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Effect of environmental conditions on flight capacity in mountain pine beetle (Coleoptera: Curculionidae: Scolytinae).

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Abstract:	<p>Mountain pine beetle (<i>Dendroctonus ponderosae</i> Coleoptera: Curculionidae: Scolytinae) is a major pest of pine (Pinaceae) in western North America. Mountain pine beetle has an obligatory dispersal phase during which beetles fly in search of new hosts to colonize. Climatic factors may influence dispersal in the expanding geographic range of the mountain pine beetle. This study tests mountain pine beetle flight capacity in the laboratory under different abiotic conditions including temperature, light and wind speed. Beetle flight capacity was tested under different temperatures before and during flight and different light regimes in separate computer-linked flight mill bioassays. A wind tunnel experiment tested the effect of wind speed on beetle flight. Pre-flight temperature and temperature during flight did not affect beetle flight capacity (distance or duration). Beetles do, however, use more energy during flight at high temperatures, which could affect host colonization following dispersal by flight of mountain pine beetle in nature. Beetles fly a greater distance and longer duration during a long (18 h) than short (16 h) photophase, suggesting that increased day length with a northern range expansion could affect beetle flight capacity. Although wind speed does not affect flight probability or duration, it affects the number of flights and flight patterns of mountain pine beetles.</p>	
Response to Reviewers:	October 08, 2020 Re: Revised version of: Effect of environmental conditions on flight capacity in mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) . Dear Drs. Allison and Cardé, Thank you very much for accepting our manuscript, "Effect of environmental conditions on flight capacity in mountain pine beetle (Coleoptera: Curculionidae: Scolytinae)" for publication in Journal of Insect Behaviour. Please find attached the revised version of	

our manuscript. We have addressed the concerns raised by the editors.

1. We notice that species authors are included and these should be removed in keeping with house style.

Authors response: We have removed species authors in the revised manuscript. [Lines 21, 47, 49, 53,86,325, 340]

2. Last reference, italicize genus, remove DOIs unless it's an online reference.

Authors response: We have italicized genus name of the last reference and DOIs were removed from references when not applicable.

3. we ask that you take a look at the text around lines 91 and 355. It seems that there could be inconsistencies here.

Authors response:

[Line 91] Emerging mountain pine beetles normally fly downwind until they encounter an odor plume at which point beetles turn to orient upwind in response to the odor source (Safranyik et al. 1992).

[Line 354-356] During the current study, beetles flew against the wind without the presence of any semiochemical cues. Mountain pine beetles fly downwind at emergence even in the presence of aggregation pheromones (Safranyik et al. 1992), before flying upwind after encountering an odor source (Gray et al. 1972).

We have removed Line 355 from the revised manuscript.

Line 354 "During the current study, beetles flew against the wind without the presence of any semiochemical cues." is same as the Line 356 " In the absence of an odor source, mountain pine beetle fly without wind or against all the different wind speeds tested in the current study". Therefore, we removed Line 354-355 to keep the flow of the discussion.

1 **Effect of environmental conditions on flight capacity in mountain pine beetle (Coleoptera: Curculionidae:**
2 **Scolytinae)**

3

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9

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19 permits were held when the research was conducted.

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Abstract

Mountain pine beetle (*Dendroctonus ponderosae* Coleoptera: Curculionidae: Scolytinae) is a major pest of pine (Pinaceae) in western North America. Mountain pine beetle has an obligatory dispersal phase during which beetles fly in search of new hosts to colonize. Climatic factors may influence dispersal in the expanding geographic range of the mountain pine beetle. This study tests mountain pine beetle flight capacity in the laboratory under different abiotic conditions including temperature, light and wind speed. Beetle flight capacity was tested under different temperatures before and during flight and different light regimes in separate computer-linked flight mill bioassays. A wind tunnel experiment tested the effect of wind speed on beetle flight. Pre-flight temperature and temperature during flight did not affect beetle flight capacity (distance or duration). Beetles do, however, use more energy during flight at high temperatures, which could affect host colonization following dispersal by flight of mountain pine beetle in nature. Beetles fly a greater distance and longer duration during a long (18 h) than short (16 h) photophase, suggesting that increased day length with a northern range expansion could affect beetle flight capacity. Although wind speed does not affect flight probability or duration, it affects the number of flights and flight patterns of mountain pine beetles.

Keywords

Dendroctonus ponderosae, light, temperature, wind speed, insect dispersal

38 Introduction

39 Dispersal is a basic element in the population dynamics of eruptive insect species (Bjornstad 2002; Aukema
40 et al. 2006; Sturtevant et al. 2013) because low resource availability at high population densities affects insect flight
41 (Elliott and Evenden 2012; Evenden et al. 2014). Dispersal is energetically costly (Zera 2009) and may reduce
42 energy availability for subsequent reproduction (Hanski et al. 2006; Wijerathna and Evenden 2019). Understanding
43 dispersal is important to predict spread and manage eruptive insect pests. Insect dispersal includes both long- and
44 short-distance movement of individuals from natal habitats (Nathan et al. 2003) to feeding or breeding habitats
45 (Loxdale and Lushai 1999; Bowler and Benton 2005). Dispersal and movement of insects is influenced by many
46 factors that can act at individual to ecosystem levels (Loxdale and Lushai 1999).

47 Mountain pine beetle (*Dendroctonus ponderosae* Coleoptera: Curculionidae: Scolytinae) is the most
48 important pest of pine (Pinaceae) in western North America. It has killed lodgepole pine (*Pinus contorta*) forest over
49 an area of 18 million hectares during the most recent outbreak that started in the late 1990s (<https://www2.gov.bc.ca>).
50 High population densities of mountain pine beetle in the most recent outbreak generated long-distance dispersal
51 events that resulted in range expansion into pine forests east and north of the Rocky Mountains in Alberta (Safranyik
52 et al. 2010). In its expanded range, mountain pine beetle has encountered the novel host, jack pine (*P. banksiana*) in
53 the boreal forest of Canada (Cullingham et al. 2011). In the new range, mountain pine beetle will encounter climatic
54 conditions that differ from its historical habitats which may influence dispersal in the new range.

55 Mountain pine beetle has an obligatory dispersal phase (Gray et al. 1972; de la Giroday et al. 2012) which
56 largely depends on short-distance or stand-level flight (Safranyik 1989). This dispersal can be influenced by weather
57 (Safranyik et al. 1992; Jackson et al. 2008; Murphy et al. 2004; Chen and Jackson 2017), host tree availability
58 (Robertson et al. 2007) and beetle physiology (Evenden et al. 2014; Wijerathna and Evenden 2019). Pioneer females
59 release an aggregation pheromone, *trans*-verbenol, after reaching a suitable host (Pureswaran and Borden 2005)
60 which attracts both sexes of mountain pine beetle to initiate the mass attack on the tree (Pitman 1968). Arriving
61 males produce a different aggregation pheromone, *exo*-brevicomin, which mainly attracts females until the attack
62 density is maximized. Both sexes produce anti-aggregation pheromone, verbenone, to discourage further
63 colonization of the host tree (Pureswaran et al. 2000). Despite our vast knowledge of mountain pine beetle ecology,

64 it is unclear how abiotic factors influence the flight capacity of mountain pine beetles during this obligatory
65 dispersal phase.

66 Weather factors are frequently correlated and have a combined effect on insect flight. Inner bark temperature
67 before flight initiation may be important for bark beetle flight in nature, as higher ambient temperatures are required
68 for flight take-off than for sustained flight in most insects (Johnson 1969; Rudinsky and Vite 1956). The minimum
69 flight initiation temperature of many *Dendroctonus* species lies between 16 to 20°C (Miller and Keen 1960;
70 McMullen and Atkins 1962; Atkins 1966; Shepherd 1966; Rasmussen 1974; Jones et al. 2019). Temperature affects
71 the flight speed, distance and the flight frequency in some bark beetle species (Henson 1962; Jones et al. 2019).
72 Flight by mountain pine beetle is severely restricted at temperatures above 38°C and no flight occurs above 41°C
73 (McCambridge 1971). The lower limit for flight initiation of mountain pine beetle is 19°C (McCambridge 1971).
74 The temperature might also affect mountain pine beetle flight through an indirect effect on the energy reserves used
75 in flight. High bark temperatures can lead to low-quality mountain pine beetle individuals (Chubaty et al. 2014) and
76 energy reserves are positively related to mountain pine beetle dispersal (Evenden et al. 2014; Wijerathna and
77 Evenden 2019). Mountain pine beetles with more fat fly further and for longer compared to those with low fat
78 reserves (Evenden et al. 2014; Wijerathna et al. 2019). Energy level can influence host selection decisions (Atkins
79 1966; Jones et al. 2019) of mountain pine beetle, as beetles with higher energy reserves are more host selective than
80 beetles with low energy reserves that accept poor quality trees (Chubaty et al. 2009; Latty and Reid 2010).

81 The current mountain pine beetle range expansion toward more northerly habitats will expose beetles to
82 longer day lengths during the summer flight period, which may change the distance and duration that beetles fly
83 during a day. Mountain pine beetles are photopositive at emergence under room temperature and more females
84 orient toward light than males (Atkins 1966). Mountain pine beetles become negatively phototactic when the
85 temperature exceeds 35°C (Shepherd 1966). *Dendroctonus armandi* also displays a photosensitive flight behavior in
86 which total flight distance is greater under artificial illumination than in natural light and dark conditions in a flight
87 mill study. Flight occurs most in the morning and afternoon and declines under dark conditions (Chen et al. 2010).

88 Insect orientation during dispersal is linked to the direction and speed of air movement. Emerging mountain
89 pine beetles normally fly downwind until they encounter an odor plume at which point beetles turn to orient upwind
90 in response to the odor source (Safranyik et al. 1992). Beetle response to attractive semiochemicals decreases with
91 increasing wind speed (Gray et al. 1972). Larger scolytids can navigate at wind speeds up to about 2 m/s (Rudinsky

92 1962; Coster and Gara 1968). Flight of *D. frontalis* ceases at wind speeds greater than ~ 2 m/s (Coster and Gara
93 1968). Hence, changes in wind speed might alter beetle flight patterns and response toward pheromones and host
94 volatiles.

95 Assessment of flight capacity in a controlled environment can indicate factors that may be driving variation
96 in the dispersal of mountain pine beetle under natural conditions. The purpose of this study is to understand
97 mountain pine beetle flight capacity under different abiotic conditions to predict how environmental factors will
98 affect dispersal in the expanded range of mountain pine beetle. We hypothesize that flight capacity of mountain pine
99 beetle is influenced by rearing and flying temperatures, light and wind speed. We use computer-linked flight mills to
100 determine the effects of variation in day length and temperature before and during flight on beetle flight capacity.
101 We measure flight distance, duration, speed, and the probability of beetles to fly under variable conditions. We
102 predict that mountain pine beetle reared and flown at low temperatures will have greater flight capacity compared to
103 those reared and flown at higher temperatures. As beetles fly during the day under natural conditions, we predict that
104 flight distance and duration will increase with day length under artificial conditions. We predict that beetle flight
105 capacity will decrease with increasing wind speeds. We use a wind tunnel bioassay to examine the effects of wind
106 speed on mountain pine beetle flight probability, duration, number of flights and flight patterns.

107

108 **Methods**

109 *Beetles*

110 Mountain pine beetle-infested lodgepole pine bolts were obtained from five different sites (3 trees/site) near
111 Grande Prairie, AB (55.1699°N, 118.7986°W) in October 2014. One 50-cm bolt from 1 m above the soil surface
112 was cut from each tree. These bolts were transported to the laboratory at the University of Alberta where the cut
113 ends were sealed with paraffin wax before storage at 5°C. Bolts were kept in cold storage for 4 to 6 months to
114 provide some winter condition for maximal mountain pine beetle development (Lusebrink et al. 2013). After
115 removal from cold storage, bolts were placed in separate 121-L bins made of opaque plastic and fitted with glass
116 emergence jars and held at room temperature. The emergent adult beetles were separated by sex (Lyon 1958) and
117 beetles were stored at 5°C in microcentrifuge tubes (2.0 ml) with a piece of paper to provide a surface to which
118 beetles could cling.

119 *Beetle flight treatment*

120 Two types of flight bioassays were used to test the effects of environmental conditions on mountain pine
121 beetle flight. To test the effects of temperature and light on beetle flight capacity, bioassays were conducted on
122 computer-linked flight mills (Evenden et al. 2014). Beetles (3-5 days post-emergence) were prepared for flight by
123 attaching a 0.4-mm-diameter loop of a tether made from 0.2-mm-diameter aluminum wire to the beetle pronotum
124 with Press-Tite Contact Cement (LePage, Mississauga, ON, Canada). Tethered beetles were attached to the distal
125 end of each flight mill arm by inserting a straight 2-cm portion of the aluminum tether at an approximately 100°
126 angle with the mill arm. The flight assay was initiated 4 h after the beginning of the photophase and lasted 23 h.
127 Beetles were flown at 621 Lux during the light cycle using high flicker frequency fluorescent bulbs. Males and
128 females were flown on alternate days (n=2-22 per day) to avoid sensory cues from the opposite sex affecting flight.
129 As beetles propelled the mill arms, a magnetic sensor on each flight mill indicated the arm rotation of each mill to
130 the computer. One revolution of the mill arm equaled 94.2 cm. The software (LabView, National Instruments
131 Corporation, Austin, TX) output included total distance flown, longest single flight, flight duration and flight speed.
132 Beetle flight status was recorded as a binary outcome (flight=1, no flight=0) for the beetles that were placed on
133 flight mills during the 23h flight period. A random sample of beetles was selected to serve as controls. Control
134 beetles were tethered in the same manner, but the tether was then removed from the beetles, and beetles were kept in
135 a perforated microcentrifuge tube (2 ml) during the flight period in the same environmental chamber that housed the
136 flight mills.

137 To test the effects of wind speed on beetle flight, a second set of flights was conducted in a small wind tunnel
138 (0.1m x 0.05m x 0.05m) (Fig. 1) positioned within a large wind tunnel (1.7m x 0.85m x 0.9m). The small wind
139 tunnel was connected to a variable-speed fan at the upwind end. The top of the wind tunnel was covered with a
140 transparent sheet (80cm x 40cm) to allow light penetration provided by 4, 100 watt incandescent lights (~650 lux).
141 A small window (30cm x 20cm) covered with a plastic transparent sheet on the side of the small tunnel allowed the
142 experimenter to observe the flight trials. Wind speed was measured at the beginning of each flight bioassay using a
143 hand-held anemometer (Model 9870, Sunshine Instruments) inserted into the wind tunnel 40 cm downwind from the
144 fan (Fig. 1).

145 *Temperature-flight bioassay*

146 A flight mill experiment tested the effects of temperature before and during flight on the flight capacity of
147 mountain pine beetle (Fig. 2). Beetles are ectotherms and lose more energy when kept at a higher temperature

148 compared to lower temperatures. Mountain pine beetles kept at 25°C lose more energy compared to those kept at
149 4°C (Chubaty et al. 2014). Therefore, we selected 5°C and 24°C as the beetle rearing temperatures for this
150 experiment. The lower limit for flight initiation of mountain pine beetle is 19°C and flight is severely restricted
151 above 38°C (McCambridge 1971). We selected two flying temperatures, 20°C and 24°C, where mountain pine
152 beetles can conduct sustained flights. Beetles (2-4 days post-emergence) were separated into different pre-flight
153 temperatures (5°C and 24°C) 23 h before the flight bioassay. After 23 h at the assigned pre-flight temperature,
154 beetles were weighed to the nearest 0.01 mg (Mettler Toledo, XS105, Columbus, OH) and the pronotum width and
155 body length (to the nearest 0.01mm) were measured using an ocular micrometer on a dissecting microscope (6.3 X
156 magnification). Tethered beetles from both pre-flight temperature treatment groups were flown at one of two flight
157 temperatures (20°C and 24°C). Beetles from both pre-flight temperature treatments were flown on a single day
158 under each flying temperature. A minimum of 50 male and 50 female beetles from each pre-flight temperature group
159 were flown at each flight temperature (total=401). Beetles were flown for 23 h under 16L: 8D at 621 Lux during the
160 light cycle. A separate set of control beetles was held at the same flight temperature for 23 h before the flight and
161 treated in the same manner as the flown beetles. Beetles were weighed to the nearest 0.01 mg after the 23 h flight.

162 *Light-flight bioassay*

163 Another flight mill experiment tested the effect of photophase duration on beetle flight (Fig. 3). Beetles 3-5
164 days post-emergence were tethered, and flights were conducted under two different photoregimes with different
165 photophase lengths (short [16L: 8D] and long [18L: 6D]). Two to 22 beetles were flown per day for 23 h at 24°C
166 under 621 Lux during the photophase. A separate set of control beetles was housed individually inside perforated
167 microcentrifuge tubes (2 ml) with a piece of paper. Control beetles were tethered in the same manner, but tethers
168 were removed and control beetles were held under the same conditions as experimental beetles during the flight
169 bioassay. Ninety-five females and 95 males were flown on the short day length cycle and 52 males and 38 females
170 were flown on the long day length cycle (total=280). The pronotum width and body length (to the nearest 0.01mm)
171 of each beetle was measured at 6.3X magnification before the flight. Pre- and post-flight weights were measured to
172 the nearest 0.01 mg (Mettler Toledo, XS105, Columbus, OH).

173 *Wind speed-flight bioassay*

174 The effect of wind speed on beetle flight probability and duration was tested in a wind tunnel flight
175 bioassay. Tethered beetles were suspended 15 cm from the roof of the wind tunnel, 40 cm from the upwind end (Fig.

176 1). Five tethered beetles of the same sex were positioned 5 cm apart in each trial. Beetles were introduced facing
177 both upwind and downwind directions within the flight chamber at one of four different wind speeds (0, 0.5, 1, 2
178 m/s) (Fig. 4). Beetles did not fly when facing downwind. Therefore, beetles were flown facing upwind during the
179 flight bioassay. Beetles were given 10 minutes to acclimatize before the experiment. Five beetles were observed for
180 50 minutes on each flight day at each wind speed. Different beetles were tested to each wind speed. The number and
181 duration of flights were recorded at each tested wind speed within the observation period. Beetle flight status was
182 recorded as a binary outcome (flight=1, no flight=0) of the beetles that were suspended from the ceiling of the wind
183 tunnel during the 50 min flight period. Wind speed treatments were alternated during the day to prevent confounding
184 effects of time of day on the beetle flight. Beetle pronotum width and body length (to the nearest 0.01mm) were
185 measured before the flight. Pre- and post-flight weight was measured to the nearest 0.01 mg (Mettler Toledo,
186 XS105, Columbus, OH). A total of 223 beetles were flown during the wind tunnel bioassay. Conditions within the
187 wind tunnel were maintained at light~650 Lux and temperature= $24\pm 2^{\circ}\text{C}$.

188 Data Analysis

189 Data were analyzed using R v. 3.5.2 2018.12.20 (R Core Development Team 2018) separately for the three
190 experiments (temperature, light and wind speed bioassays). The flight probability and flight capacity of the beetles
191 in flight assays were analyzed using generalized mixed effect models using lme4 library (Bates et al. 2015) (Table
192 1). To test flight capacity of the beetles in the temperature bioassay, flight duration, flight distance and flight speed
193 were treated as dependent variables in separate models. Pre-flight temperature, flying temperature, sex and pre-flight
194 weight were treated as fixed factors in flight probability and flight capacity models. The weight loss of the beetles
195 was analyzed using a generalized mixed effect model. Beetle weight loss was calculated by subtracting the post-
196 flight weight from pre-flight weight. Pre-flight temperature, flying temperature and sex were the fixed factors in this
197 model. Data from all pre flight- flying temperatures regimes and both sexes were averaged to visualize effects of
198 pre-flight weight on flight distance and duration.

199 In the light experiment, flight distance and duration were treated as dependent variables in separate models.
200 The light cycle (short and long), light phase (photophase or scotophase), sex and pre-flight weight were used as
201 fixed factors. In the wind speed bioassay, flight probability and total flight duration were analyzed in separate
202 generalized mixed effect models. Wind speed, beetle sex and pre-flight weight were treated as fixed factors in each
203 model. Flight duration was transformed using Tukey's Ladder power transformation (Tukey 1977) to maintain the

204 normality. In the flight duration model, wind speed was treated as a continuous variable and pre-flight weight was
205 treated as a covariate. To analyze beetle flight patterns, flights were categorized depending on the duration for each
206 flight type within the 50 min bioassay: 1) no flight; 2) burst flight <15 s; 3) intermediate flight between 15 s-25 min;
207 and 4) sustained flight for >25 min. The total number of flights conducted by all individuals under each wind speed
208 was counted. Then, the percentage of each flight type conducted under each wind speed in the 50 min bioassay was
209 calculated and used as the dependent variable in a generalized linear model. Tree bolts from which beetles emerged
210 were treated as a random factor in the above generalized mixed effect models.

211 Initial models contained all explanatory variables and interactions between all explanatory variables. In all
212 analyses, model simplification was achieved by ANOVA hypothesis testing ($p < 0.05$) for full and reduced models,
213 until the most parsimonious model remained (Table 1). Model residuals were checked for normality using the
214 Shapiro Wilk test. The models were checked for homogeneity of variance using Levene's test and for overdispersion
215 using one sample Kolmogorov–Smirnov test in DARMA package (Hartig 2018). Model fit was tested using qq-plots.
216 The pairwise comparisons were conducted using the Tukey's post hoc test to test the separation of means of each
217 model using lsmeans package (Russell 2016).

218

219 **Results**

220 **Temperature flight bioassay**

221 *Beetle flight probability*

222 Between 52 and 80% of beetles flew in experiments testing the different pre-flight temperature and flight
223 temperature combinations (Table 2). The flying temperatures had a significant effect on beetle flight probability
224 ($\chi^2=4.6020$, $df=1$, $p=0.0319$). Flight at 20°C was more likely than flight at 24°C. Pre-flight temperature, however,
225 did not affect flight probability, as beetles held at 5°C were just as likely to fly as those held at 24°C before flight.
226 Flight probability was significantly influenced by the pre-flight weight of beetles ($\chi^2= 4.2554$, $df=1$, $p=0.0391$), as
227 heavier beetles were more likely to fly than lighter beetles. Flight probability did not differ by beetle sex.

228 *Beetle flight capacity*

229 Beetle pre-flight weight significantly influenced the total distance ($\chi^2=13.5076$, $df=1$, $p=0.0002$) (Fig. 5a)
230 and the total duration ($\chi^2=7.4760$, $df=1$, $p=0.0062$) (Fig. 5b) of flight with heavier beetles flying further and for a
231 longer duration than lighter beetles. Pre-flight temperatures had no effect on flight distance ($\chi^2<0.0001$, $df=1$,

232 $p=0.9959$), flight duration ($\chi^2=0.2645$, $df=1$, $p=0.6070$), or flight speed of the beetles ($\chi^2=0.7063$, $df=1$, $p=0.4007$)
233 (Table 2). Similarly, temperature during flight had no effect on flight distance ($\chi^2=0.0515$, $df=1$, $p=0.8204$), flight
234 duration ($\chi^2=0.1130$, $df=1$, $p=0.7367$), or flight speed ($\chi^2=1.3865$, $df=1$, $p=0.2390$) of the beetles. Pre-flight
235 temperature, flying temperature and sex interacted to affect beetle weight loss as a result of flight ($\chi^2=4.9808$, $df=1$,
236 $p=0.0255$) (Fig.6). Weight loss was not different only between pre flight-flight regime combinations of 5-20°C and
237 24-20°C. Both males and females lost similar weight despite the rearing temperature. Female beetles flew at 20°C
238 lost similar weight to the males flew at 24°C (Tukey's post hoc, $p<0.05$). Females lost more weight when flown at
239 the higher temperature (24°C) compared to the lower flying temperature (20°C) ($\chi^2=57.4873$, $df=1$, $p<0.0001$). But
240 males only lost more weight when held at the lower temperature (5°C) and flown at the higher temperature (24°C)
241 ($\chi^2=7.0557$, $df=1$, $p=0.0079$).

242

243 **Light-flight bioassay**

244 *Beetle flight capacity*

245 There are interaction effects of light cycle, light phase, pre-flight weight and sex on beetle flight distance
246 and ($\chi^2=5.5717$, $df=1$, $p=0.0182$) flight duration ($\chi^2=6.8432$, $df=1$, $p=0.0089$). Female beetles flew for a longer
247 distance (Fig.7a) and duration (Fig.8a) during the longer photophase compared to the shorter photophase, but this
248 was not found in male beetles (Figs.7b and 8b) (Tukey's post hoc, $p<0.05$). Beetle flight distance and duration were
249 higher during the photophase compared to scotophase in both light cycles tested.

250

251 **Wind speed-flight bioassay**

252 *Beetle flight probability*

253 When beetles were positioned facing upwind in the wind tunnel, flight probability was not affected by the
254 wind speeds tested ($\chi^2=3.8601$, $df=3$, $p=0.2769$) nor by beetle sex ($\chi^2=0.5256$, $df=1$, $p=0.4684$). Heavier beetles
255 were more likely to fly than light beetles ($\chi^2=12.1968$, $df=1$, $p=0.0004$) in the wind tunnel assay.

256 *Beetle flight capacity*

257 The flight duration of beetles within the 50-minute observation period did not vary with wind speeds tested
258 ($\chi^2=3.0205$, $df=1$, $p=0.0822$). The total flight time during the 50-minute flight period varied with beetle pre-flight

259 weight ($\chi^2= 18.7915$, $df=1$, $p< 0.0001$). Beetles with a higher pre-flight weight flew for a longer duration compared
260 to lighter beetles. Females flew for longer durations than males at all wind speeds ($\chi^2= 4.7776$, $df=1$, $p= 0.0288$).

261 *Number of flights and flight patterns*

262 The number of flights was not affected by the wind speed ($\chi^2= 1.7575$, $df=1$, $p=0.5382$), beetle sex ($\chi^2=$
263 0.0688 , $df=1$, $p=0.7931$) or pre-flight weight ($\chi^2= 0.3742$, $df=1$, $p=0.5407$) over the 50- minute flight period. The
264 percentage of each flight type exhibited by beetles varied with wind speed ($\chi^2= 26.402$, $df=1$, $p< 0.0001$) but, not by
265 beetle sex (Fig. 9). Intermediate and burst flights were the prominent flight type in both males and females at most
266 of the wind speeds (0.5, 1 and 2 m/s). Females were capable of more sustained flights in the absence of wind than
267 males, as a large percentage of males did not fly without wind. Males conducted more intermediate flights at the
268 highest wind speed tested, 2 m/s, than females.

269

270 **Discussion**

271 Dispersal is a basic animal life history trait which allows for a change of habitat. The separation of
272 individuals by dispersal includes two major categories: movement within home range and movement beyond the
273 home range (Dingle 1996). Animals disperse in search for food (Loxdale and Lushai 1999), mates (Rudinsky 1962;
274 Dingle and Drake 2007) or to escape from deteriorating habitats (Dingle 2001) and from predatory risk (Weisser
275 2001). Dispersal is driven by a combination of individual characteristics and environmental effects (Lambin et al.
276 2001; Bowler and Benton 2005; McCauley 2010) and costs and consequences of dispersal may alter with these
277 factors. The study of dispersal is important in relation to population dynamics, because population density can affect
278 the relationship between habitat quality and individual fitness (Loxdale and Lushai 1999; Bowler and Benton 2005;
279 Clobert et al. 2012).

280 Dispersal is an important aspect of the life cycle of eruptive insects. Most bark beetles have an obligatory
281 flight period to find a new host for brood production after emergence from the natal host. Dispersal capacity is
282 crucial for beetles to find suitable host plants. Physiological, morphological, genetic and environmental conditions
283 influence bark beetle flight capacity, and these factors can be used to parametrize models to predict bark beetle
284 dispersal (Goodsman et al. 2016; Jones et al 2019). Climate conditions can affect energy metabolism and movement
285 of insects. Models that integrate abiotic factors with biotic factors that influence dispersal can help to predict

286 dispersal under changing environmental conditions (Safranyik et al. 2010). In this study, we investigate how
287 mountain pine beetle flight is affected by varying abiotic conditions.

288 Mountain pine beetle flight probability is higher at the lower flying temperature (20 °C) tested in the current
289 study, but flight probability is not affected by pre-flight temperature. These findings suggest that mountain pine
290 beetle flight probability may increase in the northern parts of the beetles' expanded range. Beetles are ectothermic
291 and expend energy more quickly at higher temperatures than at cooler temperatures. Therefore, beetle energetic
292 condition will be lower when beetles fly at high compared to low temperatures (Chubaty et al. 2014), as long as the
293 temperature is above the flight threshold. Energetic condition after flight impacts host finding, colonization
294 behaviors (Atkins 1966; Chubaty et al. 2009, 2014; Xu et al. 2016) and subsequent reproduction (Elkin and Reid
295 2005; Wijerathna et al. 2019) of bark beetles. Females with more fat reserves can successfully colonize well-
296 defended hosts (Reid et al. 2017), suggesting that a decline in energy reserves at high flying temperatures might
297 influence mountain pine beetle host acceptance and colonization. Mountain pine beetles with low energy reserves
298 accept lower quality hosts compared to beetles with more energy reserves (Chubaty et al. 2009; 2014; Latty and
299 Reid 2010). Bark beetles with high lipid content are expected to have a long adult life span (Safranyik 1976) and
300 greater flight capacity (Williams and Robertson 2008; Evenden et al. 2014) than short-lived adults. Low flight
301 probability of beetles flown at the higher temperature (24 °C), could indicate lower quality individuals with reduced
302 resources to dedicate to flight resulting in individuals, with lower capacity to tolerate tree defenses during host
303 colonization period. Flight distance and duration did not vary significantly with pre-flight and flying temperatures in
304 the current study, but beetles lost more weight when flown at the 24 °C compared to 20 °C. Energy use is lower at
305 low temperatures (Chubaty et al. 2014), and mountain pine beetle dispersal is positively correlated with energy
306 reserves used during flight (Safranyik 1976; Evenden et al. 2014; Jones et al. 2019).

307 In the current study, flight reaches a maximum of 2.7 km/h speed at the high holding and flight temperatures.
308 A field study estimate for mountain pine beetle flight velocity is approximately 2 m/s (7.2 km/h) (Safranyik 1989),
309 which is much faster than the flight velocity measured in the current study and could suggest that the tether on the
310 beetle significantly impeded flight. The temperature, light and wind speed conditions under which beetle velocity
311 was estimated, however, were not reported in the field study (Safranyik 1989). Measuring flight capacity and flight
312 probability using tethered beetles on flight mills and in wind tunnels has benefits and drawbacks. First, neither of the
313 bioassay methods mimic the natural flight conditions, as in both bioassays, insects are attached to a stiff tether.

314 Beetles flown on flight mills need to overcome inertia associated with attachment to the mill arm and flight distance
315 could be underestimated (Taylor et al. 2010). Alternatively, flight of tethered insects could be overestimated, as the
316 insect is suspended by the tether (Robertson and Roitberg 1998). Therefore, flight data should be interpreted in a
317 relative manner (Jones et al. 2019).

318 Mountain pine beetles fly for a longer distance and duration with increased day length at a constant
319 temperature. This finding suggests that the distance beetles can fly in a day will increase in the most northern parts
320 of its expanded range because of long summer days. Mountain pine beetle body lipid content decreases with flight
321 distance (Evenden et al. 2014). Greater flight distance and duration with increased day length in the most northern
322 part of its expanded range may lower the energy resources and affect subsequent host colonization (Atkins 1966;
323 Chubaty et al. 2009, 2014; Xu et al. 2016; Reid et al. 2017) and reproduction (Elkin and Reid 2005; Wijerathna et al.
324 2019). Temperature and light influence navigation during the flight phase of *D. brevicomis* and *Ips confusus* (Gara
325 and Vite 1962). Flight activity of the bark beetle *Xylosandrus germanus* is influenced by photoperiod in the field
326 where beetles prefer low light conditions for flight, but do not fly in the dark (Weber 1982). Photoperiod is the
327 major factor determining flight activity of *I. typographus*, while other environmental factors play a secondary role.
328 Swarming behavior of *I. typographus* depends on sunshine, as more beetles take flight during periods of sunshine
329 than without sunshine (Wermelinger 2004). Beetles flew more during the photophase than the scotophase in this
330 study. The time available for beetle flight in the scotophase is lower than that of photophase during the current
331 study, but beetle flight was not constrained by time during the scotophase.

332 Mountain pine beetles are photopositive at emergence under room temperature and females orient toward a
333 single light source more than males (Atkins 1966). In the current study, the length of the photophase influences the
334 flight capacity of male and female beetles differently, as females fly further and longer in the photophase during the
335 longer light cycle compared to males. Females are the pioneers in host finding and in initiating mass attack of new
336 hosts (Gitau et al. 2013). The longer flight time and distance achieved by females in the longer photophase suggests
337 the potential for successful colonization of sparsely treed landscapes in northern habitats. *Dendroctonus armandi*
338 display a phototactic flight behavior in which total flight distance and flight time is greater under artificial
339 illumination than in natural light conditions. Flight activities in the field are highest in the morning and afternoon
340 and decline with the onset of darkness (Chen et al. 2010). The bark beetle *Scolytus multistriatus* is photopositive
341 during initial flight in a wind tunnel flight assay (Choudhury and Kennedy 1980). Local flight patterns and

342 navigation by olfactory cues by *D. brevicomis* are influenced by light conditions (Gara and Vite' 1962). *Ips*
343 *typographus* fly only during conditions of sunshine and do not fly in the dark (Lobinger and Skatulla 1996). The
344 current study is the first to record an increased flight capacity of mountain pine beetle with longer day length. This
345 finding may be important in the modeling of beetle dispersal in novel habitats.

346 Mountain pine beetles fly in the presence or absence of wind and are capable of flight at all of the wind
347 speeds tested in the current study. In our study, both sexes flew at the tested wind speeds and bigger beetles were
348 more likely to fly. Beetles fly upwind against a wind of 2 m/s in the field (Safranyik et al. 1992), and under the
349 conditions of our experiment there is a slight non-significant trend for reduced flight at 2 m/s wind speed compared
350 to the 0, 0.5 and 1 m/s wind speeds tested. Some scolytid beetles cease flight at wind speeds greater than their
351 maximum flight speed (Seybert and Gara 1970; Meyer and Norris 1973). Such conditions may similarly affect flight
352 activity of mountain pine beetle. Intermediate and burst flights were more prominent in both sexes in the wind
353 tunnel as compared to sustained flight. In the absence of an odor source, mountain pine beetle fly without wind or
354 against all the different wind speeds tested in the current study. The flight behavior of beetles may vary, however,
355 with the presence and composition of semiochemicals. Mountain pine beetles fly with wind in the absence of odor
356 plumes and fly against the wind in the presence of aggregation pheromones (Gray et al. 1972).

357 We found that air temperature during flight but not pre-flight temperature influences mountain pine beetle
358 flight probability. Beetles were more likely to fly at the lower flying temperature (20 °C) than at the higher flying
359 temperature (24 °C). Pre-flight and flight temperatures did not affect the beetle flight capacity. The flight
360 temperatures tested during the current study are above the lower limits for mountain pine beetle flight and in the
361 range of beetle spontaneous flight activity. Energy use was greater at high than low flying temperatures. Longer
362 artificial day lengths increased the flight capacity of beetles and beetles showed very low flight capacity in the
363 scotophase. Mountain pine beetles flew, with and without wind, in the absence of an odor source at each tested wind
364 speed. Discoveries of beetle flight under natural conditions are difficult to conduct and the factors that initiate long
365 distance dispersal above the canopy are poorly understood (Safranyik et al. 1992). Individual flight capacity
366 measurements conditions, as measured in the current study, are likely more important for within stand dispersal and
367 are difficult to test in the natural habitat. This study provides baseline relative data on tethered beetles describing
368 individual flight capacity under varying environmental conditions. These findings will be important to incorporate
369 into models that predict mountain pine beetle dispersal in its expanded range.

Figure captions

Fig. 1 Diagram of the wind tunnel (0.1m x 0.05m x 0.05m) used for the wind speed bioassay. Beetles were tethered by attaching a beading wire to the pronotum. Tethers were attached to the roof of the wind tunnel so that beetles were apart by 5 cm and suspended 15 cm from the roof and 40 cm from the upwind end of the tunnel. Five beetles of the same sex were tested at each trial and were placed facing upwind

Fig. 2 Experimental design of the temperature flight bioassay. Mountain pine beetle flight capacity was tested at four different pre-flight and flight temperature regimes

Fig. 3 Experimental design of light flight mill bioassay. Mountain pine beetles flight capacity was tested under two different light cycles (16L:8D and 18L:6D) with different day lengths

Fig. 4 Experimental design of wind speed flight bioassay. Mountain pine beetles flight capacity was tested at four different wind speeds (0, 0.5, 1, 2 m/s)

Fig. 5 Variation of mountain pine beetle flight distance (km) (a) and flight duration (h) (b) with pre-flight weight. Female and male beetles were held separately at two pre-flight temperatures: 5°C and 24°C for 23 hours before the initiation of the flight bioassay, which was conducted at 20 or 24°C for 23 h. Beetles from both pre-flight temperatures were flown at the same time under a selected flying temperature. Beetle pre-flight weight was measured before the flight. Females and males were flown separately on alternate days. Data presented are averaged data for all pre flight- flying temperatures regimes and for both sexes. The shaded area represents the 95% confidence intervals

Fig. 6 Mountain pine beetle mean weight loss during flight (mg) under the tested pre-flight and flight temperature regimes. a) Female, b) Male. Female and male beetles were held separately at two pre-flight temperatures: 5°C and 24°C for 23 hours before the initiation of the flight bioassay, which was conducted at 20 or 24°C for 23 h. Beetles from both pre-flight temperatures were flown at the same time under a selected flying temperature. Females and males were flown separately on alternate days. Beetle weight loss was calculated subtracting the post-flight weight from pre-flight weight. Data were analyzed using a general mixed effects model. Means with different letters are significantly different (Tukey's post hoc test $p < 0.05$)

Fig. 7 Mountain pine beetle mean flight distance (km) in the photophase and scotophase of the two tested light cycles: short (16L: 8D) and long (18L: 6D). Females and males were flown separately on alternate days. a) Female,

b) Male. Data were analyzed using a general mixed effects model. Means with different letters are significantly different (Tukey's post hoc test $p < 0.05$)

Fig. 8 Mountain pine beetle mean flight duration (km/h) in the photophase and scotophase of the two tested light cycles: short (16L: 8D) and long (18L: 6D). Females and males were flown separately on alternate days. a) Female, b) Male. Data were analyzed using a general mixed effects model. Means with different letters are significantly different (Tukey's post hoc test $p < 0.05$)

Fig. 9 Mountain pine beetle flight patterns at the tested wind speeds 50 min wind tunnel bioassay. Female (a) and male (b) beetles, 3-5 days post emergence were held separately at 5°C prior to flight for 23 h. Tested wind speeds were: 0 m/s, 0.5m/s, 1m/s, 2 m/s. Females and males were flown separately on alternate days. The wind treatments were alternated during the day. Data were analyzed using a generalized linear model

Table 1: Statistical models used in temperature, light and wind speed flight bioassays. Each model includes dependent variable~ fixed effects and random effects. Symbol * indicates interactions between fixed factors and symbol + indicates no interactions between fixed factors. The models present here are the final models.

Response variable	Fixed effects	Random effects	Data distribution
<i>Temperature bioassay</i>			
Flight probability	pre-flight temperature + flying temperature +pre-flight weight +sex	bolt	binomial
Flight distance	pre-flight temperature + flying temperature +pre-flight weight +sex	bolt	Gamma
Flight duration	pre-flight temperature + flying temperature +pre-flight weight +sex	bolt	Gamma
Flight speed	pre-flight temperature + flying temperature +pre-flight weight +sex	bolt	Gamma
Total weight loss	pre-flight temperature * flying temperature *sex	bolt	Gamma
Female weight loss	pre-flight temperature + flying temperature	bolt	Gamma
Male weight loss	pre-flight temperature * flying temperature	bolt	Gamma
<i>Light flight bioassay</i>			
Flight duration	light cycle* light phase* sex* pre-flight weight	bolt	Gamma
Flight distance	light cycle* light phase* sex* pre-flight weight	bolt	Gamma
<i>Wind speed bioassay</i>			
Flight probability	wind speed+ sex+ pre-flight weight	bolt	binomial
Flight duration	wind speed+ sex+ pre-flight weight	bolt	gaussian
Number of flights	wind speed+ sex+ pre-flight weight	bolt	poisson
Flight pattern	wind speed+ sex	bolt	binomial

Table 2: The effects of temperature before and during flight on flight performance of male and female mountain pine beetle. Values are mean± SE, and sample size is stated in brackets.

Beetle sex and pre-flight- flying temperature regimes(°C)	Proportion that flew	Average distance flown (km)	Average duration (h)	Fight velocity (km/h)
Female				
5-20	0.70	5.43±5.06 (47)	3.67±3.20 (47)	2.16±4.98 (47)
5-24	0.70	3.98± 3.86(49)	2.88±2.46 (49)	1.41±0.64 (49)
24-20	0.79	4.21± 4.61(57)	3.06±3.29 (57)	1.47±0.56 (57)
24-24	0.80	4.6 ± 5.83(49)	3.02±3.15 (49)	1.62±1.23 (49)
Male				
5-20	0.72	3.65± 4.51(49)	2.37±2.77 (49)	1.82±1.47 (49)
5-24	0.69	3.35±3.20 (49)	2.74 ±2.61 (49)	1.34±0.90 (49)
24-20	0.77	3.98± 4.95(52)	2.54± 3.08 (52)	2.09±2.67 (52)
24-24	0.52	2.61± 3.55(49)	2.27± 3.06(49)	2.79±4.76 (49)

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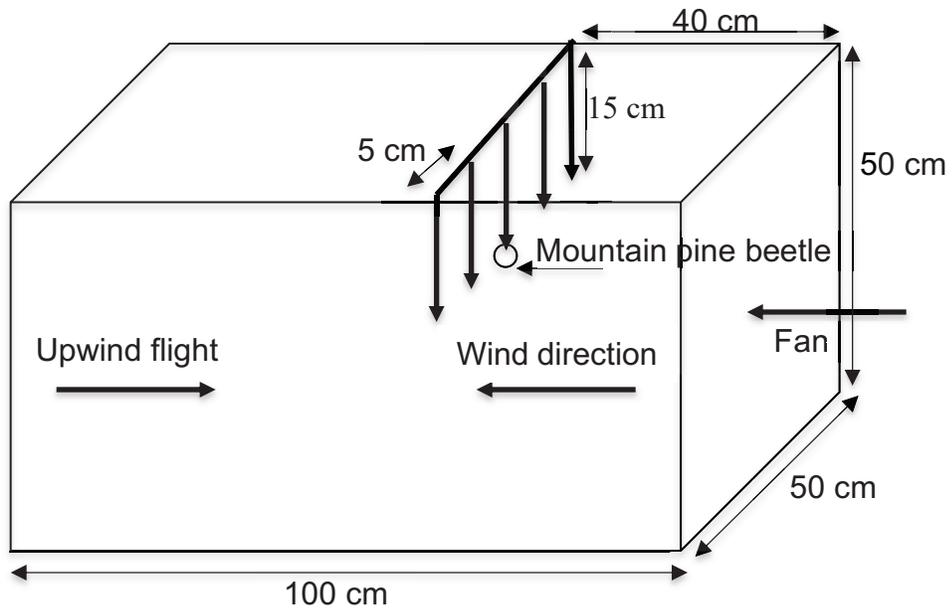


Fig. 1

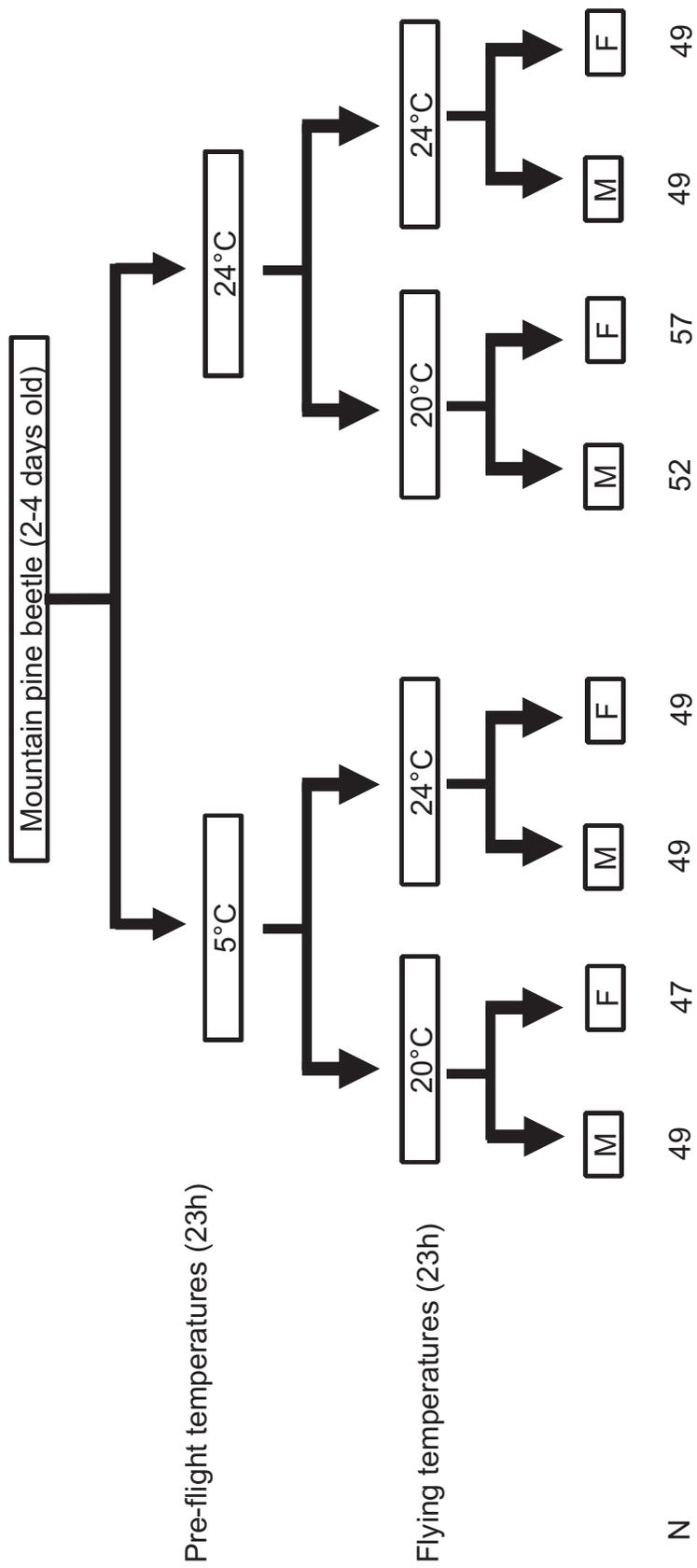


Fig. 2

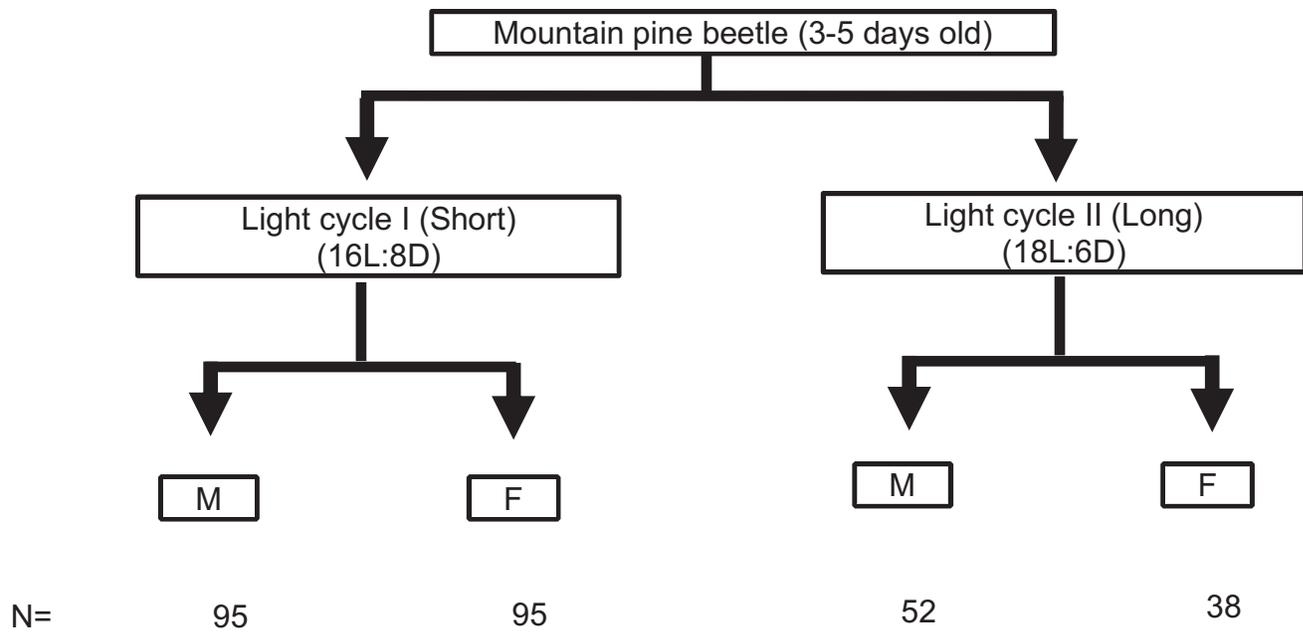
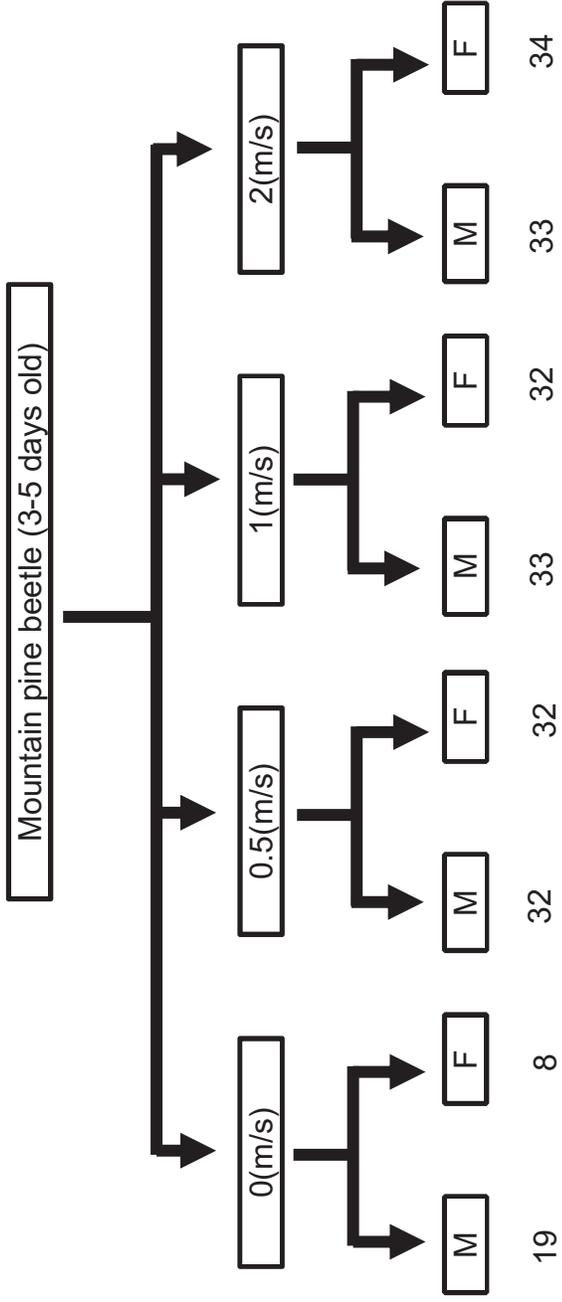


Fig. 3



N=

Fig. 4

