of escape behavior
263 and the level of metabolic costs in two fiddler crabs (Pena & Levinton, 2021; Tullis & Straube,
264 2017). Similarly, bearing large horns does not reflect male growth, mobility, or immunity in the
265 rhinoceros beetle *Trypoxylus dichotomus* (McCullough & Emlen, 2013; McCullough & Tobalske,
266 2013). It has been suggested that this apparent lack of general association may be due to the fact
267 that the performance of each weapon size depend on the environment in which the weapons are

268 used and/or because weapon sizes reflect alternative reproductive tactics (McCullough et al.,
269 2016; McCullough & Emlen, 2013). This could be the case with the European earwig. In this
270 species, males with large forceps have been suggested to be more active in guarding of females,
271 while males with small forceps are more active in sneaking into copulations (Kamimura, 2014;
272 Tomkins & Brown, 2004). Having long forceps should therefore be rewarded more frequently
273 when the encounter rate between competitors is high (Hunt & Simmons, 2001), such as in high
274 population densities. Consistent with this prediction, Tomkins & Brown (2004) found that the
275 proportion of long forceps males increased with population densities across 46 island and
276 mainland sites in the UK. Another possible explanation for our results is that the association
277 between male forceps length and the six traits measured could have been masked by differences
278 in the amount of resources available to each male and/or used by each male for these traits (van
279 Noordwijk & de Jong, 1986). In our study, all males were kept under identical laboratory conditions
280 and fed *ad libitum* for three months prior to our measurement. This explanation would therefore
281 suggest that the variation in resources influencing investment decisions is determined prior to
282 field sampling, e.g. during development or early adulthood. Previous data suggest that it could be
283 the case in the European earwig. In this species, early life conditions have long-term effects on the
284 physiology and behaviour of adults (Raveh et al., 2016; Thesing et al., 2015; Wong & Kölliker, 2014)
285 and inter-individual variation in female condition can mask investment trade-off between egg
286 quantity and quality (Koch & Meunier, 2014). Overall, our findings call for future studies to confirm
287 whether males with short or long forceps have alternative reproductive tactics, whether their
288 reproductive success depends on population densities and whether early life conditions can affect
289 the likelihood to detect the association between forceps length and the six traits measured.

290 Notwithstanding these underlying mechanisms, they also emphasize that forceps size is not a good
291 predictor of the six behavioural and physiological traits measured in males.

292 While we found no overall difference between short- and long-forceps males, our data
293 reveal population differences in terms of males' boldness and resistance to starvation. Cinais had
294 males that were generally bolder, as well as males with long forceps that survived food deprivation
295 better than Valence. These effects are unlikely to reflect a plastic response to the direct
296 environment of the males tested (e.g. population differences in terms of nutritional status), as
297 they were all reared under common laboratory conditions for months prior to the start of our
298 experiments. Instead, it could reflect population idiosyncrasies that have affected their
299 development, such as climatic conditions (Valence is warmer than Cinais), exposure to
300 phytosanitary products (e.g. Valence is a cultivated orchard, whereas Cinais is an uncultivated
301 forest edge) or population-specific genetic background. In line with this hypothesis, several life
302 history traits of the European earwig are shaped by the duration of cold during egg development,
303 the level of warm temperatures during nymph development and, more generally, by seasonal
304 parameters encountered by offspring during development (Coulm & Meunier, 2021; Körner et al.,
305 2018; Tourneur & Meunier, 2020). Similarly, recent studies have shown that the European earwig
306 can be sensitive to exposure to even low levels of pesticides, which can lead to populations
307 specificities in terms of earwig physiology, morphology and behaviour (Fricaux et al., 2023; Le
308 Navenant et al., 2019; Malagnoux, Capowiez, et al., 2015; Malagnoux, Marliac, et al., 2015;
309 Mauduit et al., 2021; Meunier et al., 2020). Regardless of the nature of these population
310 idiosyncrasies, our study shows that they do not affect the (lack of) association between forceps
311 length and the six traits measured.

312 Overall, our findings questions the robustness of our understanding of forceps length
313 diversity in terms of function, maintenance and use as a possible quality signal in the European
314 earwig (McCullough et al., 2016). To date, our knowledge of these questions is exclusively based
315 on laboratory experiments in which females were presented to one or two males (reviewed in
316 Kamimura, 2014). While the results of these studies suggest that males can gain fitness benefit
317 from growing long compared to short forceps (Forslund, 2000, 2003; Radesäter & Halldórsdóttir,
318 1993; Styrsky & Rhein, 1999; Walker & Fell, 2001), they contain two important limitations. First,
319 they considered mating success (i.e., success in gaining copulation) and not reproductive success
320 (i.e. success in producing offspring). As these two parameters are not necessarily related
321 (Thompson et al., 2011), it cannot be excluded that short forceps males have a similar or even
322 higher reproductive output than their counterparts. This could be because mating is more efficient
323 in short compared to long forceps males (Brown, 2006), or because short forceps males have
324 alternative reproductive tactics to long forceps males (see above; Tomkins & Brown, 2004). One
325 study used a genetic approach to study reproductive success and found no association between
326 male forceps length and the number of offspring sired (Sandrin et al., 2015). However, this study
327 only focused on length variation within short forceps males. The second limitation is that all these
328 studies have examined mating success in groups of a maximum of two males. This number is far
329 less than the hundreds of individuals that typically constitute earwig aggregates (Meunier, 2024)
330 and thus cannot rule out the possibility that the apparent advantage of long-forceps males in pairs
331 or trios may disappear or even become a disadvantage under different demographic conditions
332 (Hunt & Simmons, 2001; Oliveira et al., 2008; Tomkins & Brown, 2004). Hence, our current
333 understanding of the relationship between forceps length and male fitness should be treated with

caution in the European earwig. Our results thus call for future studies to determine the function and reliability of male forceps length under natural conditions, and the evolutionary drivers that explain the maintenance of its diversity within and between populations.

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Data accessibility

All data and R script are available online: https://doi.org/10.5281/zenodo.10843578

Conflict of interest disclosure

The authors declare that they have no financial conflict of interest with the content of this article.

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529 **Table 1** – Number of males used for each measurement. The observed reduction over days reflects

530 their mortality during isolation and in absence of any food source. Males are distributed according

531 to their forceps-length category and their population of origin.

532

		Large forceps males		Short forceps males	
Measurement day	Type of measurement	Cinais	Valence	Cinais	Valence
0	Male isolation	30	30	30	30
5	Locomotor performance	30	29	30	30
10	Response to physical disturbance	30	29	30	30
24	Aggregation	18	28	22	24
31	Sperm count & survival to pathogen	17	28	22	24

533

534 **Table 2** – Effects of male forceps length and population of origin of the three physiological and

535 three behaviours measured in this study. Significant p-values are in bold.

536

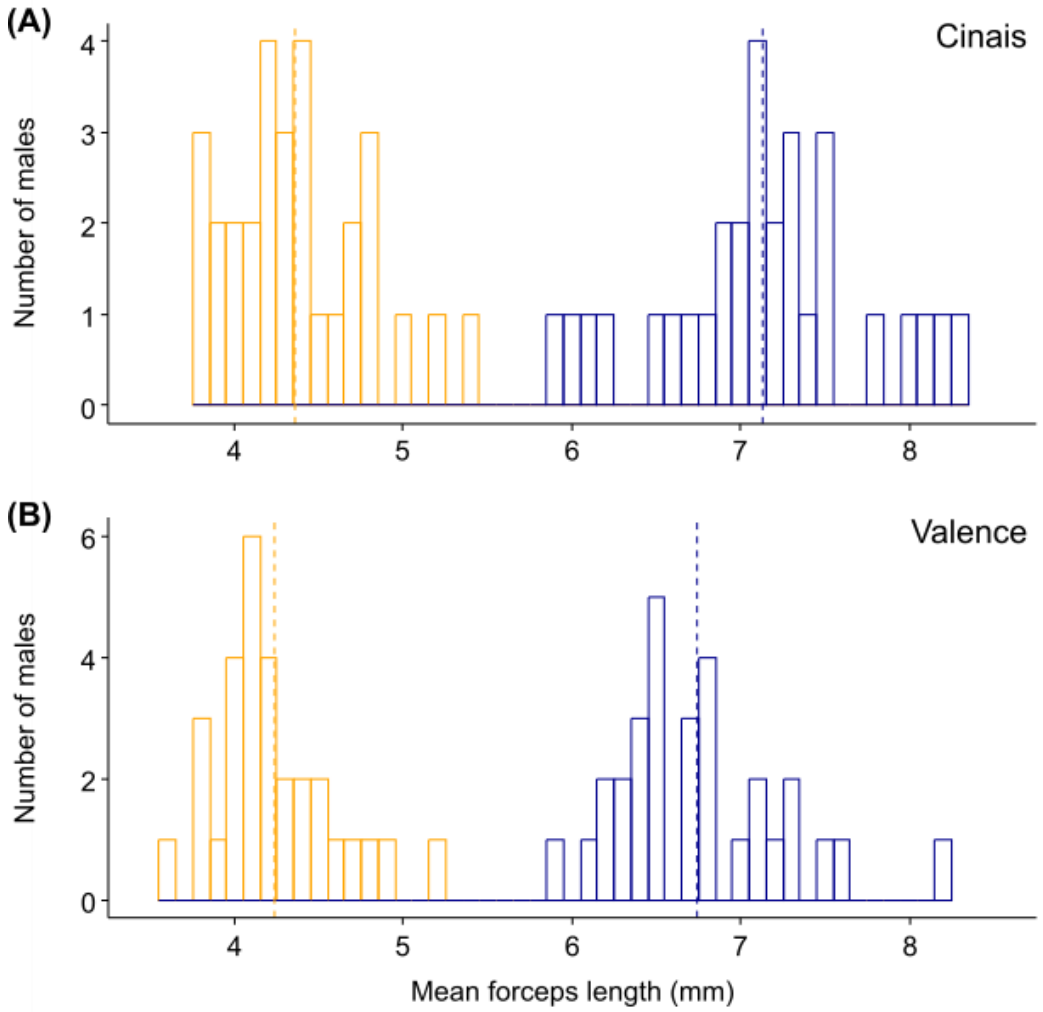
	Population of origin	Forceps length	Interaction
Locomotor performance	$F_{1,115}$ = 0.21; P = 0.648	$F_{1,115}$ = 1.14 P = 0.287	$F_{1,115}$ = 1.25; P = 0.265
Likelihood of fleeing away after a physical disturbance	LR χ^2_1 = 8.74; P = **0.003**	LR χ^2_1 = 1.06; P = 0.303	LR χ^2_1 = 0.57; P = 0.450
Aggregation score	$F_{1,88}$ = 3.83; P = 0.054	$F_{1,88}$ = 0.004; P = 0.948	$F_{1,88}$ = 0.02; P = 0.878
Survival rate under harsh environmental conditions	LR χ^2_1 = 7.88; P = **0.005**	LR χ^2_1 = 0.02; P = 0.885	LR χ^2_1 = 4.22; P = **0.039**
Sperm count	$F_{1,35}$ = 0.42; P = 0.522	$F_{1,35}$ = 0.19; P = 0.667	$F_{1,35}$ = 0.75; P = 0.391
Survival rate after infection	LR χ^2_1 = 0.02; P = 0.891	LR χ^2_1 = 0.15; P = 0.695	LR χ^2_1 = 0.46; P = 0.496

537

538 **Figure 1** – Forceps length distribution of the 120 selected males with (blue) short and (orange)

539 long forceps in (A) Cinais and (B) Valence populations. Dashed lines show the mean values per

540 forceps category for each population.



541

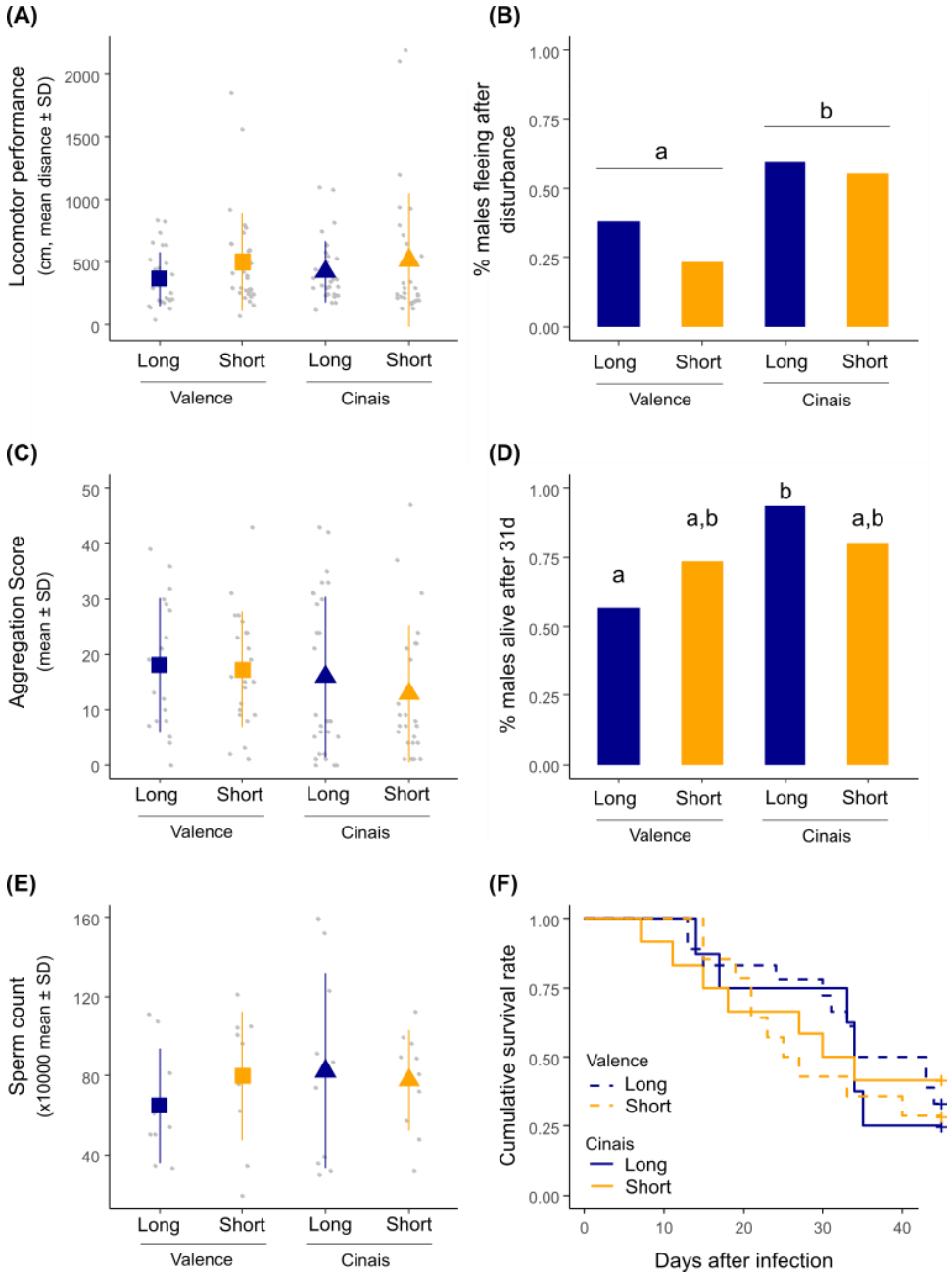
542 **Figure 2** – Association between forceps length and male (A) locomotor performance, (B) likelihood

543 of fleeing after a physical disturbance, (C) propensity to aggregate with conspecifics, (D) likelihood

544 of being alive after 31 days in social isolation and without food access, (E) sperm count in the

545 vesicle and (F) survival rate after pathogen infection. Males came from Cinais (square) or Valence

546 (triangle). Different letters *P* <0.05.



547