

1 **Title:** Ontogeny of familiarity with foraging landscape and foraging abilities in the tropical
2 social wasp *Ropalidia marginata*

3 **Running title:** Social wasp: ontogeny of foraging ability

4

5 **Authors:** Souvik Mandal, Anindita Brahma and Raghavendra Gadagkar

6 **Authors' affiliation:** Centre for Ecological Sciences, Indian Institute of Science, Bangalore,
7 560012, India.

8

9 **Correspondence:** Souvik Mandal

10 E-mail: souvikmandal@iisc.ac.in

11 Postal address: Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012,
12 India.

13 Telephone: +91 80 23601429, Fax: +91 80 23602121.

14 **Keywords:** Spatial familiarity; Foraging strategies; *Ropalidia marginata*; Social wasps; Social
15 Hymenoptera

16 **TITLE:** Ontogeny of familiarity with foraging landscape and foraging abilities in the tropical
17 social wasp *Ropalidia marginata*

18

19 **SUMMARY STATEMENT:** Contrary to insects inhabiting less-featured landscapes, tropical social
20 wasps invest weeks to get familiar with foraging landscapes during their early foraging lives.
21 This eventually enables them to increase foraging gain with reduced effort.

22

23 **ABSTRACT**

24 Possessing spatial familiarity with their foraging landscape may enable animals to reduce
25 foraging effort without compromising on foraging benefits. For animals inhabiting feature-rich
26 landscapes, spatial familiarity can increase with increasing age/experience. To check whether
27 this holds for individually foraging tropical social wasp *Ropalidia marginata*, we recorded the
28 number and duration of all foraging trips, the identity of the materials brought to the nest
29 (building material, water or food) and the directions of outbound and inbound flights
30 (relative to their nests) of known-age foragers from three natural colonies, each for three
31 consecutive days. The average trip duration and time spent daily in foraging increased rapidly
32 until about first four weeks of their life, during which they rarely brought food to their nest,
33 although many of them brought building material and water. Thereafter, their average as well as
34 per day duration of foraging trip started decreasing gradually. Nevertheless, their foraging
35 efficiency and success for food kept on increasing monotonically with age. These results suggest
36 that older wasps were more efficient in foraging despite spending less time doing so. With
37 increasing age, wasps developed individual preferences for the direction of their outbound
38 flights, increased directionality of their inbound trips as well as the angular difference between
39 their outbound and subsequent inbound flights, indicating development of spatial memory. We
40 conclude that wasps acquire familiarity with their foraging landscape in their initial foraging
41 phase and gradually develop robust memory for rewarding sites and routes to those sites, which
42 enables them to increase their foraging capabilities.

43

44 **KEY WORDS**

45 Spatial familiarity; Foraging strategies; *Ropalidia marginata*; Social wasps; Social Hymenoptera

46

47 INTRODUCTION

48 Minimizing foraging effort without compromising foraging benefit is a perpetual
49 challenge for foraging animals. For animals inhabiting feature-rich landscapes, learning
50 and memorising features of foraging landscapes, especially those related to the locations
51 of rewards may eventually enable them to collect substantial foraged materials with a
52 minimal investment in foraging effort (Caraco, 1980; Kamil and Roitblat, 1985). It has
53 been postulated that more the time an animal travels within a landscape, more would be
54 its spatial familiarity with the surrounding (Boyer and Walsh, 2010), and thus, better
55 would be its homing capabilities (Dyer, 1996). This in turn may enable them to attain
56 higher foraging benefits (Bracis et al., 2015; Dukas and Visscher, 1994; Pyke et al., 1977;
57 Raine and Chittka, 2008). On the other hand, foraging is a costly affair in terms of time,
58 energy and associated risks like predation. Thus, it would be a proficient strategy for
59 animals to strike an optimum balance between the time they spend to gain familiarity
60 with their foraging landscapes and on foraging, and the amount of foraged materials
61 (Abrams, 1991; Norberg, 1977).

62 To acquire such spatial familiarity, foragers of social hymenopterans like ants
63 (Fleischmann et al., 2016), honey bees (Capaldi et al., 2000; Degen et al., 2015), and
64 bumble bees (Osborne et al., 2013; Woodgate et al., 2016) begin their foraging life with a
65 few exploratory flights/walks, and very soon they begin to forage for food. The Saharan
66 desert ants, which scavenge in featureless and non-patchy desert landscapes, increase
67 their foraging success as well as their foraging duration with the advancement of their
68 short foraging life (Wehner et al., 2004). Similarly, honey bees inhabiting temperate
69 landscape also increase foraging gain with age but they also cover more foraging area
70 per trip and increase their flight speed (Capaldi et al., 2000). Thus, their foraging success
71 seems to depend much on their current foraging effort (and not on the effort they put on
72 the exploratory/learning phase), which might be an ideal strategy for foragers evolved
73 in such less-featured non-patchy landscapes. On the other hand, landscapes with high
74 density of features, like the tropics, probably offer much more spatial information but
75 much less visual continuity (Cartwright and Collett, 1987; Zeil, 2012). Thus, insects
76 inhabiting complex feature-rich terrains encounter homing challenges different from the
77 insects inhabiting less-featured terrains – and thus they may evolve with different
78 homing and foraging strategies. Interestingly, whereas insects inhabiting less-featured

79 landscapes rely heavily on their path integration system for homing, foragers of the
80 Australian ant *Melophorus bagoti* (Narendra, 2007) inhabiting semi-desert cluttered
81 landscape or the tropical ant *Gigantiops destructor* (Macquart et al., 2006) inhabiting
82 complex tropical rain forests rely heavily on the learnt visual features of their foraging
83 landscape. However, we are yet to know the strategies by which social insects evolved in
84 feature-rich landscapes develop their familiarity with their foraging landscape and
85 whether such spatial familiarity contributes to their future foraging abilities. We
86 postulate that they may invest much effort (for instance, spending greater amount of
87 time out of their nest) during their initial foraging phase to obtain adequate spatial
88 familiarity and spatial memory of rewarding patches. This may eventually enable them
89 to find rewarding sites with much less or even no large-scale searching.

90 *Ropalidia marginata* is an aseasonal predatory social wasp inhabiting feature-rich
91 tropical landscapes. Females typically survive for 9 to 329 days (mean \pm s.d. = $135.9 \pm$
92 86.3) in laboratory conditions (Sen and Gadagkar, 2010) and colonies typically consist of
93 1 to 200 females (mean \pm s.d. = 21.9 ± 22.3) (Gadagkar, 2001). Upon eclosion, workers
94 first perform intranidal tasks and then gradually increase the proportion of extranidal
95 tasks (i.e. foraging) with the advancement of their age (Naug and Gadagkar, 1998). They
96 forage solitarily for food (spiders, larvae of other insects etc.), plant fibres (as building
97 materials) and water. If a prey is too big to carry, they cut the prey into pieces and bring
98 those pieces to their nest in multiple bouts. They typically forage within about 500 m
99 from their nests (Mandal and Gadagkar, 2015) and experienced foragers possess
100 comprehensive spatial familiarity with their foraging landscape (Mandal et al., 2017).
101 Each forager has to acquire this spatial familiarity as they forage solitarily. This makes
102 all the foragers of a colony equally suitable for our experiment.

103 To test whether they spend a substantial amount of time outside their nest during
104 the initial phase of their foraging life (probably for exploring and learning the features of
105 the foraging landscape), and whether they reduce their foraging effort without affecting
106 their foraging benefits at the later stage, we first checked whether the number of trips
107 per day, proportion of time that the forager wasps spent daily on foraging or the average
108 foraging duration per trip change with their age following a pattern that has an initial
109 ascent followed by a descent, and whether these patterns explain the data better than a
110 linear function. In parallel, we checked whether their foraging benefits increased with

111 the advancement of their age. We also predicted that individual foraging wasps, like ants
112 (Wehner et al., 2004) and bees (Capaldi et al., 2000), might develop fidelity for a
113 particular (rewarding) direction to go for foraging with age; young wasps may not
114 develop such a choice for any particular direction during their explorative phase until
115 they come across a rewarding patch (for instance, a food source). We tested this
116 prediction by analysing all the outbound flight directions of individual wasps. Also,
117 though insects rely heavily on path integration during early foraging bouts, with the
118 advancement of their age/experience, they tend to rely more on learnt information
119 acquired from their foraging landscape, if available (Bühlmann et al., 2011; Cheng et al.,
120 2012; Kohler and Wehner, 2005; Menzel and Greggers, 2015; Müller and Wehner, 2010;
121 Narendra, 2007; Wystrach et al., 2014). Since path integration is an error-prone system
122 and the error increases with directional changes during a trip, young and inexperienced
123 foragers are expected to stick to a particular relative direction for a particular trip, i.e.
124 going out and returning along the same path (though they may choose a different
125 direction for subsequent trips) (Capaldi et al., 2000). On the other hand, familiarity with
126 the landscape may enable experienced foragers to explore several places in different
127 directions during a single trip (Hassell and Southwood, 1978). This may be possible by
128 developing preference for habitual foraging directions (Osborne et al., 2013; Woodgate
129 et al., 2016) and eventually using trapline routes (Buatois and Lihoreau, 2016; Lihoreau
130 et al., 2012; Saleh and Chittka, 2007) and novel foraging routes (Menzel et al., 1998).
131 Thus, after each foraging bout, they may return from the direction of sites of their last
132 preference. Therefore, we have checked whether wasps developed any directional
133 preference for their incoming flights and whether the angular difference between the
134 outbound and subsequent inbound directions increased with advancing age.

135

136 **MATERIALS AND METHODS**

137 We performed this experiment using three naturally occurring nests (N17, N18
138 and N21), of *Ropalidia marginata* (Lepeletier 1836) (Vespidae, Polistinae) located at the
139 Indian Institute of Science campus, Bangalore, India (13°01' N, 077°34' E). The
140 landscape of the main campus is spread over an area of about 1.55 km² and dominated
141 by densely distributed trees (with an average height of about 30 m) and shrubs covering

142 about 75% area of the landscape, along with small to medium sized (i.e. maximum
143 height of about 35 m) academic and residential buildings, limiting a continuous view
144 within a maximum distance to about 30 m on ground. Uninterrupted view for much
145 longer distance could only be accessed on roads that had varied lengths with a width of
146 3-6 m, and with light motor traffic. Such a landscape is of special interest, as foraging
147 wasps typically cruise within a height of 2-10 m from ground and thus can access very
148 small visual catchment area during their regular foraging trips.

149 We found all the three experimental nests inside electrical-fuse boxes attached to
150 roadside lampposts at a height of about 50 cm from ground. Immediately after locating
151 the nests, we sealed all the holes of those boxes except the one on the frontal lid of the
152 boxes to get the wasps accustomed with it as the only exit and entrance. We also placed
153 a mimic camera set-up 30 cm away from the frontal lid of the boxes to get the foraging
154 wasps used to it and kept it until we replaced it with a real look-alike video camera for
155 data collection (Figure 1). We carried out the experiment in three consecutive steps,

156 **Step 1. Accounting for the age of the wasps**

157 Since we required to know the age of the wasps as the first step of our experiment,
158 after finding a colony, we took daily census of the wasp colonies at night until we knew
159 the age of all the resident wasps of the colony. We uniquely colour-marked all the newly
160 eclosed wasps on their thorax and/or abdomen using Testors® quick drying enamel
161 paints along with recording their date of eclosion. We started taking the daily census of
162 N17, N18 and N21 on October 1, November 11 and December 23, 2013, respectively.

163 **Step 2. Data collection**

164 Next, we replaced the dummy camera set-up with a real motion sensitive web
165 camera and connected that to a laptop kept at least 5 m away from the lampposts. The
166 camera was set to start recording (with 2 seconds of pre-recording function, using
167 Webcam Zone Trigger™ software) upon detection of any movement within its field of
168 view (which included the hole on the frontal lid of the box and part of the frontal lid, see
169 Figure 2). Thus, the video captured the identity of all the outgoing/incoming wasps
170 when it appeared within its visual field as well as the time of their departure and arrival,
171 and the identity of foraged materials, if any. An observer sat near the laptop in
172 camouflage attire and recorded data on the vanishing bearing of the outbound and

204 2008). The last was fitted to the data with nonlinear least squares (nls) regression and
205 was expressed as $(A \times \text{age}^2) / (B + C \times \text{age} + \text{age}^2)$, where A is the value of the proportion of
206 time spent outside when the curve reaches asymptote, and $-2 \times B / C$ demarcates the age at
207 the peak of the curve. Similarly, we calculated the average duration of foraging trips by
208 dividing the total time a wasp spent on foraging in three days with the total number of
209 trips she had made in these three days and fitted linear, quadratic and Holling type IV
210 function to the data for checking its possible relationships with the age of the wasps.

211 We computed 'foraging success' as 'the ratio of the number of trips in which a wasp
212 brought food to her nest and the total number of trips she made'. We computed 'foraging
213 efficiency' as 'the number of times the wasp brought food to the nest divided by the
214 proportion of time she spends outside of her nest'. We first fitted a linear and then a
215 quadratic function to explore the relationships between both foraging success and
216 foraging efficiency with the age of the wasps, separately for the three nests.

217 Next, we tested whether with age, wasps developed a preference toward any
218 particular direction to go out for foraging. We measured their age in days and directional
219 preference as the length of the mean vector (r value) (Batschelet, 1981) of all the
220 outbound directions shown by each wasp on a day and averaged over three days. We
221 eliminated those wasps from our analysis for which we had data for only one outbound
222 trip in a day. Thus, our dataset for this analysis comprised of 54 (for N17), 71 (for N18)
223 and 68 (for N21) unique wasps. We fitted a linear and a saturating function namely
224 Michaelis-Menten to the data and checked which one explained the data better. The
225 expression of Michaelis-Menten function was $(A \times \text{age}) / (B + \text{age})$, where A defines the
226 value of dependent variable (r value) at asymptote and B defines the value of the
227 independent variable (age of wasps) at $A/2$. Similarly, we have checked whether with
228 age, wasps developed any directionality for their inbound trips. Here, the data set
229 comprised of 51, 71 and 80 unique wasps from N17, N18 and N21, respectively. Since
230 we wanted to check whether after an initial increase, wasps reduced the directionality of
231 their inbound trips, we also fitted a quadratic function along with linear and Michaelis-
232 Menten function to the data and checked for the best fit.

233 To know whether the wasps started taking detours with increasing age, we
234 checked the angular difference between the direction of outbound and subsequent

235 inbound flights for each trip of each wasp. The angular difference ranged from 0° to
236 180°. Though we agree that reaching to a conclusion about their entire foraging route
237 from the outbound and inbound directional data acquired only from a distance of 5 m
238 around their nests is a bit over-speculation, we still used the data to get a rough proxy of
239 the foraging route during a trip, assuming more angular difference as the indication of
240 greater detour during their foraging trip. Since we had several data points from the
241 same wasp and we had three experimental nests, we fitted a generalized linear mixed-
242 effects model (lme4 package) with a Poisson error family and log link, taking data from
243 all the wasps of all the nests together. For better explanatory power of the model, we
244 took the rescaled value (and not transformed value) of the angular difference between
245 outbound and inbound direction as the response variable (using the ‘scales’ package;
246 Wickham, 2016), the age of the wasps as the explanatory variable and the identity of the
247 wasps nested within their colony ID as random effects.

248

249 **RESULTS**

250 During the three days of observation, 78, 89 and 105 unique wasps from nest N17,
251 N18 and N21 made a total of 607, 1173 and 2407 foraging trips, respectively. On the
252 basis of the material that a wasp brought back to her nest, most of the wasps (100%,
253 95.5% and 92.37% from N17, N18 and N21, respectively) could be classified into four
254 categories: wasps that did not bring anything, brought building material, water or food
255 to their nests. However, there were few cases in which a single wasp brought more than
256 one material (see Table S1 in supplementary materials). We found that the water
257 foragers (defined as wasps that brought water more than once and more than anything
258 else) (2, 1 and 8 wasps in N17, N18 and N21, respectively), made much higher numbers
259 of trips than other foragers – in fact water foragers were outliers in the number of trips
260 they made. Compared to foragers that brought other things, trip duration of the water
261 foragers was much shorter (GLMM, Estimate: 0.765, z value: 141.72 $P < 0.01$) and their
262 success rate was much higher (χ^2 test, $P < 0.01$) (Table S1). They showed high
263 directionality for outbound as well as inbound trips (r value on any given day was
264 greater than 0.9 for all the water foragers), and had much less angular difference
265 between outbound trips and subsequent inbound trip than the other foragers (GLMM,

266 Estimate: 0.3545, z value: 10.60 $P < 0.01$). Because of these reasons, we excluded water
267 foragers from all the analyses except the analyses that we performed to check for
268 relationships between age of the wasps and the proportion of time they spent outside
269 their nest as well as the average duration of their foraging trips. For an overview of the
270 foraging activities on these three nests, see Figure 3 and Table S1.

271 [--Figure 3 approximately here--]

272 **Change in number of foraging trips per day with age**

273 Wasps from all three nests initially increased and later decreased their number of
274 foraging trips per day with increasing age. A quadratic function explained the rate of
275 change better compared to a linear function (ANOVA, $P < 0.05$) (Figure 4).

276 [--Figure 4 approximately here--]

277 **Change in the proportion of time spent on foraging with age**

278 A linear fit explained only 14.91% (AIC = -64.09), 18.28% (AIC = -8.44) and 26%
279 (AIC = -16.92) of the total variation of the relationship between the age of the wasps and
280 the proportion of time wasps spent outside their nests for N17, N18 and N21,
281 respectively. The quadratic model explained 46.29% (AIC = -98.98), 53.10 % (AIC = -
282 55.86) and 55.31% (AIC = -67.87) of the total variation of the data from N17, N18 and
283 N21, respectively. When we fitted the function Holling type IV to the data, which has a
284 characteristic of initial rapid ascent and after reaching to a peak, a gradual descent,
285 greater amount of variation in the data was explained with decreased AIC values (N17:
286 54.46%, AIC = -111.85; N18: 54.74%, AIC = -59.02; N21: 55.98%, AIC = -69.45) (Figure
287 5). It may be noted that the few young individuals that brought food (red circles in
288 Figure 5) generally spent more time outside of their nest while older individuals that
289 brought food spent varied amount of time outside nest.

290 [--Figure 5 approximately here--]

291 **Change in average foraging duration per trip with age**

292 Similarly, we checked for the relationship between the age and the average foraging
293 duration per trip of the wasps by fitting a linear, quadratic and Holling type IV function

294 to the dataset. Here also, Holling type IV provided the best fit for the data from all three
295 nests; it explained 31.45% (AIC = 857.68) of the variation of the data (compared to
296 0.124% (AIC = 885.04) by linear and 14.51% (AIC = 874.90) by quadratic function) from
297 N17, 41.49% (AIC = 973.52) of the variation of the data (compared to 5.03% (AIC =
298 1014.62) by linear and 32.4% (AIC = 986.36) by quadratic function) from N18, and
299 15.45% (AIC = 1164.27) of the variation of the data (compared to 4.08% (1175.52) by
300 linear and 11% (AIC = 1169.66) by quadratic function) from N21 (Figure 6).

301 [--Figure 6 approximately here--]

302 **Change in foraging success with age**

303 With the increase in their age, foraging success (i.e. proportion of trips in which
304 wasps brought food) of wasps from all the three nests increased significantly ($P < 0.05$)
305 (Figure 7). A linear model explained 57.17%, 47.73% and 40.95% of the variation of the
306 data from N17, N18 and N21, respectively. Attempt to fit a quadratic function to the data
307 revealed insignificant p values (i.e. $P > 0.05$) for all the parameters for N17 and N21, and
308 a p value less than 0.05 (i.e. 0.027) only for the quadratic term for N18.

309 [--Figure 7 approximately here--]

310 **Change in foraging efficiency with age**

311 Likewise, foraging efficiency (i.e. the number of times a wasp brought food to her
312 nest in unit time she spent on foraging) also increased with the advancement of their age
313 (Figure 8). While all the parameters of linear models for all the nests were significant (P
314 < 0.05) (and explained 61.08%, 65.5% and 63% of the variation of the data from N17,
315 N18 and N21, respectively), no parameters of a quadratic model were significant for
316 N17, and only the quadratic term was significant for N18 and N21.

317 [--Figure 8 approximately here--]

318 **Developing directional fidelity for outbound trips with age**

319 The average of mean vector length (r value) of the outbound flight directions
320 increased with the age of the wasps from all the three nests. We found that Michaelis-
321 Menten function (Figure 9) fitted better than linear function to the data from all the
322 three nests. The former function explained 40.67%, 51.30% and 54.58% of the total

323 variation of the data from N17, N18 and N21 respectively (AIC: -9.17 for N17, -26.66 for
324 N18 and -48.01 for N21) whereas the latter explained 22.9%, 42.55% and 54.74% of the
325 total variation in the data from N17, N18 and N21 respectively (AIC: 4.98 for N17, -15.95
326 for N18, -33.81 for N21).

327 [--Figure 9 approximately here--]

328 **Developing directional fidelity for inbound trips with age**

329 Interestingly, the average of the mean vector length (r value) of the inbound flights
330 made by wasps also increased with their age. Whereas the Michaelis-Menten function
331 best explained the data from N17 and N18, a quadratic function best explained the data
332 from N21 (Figure 10). While the linear function explained 16.92% (AIC=-14.44), 16.64%
333 (AIC=-18.72), 13.91% (AIC=-18.48) of the variation of the data from N17, N18 and N21
334 respectively, a quadratic function explained 24.6% (AIC=-17.38), 30.91% (AIC=-30.05),
335 43.19% (AIC=-49.73), and the Michaelis-Menten function explained 24.6% (AIC=-19.36),
336 32.07% (AIC=-33.25), 37.02% (AIC=-43.48) of the variation of the data from these three
337 nests.

338 [--Figure 10 approximately here--]

339 **Change in angular difference between outbound and subsequent inbound** 340 **direction with age**

341 When we checked for the relationship between the angular difference in the
342 outbound and subsequent inbound flight direction with the age of the wasps using a
343 generalized linear mixed model, we found that the angular difference increased with the
344 advancement of age. In the model, we found the estimate of intercept as 3.55 ± 0.11 (SE),
345 and estimate of age as 0.009 ± 0.002 (SE), $P < 0.05$ for both intercept and age.

346

347 **DISCUSSION**

348 In a previous study, we have shown that spatial familiarity with their foraging
349 landscape boosts homing performance in the tropical social wasp *Ropalidia marginata*
350 significantly (Mandal et al., 2017). The same has also been shown in several other social
351 insects (Collett et al., 2013; Narendra et al., 2013; Palikij et al., 2012). Possessing spatial

352 familiarity with the foraging landscape can enable animals to minimize foraging effort
353 without affecting their foraging benefits, which can be a great advantage in natural
354 contexts. In an attempt to investigate the ontogeny of spatial familiarity with foraging
355 landscape and foraging capabilities in the tropical social wasp *Ropalidia marginata*,
356 especially to know whether *R. marginata* foragers reduce their foraging effort but
357 increase their foraging gain with an increase in their experience with the foraging
358 landscape, first we checked how the number of foraging trips per day, average duration
359 of their foraging trip and the total time they spent on foraging changed with the
360 advancement of the age of free-foraging wasps from three nests, along with recording
361 the materials that they brought to their nest. We found that most of the wasps started
362 going out of their nest within about the first two weeks of their lives. They began their
363 foraging life with few short duration trips and gradually increased the number of
364 foraging trips per day till about the middle of their foraging career, and then they
365 reduced that. The relationship between the number of trips per day and their age was
366 best explained by a quadratic function. During their initial foraging life, they also rapidly
367 increased the average duration of their foraging trips and the total time that they spent
368 daily on foraging. However, after about four weeks of age, their average foraging
369 duration per trip and the proportion of time they spent in foraging per day followed a
370 gradual decrease. Such an initial rapid increase followed by a gradual decrease in their
371 foraging effort indicate that wasps invest great amount of effort in the initial phase of
372 their foraging life probably for learning/exploring their foraging landscape; once the
373 foragers acquire sufficient familiarity with their foraging landscape, they decrease their
374 foraging effort.

375 It is noteworthy that during this initial phase of learning/exploring, which is till
376 about four weeks of their age, they rarely brought food to their nests although several
377 wasps brought building materials and water. Compared to desert ants (Narendra et al.,
378 2013; Wehner et al., 2004), honey bees (Capaldi and Dyer, 1999) and bumblebees
379 (Osborne et al., 2013; Woodgate et al., 2016), which start bringing food to their nest
380 after only a few exploration flights/walks, the exploration period in this wasp seems to
381 be much longer. However, this is not surprising if the duration of the exploratory phase
382 can be contributed to the complexity of the foraging landscape and the distribution of
383 the foraged materials. Compared to tropical insects like this wasp, desert ants, for

384 instance, encounter fewer visual features to learn from their foraging landscape (which
385 include occasional small bushes and minor variation on the surface of the land) and so
386 once they get accustomed to being outside their nest, they get ready to forage for food
387 depending heavily on path integration system. The chance of encountering food, i.e. dead
388 insects may also be higher for these short-lived thermophilic ants in such an extreme
389 environment than finding camouflaging prey by the wasps in tropics. Thus, these ants
390 can start foraging for food much earlier.

391 On the other hand, *R. marginata* wasps live for much longer time and typically
392 bring building materials or water before bringing food to their nest (Naug and Gadagkar,
393 1998). Such age-based polyethism has been reported in other paper-wasps as well
394 (Jeanne and Taylor, 2009). Apparently building materials (i.e. plant fibres) were
395 abundantly available in all the directions throughout the landscape. Thus, to collect
396 building materials, wasps need not to go for any particular place and foragers with very
397 little experience of the landscape could also accomplish this task. In fact, we found that
398 the foragers that collected building materials were indeed among the youngest foragers
399 of their colony. Compared to finding building material, finding a source of water needed
400 more exploration and bringing water repeatedly from the same place implies that they
401 have learnt the location of the water source. We found that the water foragers had
402 several successful short-duration trips per day and the mean direction of their outbound
403 flights was toward directions in which there was at least one permanent source of water
404 (for instance, fountain or small water reservoir) within about 100 m. Wasps that
405 brought food were among the oldest individuals of their colony. This may be because
406 finding a prey may need much more searching, which includes visits to several places
407 with potential of prey-availability. Several times, wasps took great time (more than 2
408 hours) to bring food once, followed by few trips when they brought food quite quickly
409 (about 10 minutes). Several times, they brought food spending more or less equal
410 amount of time on all the trips (all more than 2 hours). When they take greater time to
411 bring food to their nest, they probably first find the prey by searching and then hunt it.
412 Next time onwards, they bring the pieces of the kill, so it takes much less time. Also,
413 since their kill is lucrative food for several ants, wasps might hunt for bigger prey when
414 they are close to their nests (so that they can reach back quickly to the hunting site
415 before ants claim the kill) but may kill only smaller prey (which can be carried in a single

416 bout) when they are far from their nest. Thus, to collect food, a thorough familiarity with
417 the foraging landscape might be very necessary for the wasps.

418 The European honey bees and bumblebees inhabit temperate landscapes that are
419 more complex than deserts but less complex than tropics in which the wasps inhabit,
420 and forage for nectar/pollen. Additionally, flowers are stationary and advertise
421 themselves to attract pollinators like bees, contrary to the mobile prey of the wasps that
422 probably attempt to not getting discovered by the wasps. Also, unlike these wasps that
423 practice solitary foraging, honey bee foragers can get information about rewarding
424 patches from a nest-mate. Putting all together, wasps might need to search for food
425 much more vigorously than bees need to do - bees may not need to acquire a detailed
426 familiarity of their foraging landscape to find their food and they may acquire the
427 required familiarity with the foraging landscape within much shorter time enabling
428 them to start bringing food early in life. Thus, a prolonged exploratory phase can be
429 expected for a predatory wasp that inhabits highly dense tropical landscape and does
430 not have the advantage of conspecific recruitment. However, such a high investment in
431 learning during early foraging life can only be balanced if the forager wasps (can use the
432 acquired spatial familiarity to) increase their foraging benefits with their increasing age.

433 Interestingly, we found that both foraging success (measured by the ratio of the
434 number of trips in which a wasp brought food and all the trips that she made) and
435 foraging efficiency (measured by the number of times a wasp brought food per unit time
436 she spent on foraging) of the wasps increased with their age. The reduction in their
437 foraging effort and the increase in foraging benefit with increasing age indicate learning
438 and memorising of the features of the landscape in early foraging life, and using the
439 spatial familiarity later for foraging; this might be a stable strategy for predatory
440 animals inhabiting highly dense landscapes. On the contrary, although desert ants
441 (Wehner et al., 2004) and honey bees (Dukas and Visscher, 1994) are also known to
442 increase their foraging benefits with the advancement of their foraging life, both of these
443 insects do so by increasing their foraging effort; desert ants increase their number of
444 foraging trips (Wehner et al., 2004) and honey bees increase their foraging speed and
445 distance (from hive) with increasing age (Capaldi et al., 2000).

446 In a landscape where food is randomly distributed into patches, animals can
447 achieve foraging competence by memorising the locations of rewarding patches and
448 reaching those places directly (instead of searching for prey every time randomly). We
449 found that wasps indeed developed directional fidelity for the outbound flights with
450 increasing age. The relationship between the consistency in their outbound direction
451 and their age can be explained best by the saturating Michaelis-Menten function. This
452 suggests that the wasps fly in many directions, probably for learning/exploring in the
453 initial foraging stages (and therefore show less directional fidelity), but soon develop a
454 choice for particular direction, maybe after encountering prey in that particular
455 direction. Wasps prefer to begin their search for prey in that direction or in a direction
456 we they have encountered prey in recent past, at least for some days. The saturation of
457 high directional preference in the older wasps may also indicate that a rewarding patch
458 continues to be rewarding at least for three days.

459 Since young wasps do not show any directional preference for their outbound
460 trips, if they return from the same direction, they should not have any directionality for
461 their inbound flights as well, and the angular difference between the outbound and
462 subsequent inbound flights should be low. On the other hand, since experienced foragers
463 develop a directional preference for outbound trips, if they forage by following a trapline
464 foraging route as bees are known to do (Buatois and Lihoreau, 2016; Lihoreau et al.,
465 2012; Saleh and Chittka, 2007), they should also show an increase in the directionality of
466 inbound trips. However, following more than a single trapline may again reduce the
467 directionality of the inbound trips. With age, wasps from two nests in fact showed an
468 increase in their directionality of inbound trips following the saturating Michaelis-
469 Menten function and wasps of the other nest showed an initial increase followed by
470 decrease in older age. Though our data on the direction of the inbound flights were
471 collected on the basis of the very last stages of the flights and therefore may just indicate
472 the best approach to the nest (and might be unrelated to foraging path), these results
473 might also suggest that depending on the distribution of resources, which in turn
474 depends on many factors including the landscape, wasps might develop one or more
475 trapline foraging routes in different directions. Quite interestingly, we have also found
476 that the angular difference between the direction of outbound flight and subsequent
477 inbound flight increased with the advancement of age of the wasps. This suggests that

478 the young foragers returned from the same direction in which they had their outbound
479 foraging trip, whereas the older wasps returned to their nest from directions different
480 from the direction of their outbound trip. This may have happened because during their
481 learning phase, young wasps probably relied mostly on error-prone path integration, the
482 degree of error of which increases with the change of the angular direction in a single
483 foraging trip. Thus, young foragers did not make much angular deviation during a single
484 trip; similar results has been shown in honey bees (Capaldi et al., 2000). With
485 experience, wasps may enhance their skill in path integration and also they may start
486 using the acquired familiarity with the foraging landscape much more efficiently for
487 navigational guidance, as observed in ants (Mangan and Webb, 2012) and honey bees
488 (Zhang et al., 1999).

489

490 **CONCLUSIONS**

491 All these results indicate that these wasps acquire spatial familiarity with their
492 foraging landscape in their initial phase of foraging. They do so probably by learning and
493 developing a long-term memory of the features of the landscape. This memory in turn
494 enables the wasps to reduce their foraging effort and yet increase their foraging benefits.
495 Such an ontogeny of foraging capability that is strongly influenced by the memory of
496 their surrounding landscapes may be a reflection of their evolution in the landmark-rich
497 tropical ecosystem.

498

499 **Acknowledgements**

500 We thank Kavita Isvaran for her help with statistical analyses, and Thomas S. Collett
501 for many helpful discussions.

502

503 **Funding**

504 This work was supported by the Department of Science and Technology,
505 Department of Biotechnology, Ministry of Environment and Forests, and Council of
506 Scientific and Industrial Research, Government of India (to RG).

507

508 **Disclaimer**

509 SM and RG designed the study, SM and AB conducted the study, SM analysed the
510 data and SM and RG co-wrote the paper. The authors declare no competing interest.
511 The research adheres to the guidelines for the Use of Animals in Research, the legal
512 requirements of the country in which the work was carried out, and all institutional
513 guidelines.

514

515

516

517 **REFERENCES**

- 518 **Abrams, P. A.** (1991). Life History and the Relationship Between Food Availability and
519 Foraging Effort. *Ecology* **72**, 1242–1252.
- 520 **Batschelet, E.** (1981). *Circular statistics in biology*. London: Academic press.
- 521 **Bolker, B. M.** (2008). *Ecological models and data in R*. Princeton and Oxford: Princeton
522 University Press.
- 523 **Boyer, D. and Walsh, P. D.** (2010). Modelling the mobility of living organisms in
524 heterogeneous landscapes: does memory improve foraging success? *Philos. Trans. A.*
525 *Math. Phys. Eng. Sci.* **368**, 5645–5659.
- 526 **Bracis, C., Gurarie, E., Van Moorter, B. and Goodwin, R. A.** (2015). Memory effects on
527 movement behavior in animal foraging. *PLoS One* **10**, 1–21.
- 528 **Buatois, A. and Lihoreau, M.** (2016). Evidence of trapline foraging in honeybees. *J. Exp.*
529 *Biol.* **219**, 2426–9.
- 530 **Bühlmann, C., Cheng, K. and Wehner, R.** (2011). Vector-based and landmark-guided
531 navigation in desert ants inhabiting landmark-free and landmark-rich
532 environments. *J. Exp. Biol.* **214**, 2845–53.
- 533 **Capaldi, E. A. and Dyer, F. C.** (1999). The role of orientation flights on homing
534 performance in honeybees. *J. Exp. Biol.* **202**, 1655–66.
- 535 **Capaldi, E. A., Smith, a D., Osborne, J. L., Fahrbach, S. E., Farris, S. M., Reynolds, D. R.,**
536 **Edwards, a S., Martin, A., Robinson, G. E., Poppy, G. M., et al.** (2000). Ontogeny of
537 orientation flight in the honeybee revealed by harmonic radar. *Nature* **403**, 537–40.
- 538 **Caraco, T.** (1980). On Foraging Time Allocation in a Stochastic Environment. *Ecology* **61**,
539 119–128.
- 540 **Cartwright, B. A. and Collett, T. S.** (1987). Landmark Maps for Honeybees. *Biol. Cybern.*
541 **57**, 85–93.
- 542 **Cheng, K., Middleton, E. J. T. and Wehner, R.** (2012). Vector-based and landmark-
543 guided navigation in desert ants of the same species inhabiting landmark-free and
544 landmark-rich environments. *J. Exp. Biol.* **215**, 3169–74.
- 545 **Collett, M., Chittka, L. and Collett, T. S.** (2013). Spatial Memory in Insect Navigation.

- 546 *Curr. Biol.* **23**, R789–R800.
- 547 **Degen, J., Kirbach, A., Reiter, L., Lehmann, K., Norton, P., Storms, M., Koblöfsky, M.,**
548 **Winter, S., Georgieva, P. B., Nguyen, H., et al.** (2015). Exploratory behaviour of
549 honeybees during orientation flights. *Anim. Behav.* **102**, 45–57.
- 550 **Dukas, R. and Visscher, P. K.** (1994). Lifetime learning by foraging honey bees. *Anim.*
551 *Behav.* **48**, 1007–1012.
- 552 **Dyer, F. C.** (1996). Spatial memory and navigation by honeybees on the scale of the
553 foraging range. *J. Exp. Biol.* **199**, 147–54.
- 554 **Fleischmann, P. N., Christian, M., Müller, V. L., Rössler, W. and Wehner, R.** (2016).
555 Ontogeny of learning walks and the acquisition of landmark information in desert
556 ants, *Cataglyphis fortis*. *J. Exp. Biol.* jeb.140459.
- 557 **Gadagkar, R.** (2001). *The Social Biology of Ropalidia marginata: Toward Understanding*
558 *the Evolution of Eusociality*. Cambridge, Massachusetts; London, England: Harvard
559 University Press.
- 560 **Hassell, M. . P. . and Southwood, T. R. E.** (1978). Foraging Strategies of Insects. *Annu.*
561 *Rev. Ecol. Syst.* **9**, 75–98.
- 562 **Jeanne, R. L. and Taylor, B. J.** (2009). Individual and social foraging in social wasps. In
563 *Food Exploitation By Social Insects: Ecological, Behavioral, and Theoretical*
564 *Approaches*, pp. 53–79. Boca Raton: CRC Press.
- 565 **Kamil, A. C. and Roitblat, H. L.** (1985). The ecology of foraging behavior: implications
566 for animal learning and memory. *Annu. Rev. Psychol.* **36**, 141–169.
- 567 **Kohler, M. and Wehner, R.** (2005). Idiosyncratic route-based memories in desert ants,
568 *Melophorus bagoti*: How do they interact with path-integration vectors? *Neurobiol.*
569 *Learn. Mem.* **83**, 1–12.
- 570 **Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J., Lim, K. S., Smith, A. D.,**
571 **Osborne, J. L. and Chittka, L.** (2012). Radar Tracking and Motion-Sensitive
572 Cameras on Flowers Reveal the Development of Pollinator Multi-Destination Routes
573 over Large Spatial Scales. *PLoS Biol.* **10**, 19–21.
- 574 **Macquart, D., Garnier, L., Combe, M. and Beugnon, G.** (2006). Ant navigation en route
575 to the goal: Signature routes facilitate way-finding of *Gigantiops destructor*. *J. Comp.*

- 576 *Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **192**, 221–234.
- 577 **Mandal, S. and Gadagkar, R.** (2015). Homing abilities of the tropical primitively
578 eusocial paper wasp *Ropalidia marginata*. *J. Comp. Physiol. A* **201**, 795–802.
- 579 **Mandal, S., Brahma, A. and Gadagkar, R.** (2017). Homing in a tropical social wasp: role
580 of spatial familiarity, motivation and age. *J. Comp. Physiol. A Neuroethol. Sensory,*
581 *Neural, Behav. Physiol.* **203**, 1–13.
- 582 **Mangan, M. and Webb, B.** (2012). Spontaneous formation of multiple routes in
583 individual desert ants (*Cataglyphis velox*). *Behav. Ecol.* **23**, 944–954.
- 584 **Menzel, R. and Greggers, U.** (2015). The memory structure of navigation in honeybees.
585 *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **201**, 547–61.
- 586 **Menzel, R., Geiger, K., Joerges, J., Muller, U. and Chittka, L.** (1998). Bees travel novel
587 homeward routes by integrating separately acquired vector memories. *Anim. Behav.*
588 **55**, 139–52.
- 589 **Müller, M. and Wehner, R.** (2010). Path Integration Provides a Scaffold for Landmark
590 Learning in Desert Ants. *Curr. Biol.* **20**, 1368–1371.
- 591 **Narendra, A.** (2007). Homing strategies of the Australian desert ant *Melophorus bagoti*
592 II. Interaction of the path integrator with visual cue information. *J. Exp. Biol.* **210**,
593 1804–12.
- 594 **Narendra, A., Gourmaud, S. and Zeil, J.** (2013). Mapping the navigational knowledge of
595 individually foraging ants, *Myrmecia croslandi*. *Proc. R. Soc. B* **280**,
- 596 **Naug, D. and Gadagkar, R.** (1998). The Role of Age in Temporal Polyethism in a
597 Primitively Eusocial Wasp. *Behav. Ecol. Sociobiol.* **42**, 37–47.
- 598 **Norberg, R. A.** (1977). An Ecological Theory on Foraging Time and Energetics and
599 Choice of Optimal Food-Searching Method. *J. Anim. Ecol.* **46**, 511–529.
- 600 **Osborne, J. L., Smith, A., Clark, S. J., Reynolds, D. R., Barron, M. C., Lim, K. S. and**
601 **Reynolds, A. M.** (2013). The ontogeny of bumblebee flight trajectories: From Naive
602 explorers to experienced foragers. *PLoS One* **8**,
- 603 **Palikij, J., Ebert, E., Preston, M., McBride, A. and Jander, R.** (2012). Evidence for the
604 honeybee’s place knowledge in the vicinity of the hive. *J. Insect Physiol.* **58**, 1289–98.

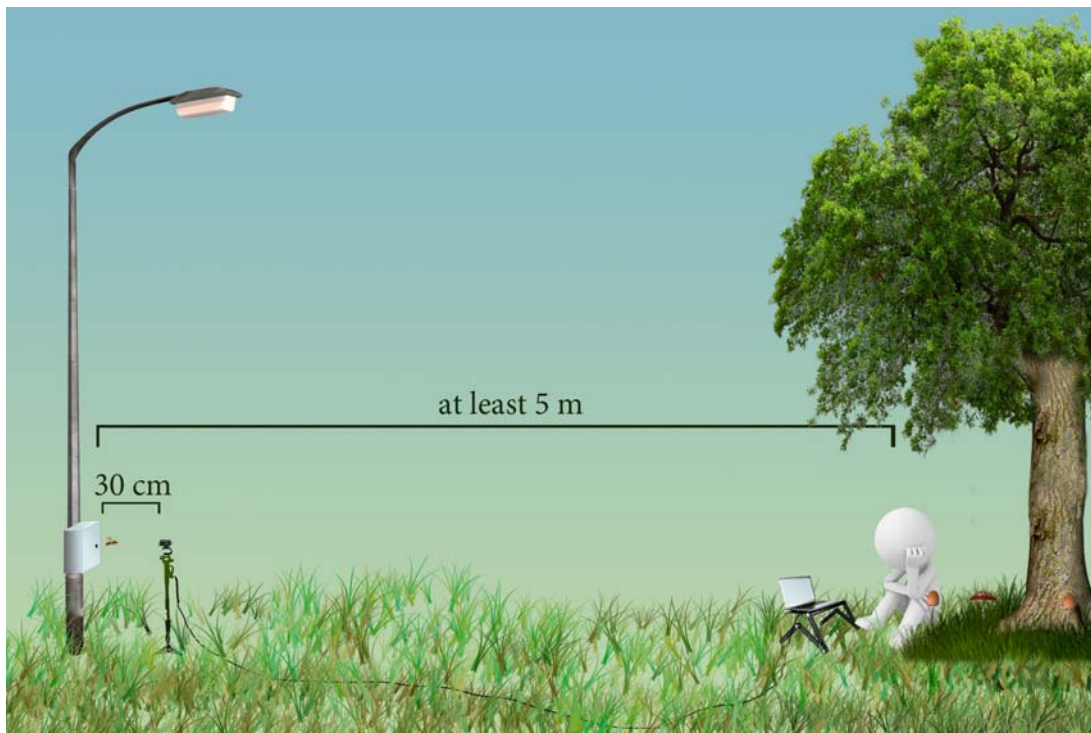
- 605 **Pyke, G. H., Pulliam, H. R. and Charnov, E. L.** (1977). Optimal foraging: A selective
606 review of theory and tests. *Q. Rev. Biol.* **52**, 137–154.
- 607 **Raine, N. E. and Chittka, L.** (2008). The correlation of learning speed and natural
608 foraging success in bumble-bees. *Proc. R. Soc. B-Biological Sci.* **275**, 803–808.
- 609 **Saleh, N. and Chittka, L.** (2007). Traplining in bumblebees (*Bombus impatiens*): A
610 foraging strategy's ontogeny and the importance of spatial reference memory in
611 short-range foraging. *Oecologia* **151**, 719–730.
- 612 **Sen, R. and Gadagkar, R.** (2010). Natural history and behaviour of the primitively
613 eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae): a comparison of
614 the two sexes. *J. Nat. Hist.* **44**, 959–968.
- 615 **Wehner, R., Meier, C. and Zollikofer, C.** (2004). The ontogeny of foraging behaviour in
616 desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* **29**, 240–250.
- 617 **Wickham, H.** (2016). scales: Scale Functions for Visualization.
- 618 **Woodgate, J. L., Makinson, J. C., Lim, K. S., Reynolds, A. M. and Chittka, L.** (2016). Life-
619 Long Radar Tracking of Bumblebees. *PLoS One* 1–22.
- 620 **Wystrach, A., Philippides, A., Aurejac, A., Cheng, K. and Graham, P.** (2014). Visual
621 scanning behaviours and their role in the navigation of the Australian desert ant
622 *Melophorus bagoti*. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.*
623 **200**, 615–626.
- 624 **Zeil, J.** (2012). Visual homing: an insect perspective. *Curr. Opin. Neurobiol.* **22**, 285–93.
- 625 **Zhang, S., Lehrer, M. and Srinivasan, M. V.** (1999). Honeybee Memory: Navigation by
626 Associative Grouping and Recall of Visual Stimuli. *Neurobiol. Learn. Mem.* **72**, 180–
627 201.
- 628
- 629

630 **Supplementary materials: Table S1.** Overview of the data collected from three wasp nests.

Nest →		N17	N18	N21
All wasps	Number of unique foraging wasps	78	89	105
	Mean age of foragers (in days)	40.00	36.46	32.06
	Total number of trips (3 days)	607	1173	2407
	Mean number of trips/wasp/day	2.59	4.39	7.64
	Mean trip duration (minutes)	87.59	71.23	74.05
foragers that brought food	Number (and percentage among all foraging wasps)	43 (55.13%)	37 (41.57%)	44 (41.90%)
	Mean age (in days)	55.28	57.08	48.41
	Total number of trips (3 days)	358	477	759
	Successful trips	146	197	217
	Proportion of successful trips	0.41	0.41	0.29
	Mean number of trips/wasp/day	2.78	4.30	5.75
	Mean trip duration (minutes)	91.30	98.86	86.43
foragers that brought water	Number (and percentage among all foraging wasps)	2 (2.56%)	1 (1.12%)	3 (2.86%)
	Mean age (in days)	30.00	22	30.33
	Total number of trips (3 days)	90	321	188
	Successful trips	54	311	61
	Proportion of successful trips	0.60	0.97	0.32
	Mean number of trips/wasp/day	15.00	107.00	20.89
	Mean trip duration (minutes)	9.50	1.58	25.51
foragers that brought building material	Number (and percentage among all foraging wasps)	4 (5.13%)	8 (8.99%)	10 (9.52%)
	Mean age (in days)	20.00	22.75	19.00
	Total number of trips (3 days)	38	98	140
	Successful trips	6	14	19
	Proportion of successful trips	0.16	0.14	0.14
	Mean number of trips/wasp/day	3.17	4.08	4.67
	Mean trip duration (minutes)	64.17	27.63	66.78
Wasps that did not bring anything	Number (and percentage among all foraging wasps)	29 (37.18%)	39 (43.82%)	40 (38.09%)
	Mean age (in days)	20.79	20.41	17.05
	Total number of trips (3 days)	121	226	373
	Mean number of trips/wasp/day	1.39	1.93	3.11
	Mean trip duration (minutes)	90.69	52.32	72.27
Wasps that brought building material (B) and water (W)	Number (and percentage among all foraging wasps)		1 (1.12%)	3 (2.86%)
	Mean age (in days)		21	23.00
	Total number of trips (3 days)		12	511
	Successful trips	NA	B = 1, W = 1	B=5, W=347
	Proportion of successful trips		0.17	0.69
	Mean number of trips/wasp/day		4.00	56.78
	Mean trip duration (minutes)		40.91	5.93
Wasps that brought water (W) and food (F)	Number (and percentage among all foraging wasps)		1 (1.12%)	1 (0.95%)
	Age (in days)		39	64
	Total number of trips (3 days)		12	178
	Successful trips	NA	W = 1, F = 1	F = 3, W=135
	Proportion of successful trips		0.17	0.78
	Mean number of trips/wasp/day		4.00	59.33
	Mean trip duration (minutes)		189.73	4.78
Wasps that brought building material (B) and food (F)	Number (and percentage among all foraging wasps)		2 (2.24%)	3 (2.86%)
	Mean age (in days)		36.5	31.00
	Total number of trips (3 days)		27	47
	Successful trips	NA	B=2, F=12	B=3, F=12
	Proportion of successful trips		0.52	0.32
	Mean number of trips/wasp/day		4.5	5.22
	Mean trip duration (minutes)		93.86	103.56
Wasps that brought building material (B), water (W) and food (F)	Number (and percentage among all foraging wasps)			1 (0.95%)
	Age (in days)			47
	Total number of trips (3 days)			221
	Successful trips	NA	NA	B=1, W=128, F=2
	Proportion of successful trips			0.62
	Mean number of trips/wasp/day			73.67
	Mean trip duration (minutes)			3.84

631

632 **Figures**



633

634 **Figure 1. A schematic representation of the experimental set-up.** We found all the three
635 experimental colonies of wasps within electric boxes attached to roadside lampposts. By
636 default, these boxes had two holes, one on the frontal lid of the box another at the bottom of
637 the box. We sealed the hole at the bottom so that wasps use the frontal hole as their only
638 entrance and exit. A motion sensitive video camera was placed 30 cm away in front of the
639 frontal hole, so that whenever a wasp came out or went inside the box, the camera started
640 recording the video. The timing of departure and arrival of the wasps, as well as the foraged
641 material could be retrieved from the video. The video was stored into a laptop computer
642 connected to the camera and placed at least 5 m away from the lamppost. An observer, clad in
643 camouflage attire, sat near the laptop and recorded the vanishing direction of the outbound
644 and inbound foraging trips.

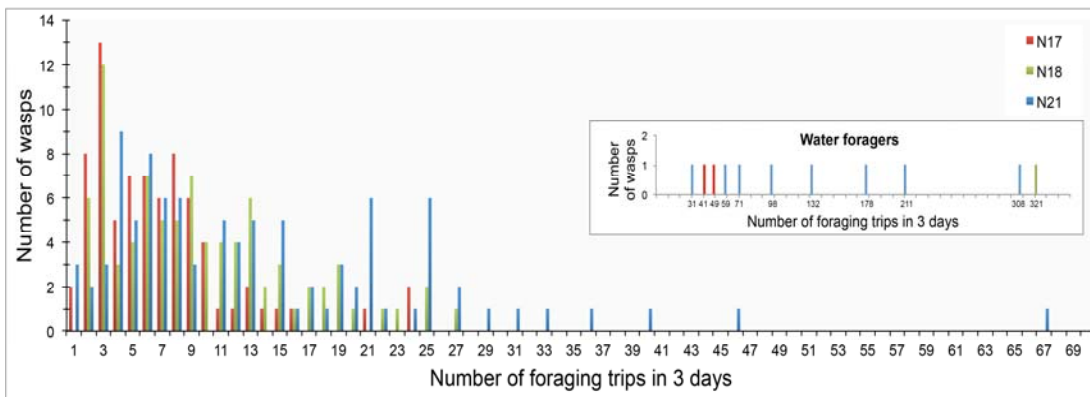


645

2014/04/08 16:17:56.36

646 **Figure 2. A still frame from the collected video data of the nest N21.** In this frame,
647 recorded at 16:17:56.36 hrs (mentioned at the bottom right corner of the frame), a wasp with
648 light blue (coded as L) on top of the thorax and dark green (coded as D) below as well as on
649 her abdomen (hence named as LD) is going inside the box through the exit/entrance hole,
650 while wasp with light blue on thorax as well as on abdomen (hence named as LL) is going out
651 for a foraging trip. None of them is carrying anything.

652

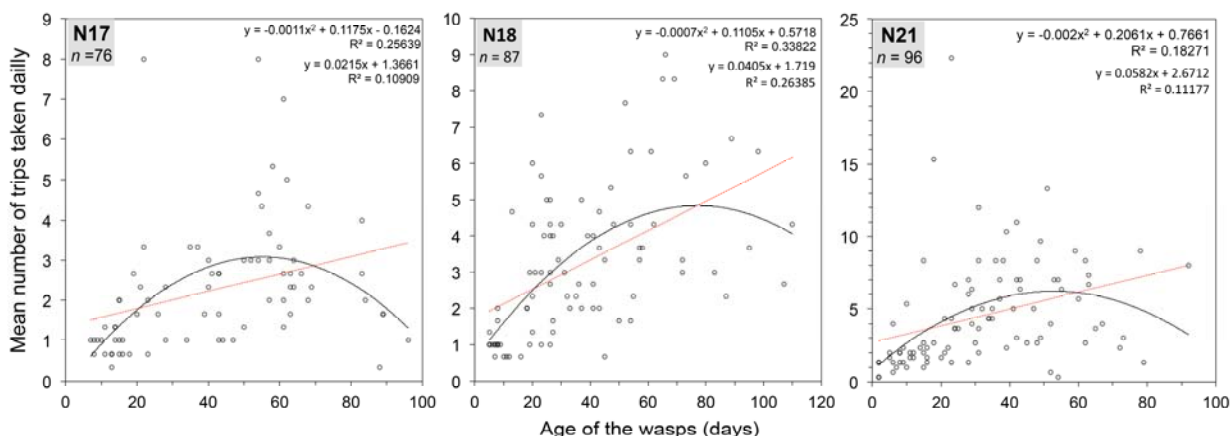


653

654 **Figure 3. The number of foraging trips performed by wasps from three nests (N17, N18**
 655 **and N21) during the three days of observation.** Number of trips made by the water
 656 foragers was much higher than other foragers (see Table S1), and an inclusion of those into
 657 this graph would have made visualization of data from other wasps difficult. While data on
 658 water foragers are presented in the inset, data on other wasps are in the main graph.

659

660



662 **Figure 4. Change in the number of foraging trips taken daily by wasps with their age.** For
 663 all the three nests, the quadratic model explained more variation of the data than the linear
 664 model. Comparison of AIC values of linear (N17=282.36, N18=348.82, N21=512.95) and
 665 quadratic model (N17=270.63, N18=341.56, N21=506.96) reconfirms the better fit of the
 666 quadratic model (ANOVA, $P < 0.05$). An attempt to fit a Holling type IV function revealed non-
 667 significant values of the parameters for all three nests. It is noteworthy that we have not
 668 included water foragers in this analysis.

669

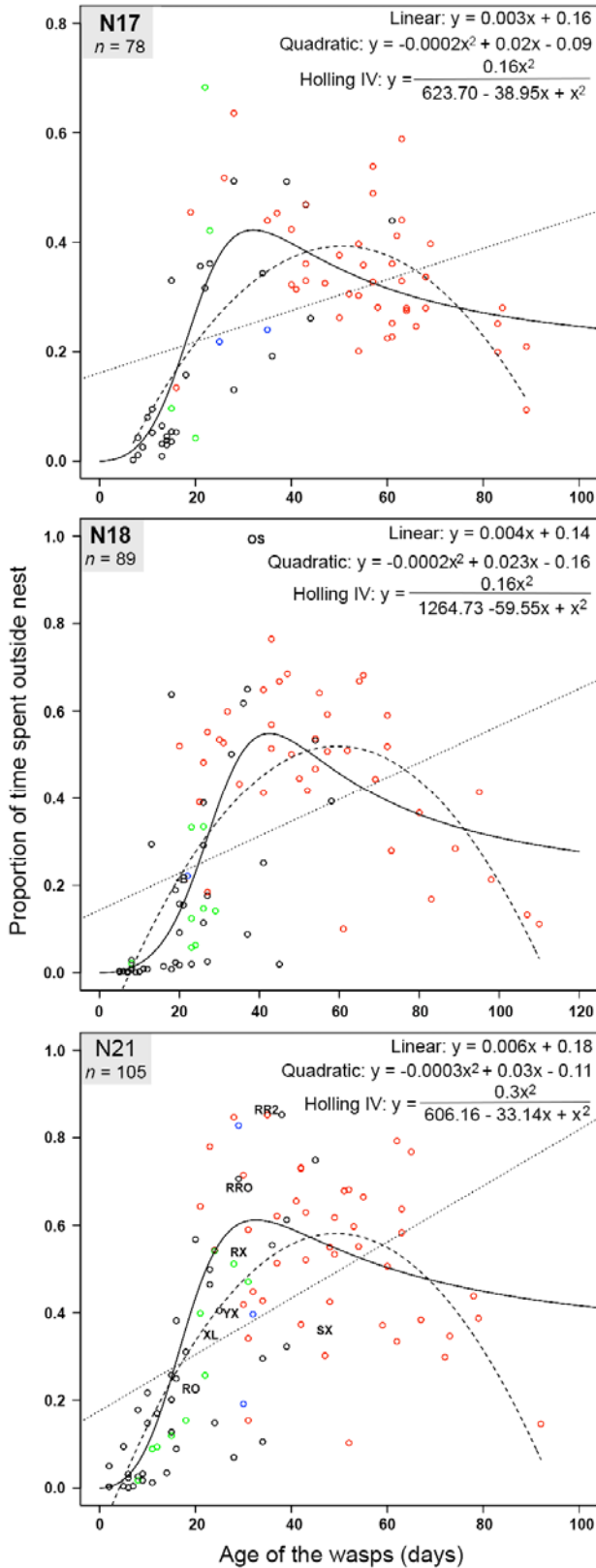


Figure 5. With increasing age, the change in the proportion of the time *Ropalidia marginata* wasps spent on foraging (time spent outside their nests) in three natural colonies (namely N17, N18 and N21). In the plots, black circles represent wasps that did not bring anything to their nest during the three days of observation. Likewise, green, blue and red circles represent wasps that brought building material, water and food at least once to their nest, respectively. One wasp (named as -B) in N18 and three wasps (named RO, XL, YX) in N21 brought both building material and water; one wasp (named OS) in N18 brought both water and food; three wasps (RR2, RRO, RX) from N21 brought building material and food; one wasp (SX) from N21 brought building material, water and food. Three mathematical functions (linear, quadratic and Holling type IV) were fitted to the data from each nest. For all the three nests, Holling type IV provided the best fit. For all the parameters of this function, p value was <0.05 for all the nests.

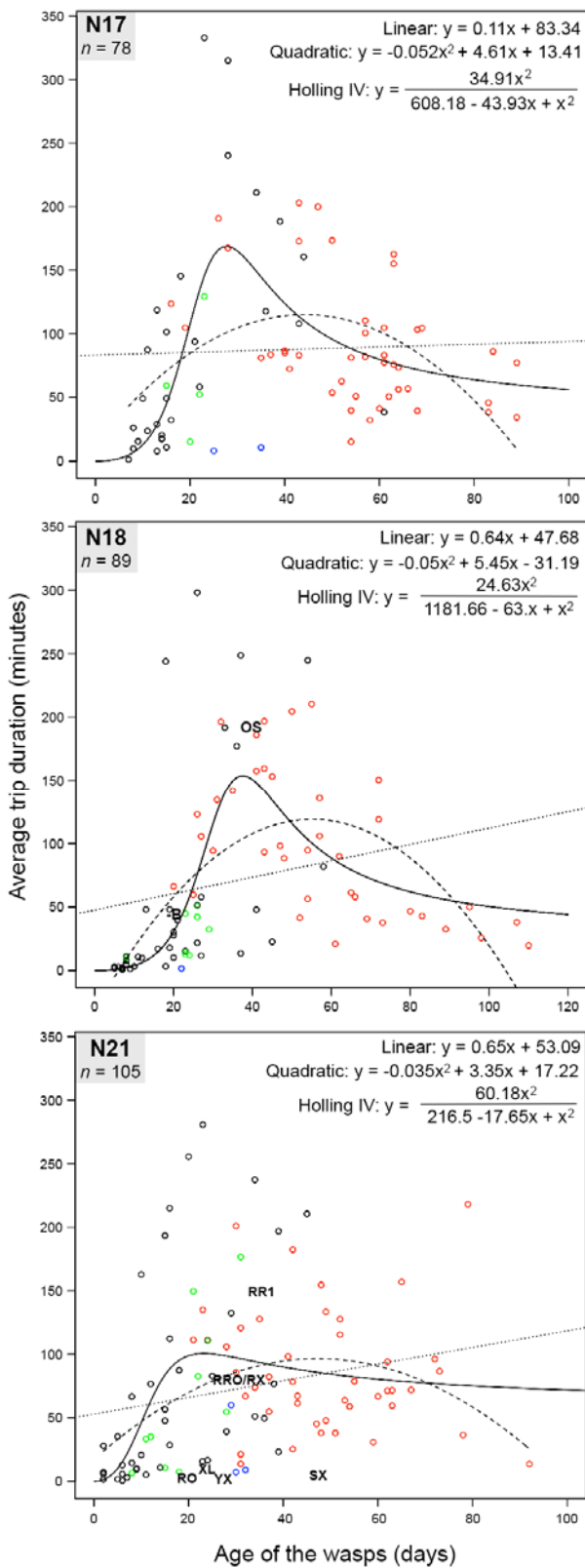
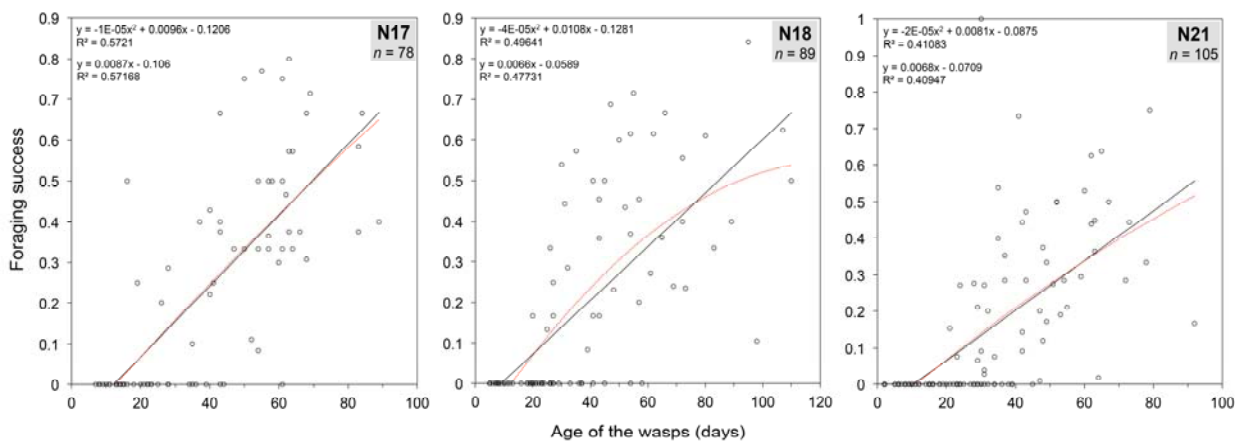


Figure 6. Average foraging duration per trip is also explained best by Holling type IV function, which has a characteristic of rapid initial ascent and after reaching a peak, a gradual descent. For all the parameters of this function, P value was <0.05 for all the nests. As represented in Figure 5, black, green, blue and red circles represent wasps that did not bring anything, and wasps that brought building material, water and food at least once to their nest, respectively during the three days of observation. Similarly, one wasp (named as -B) in N18 and three wasps (named RO, XL, YX) in N21 brought both building material and water; one wasp (named OS) in N18 brought both water and food; three wasps (RR2, RRO, RX) from N21 brought building material and food; one wasp (SX) from N21 brought building material, water and food.

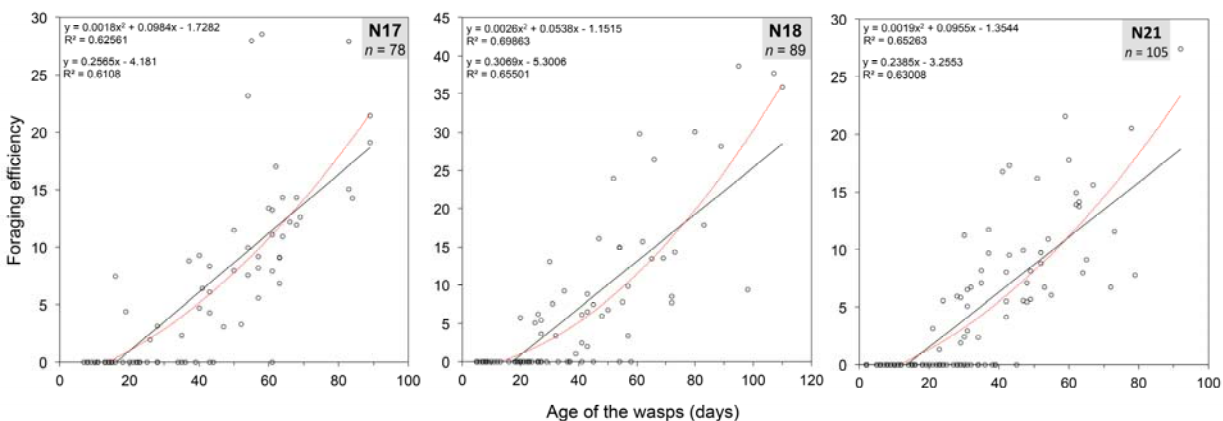


6'

673 **Figure 7. Foraging success (calculated by the ratio of the trips in which a wasp brought**
 674 **food and all the trips that the wasp made) of the wasps increased linearly with increase**
 675 **in their age.**

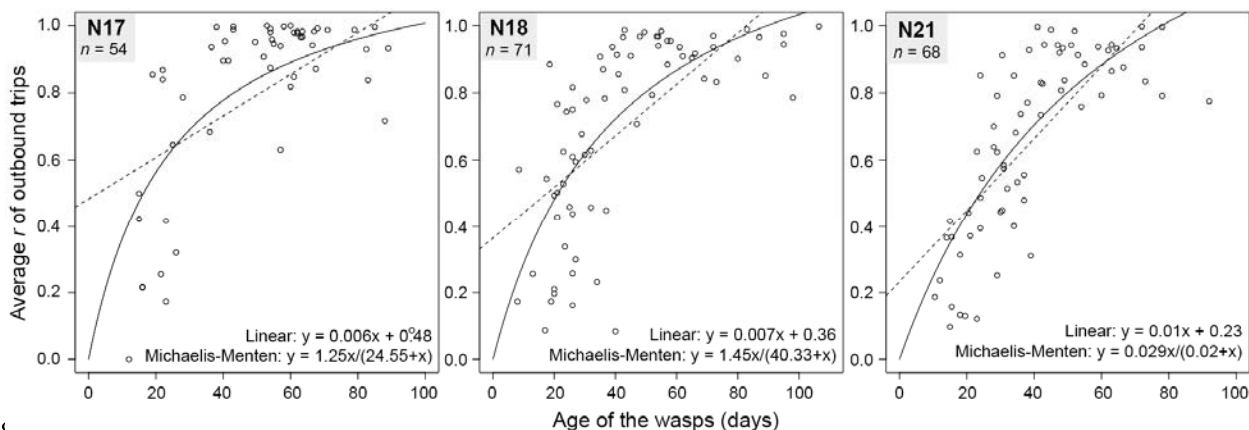
676

677



6'

679 **Figure 8. Foraging efficiency, computed by the number of times a wasp brought food to**
 680 **her nest divided by the proportion of time it spent outside of her nest, increased linearly**
 681 **with the advancement of their age ($P < 0.05$ for all the three nests).**

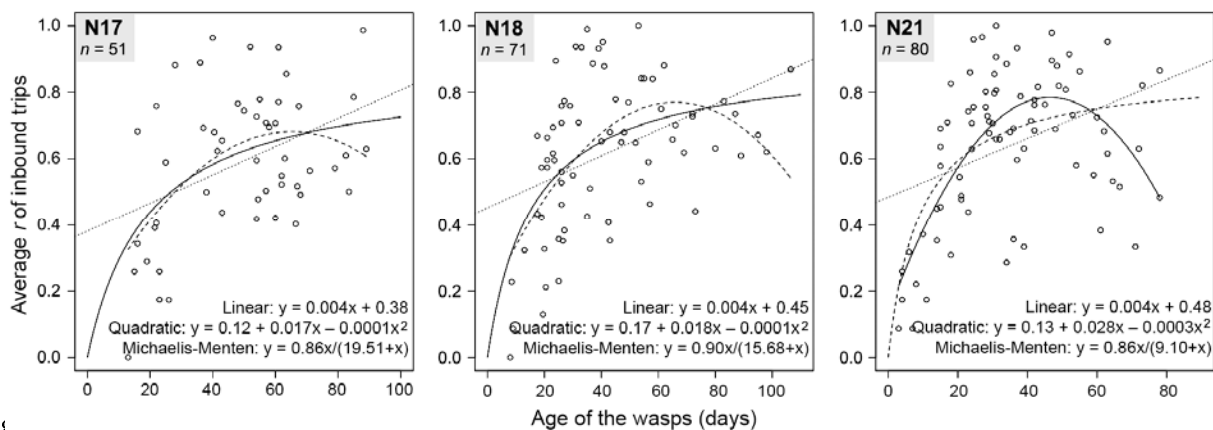


61

683 **Figure 9. Directional fidelity to go for foraging, calculated by averaging the mean vector**
 684 **length of the outbound directions (r) shown by each wasp each day, increased with age**
 685 **of the wasps following a Michaelis-Menten function, average $r = (A \times \text{age}) / (B + \text{age})$. For**
 686 **all the values of A and B for all the nests, $P < 0.05$.**

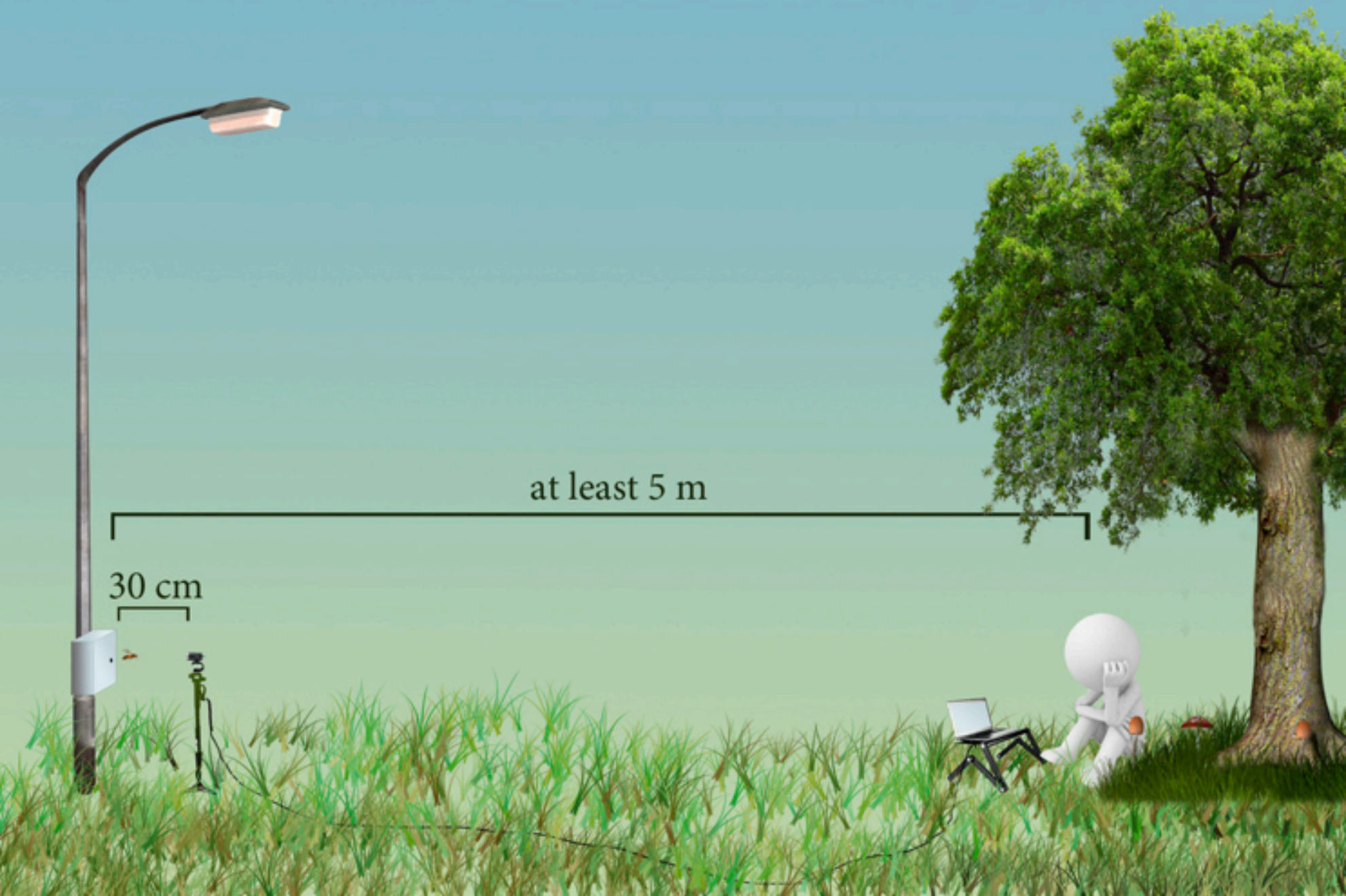
687

688



61

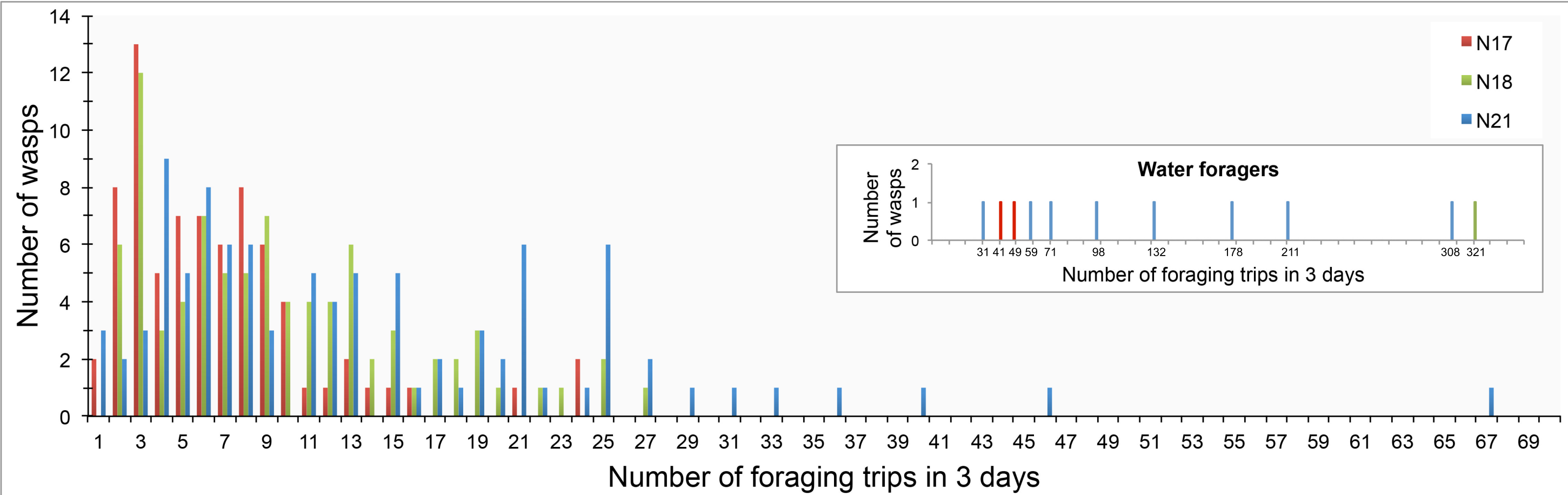
690 **Figure 10. Directional fidelity of the inbound trips increased with age.** Though slopes and
 691 intercepts of linear functions were significant ($P < 0.05$) for all the three nests, data from N17
 692 and N18 were best explained by the Michaelis-Menten function ($P < 0.05$ for all the
 693 parameters), and data from N21 were best explained by a quadratic function ($P < 0.05$ for all
 694 the parameters).



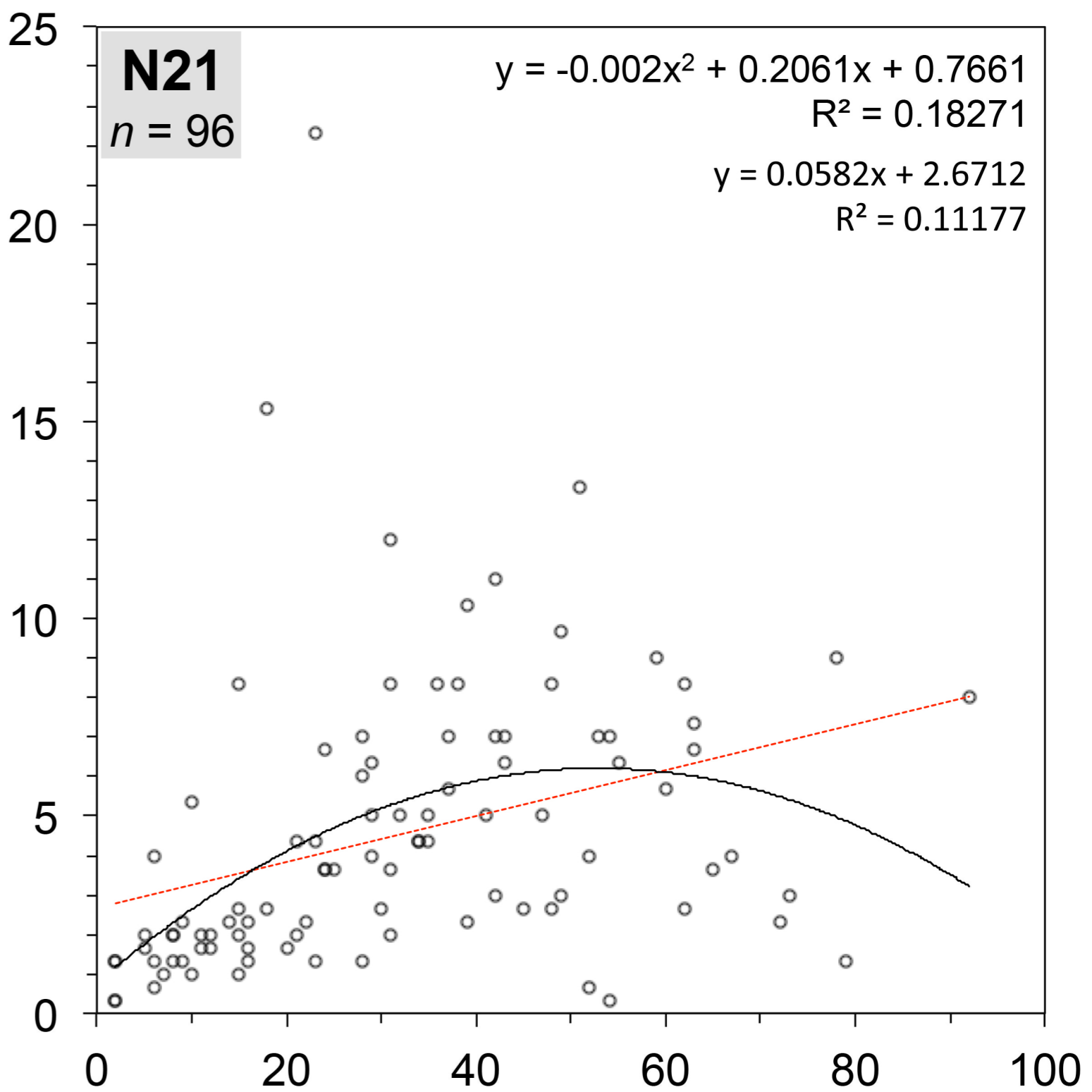
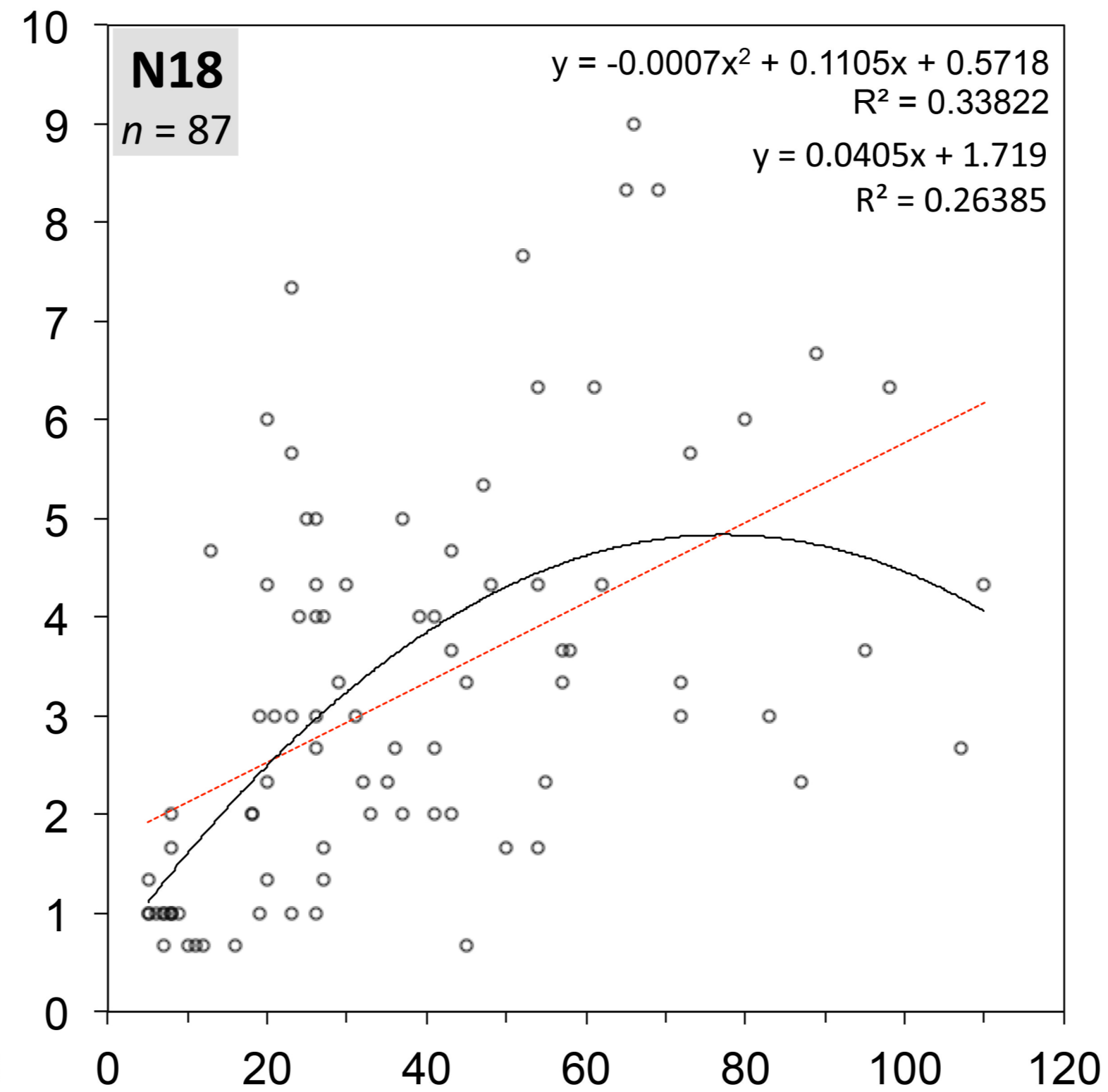
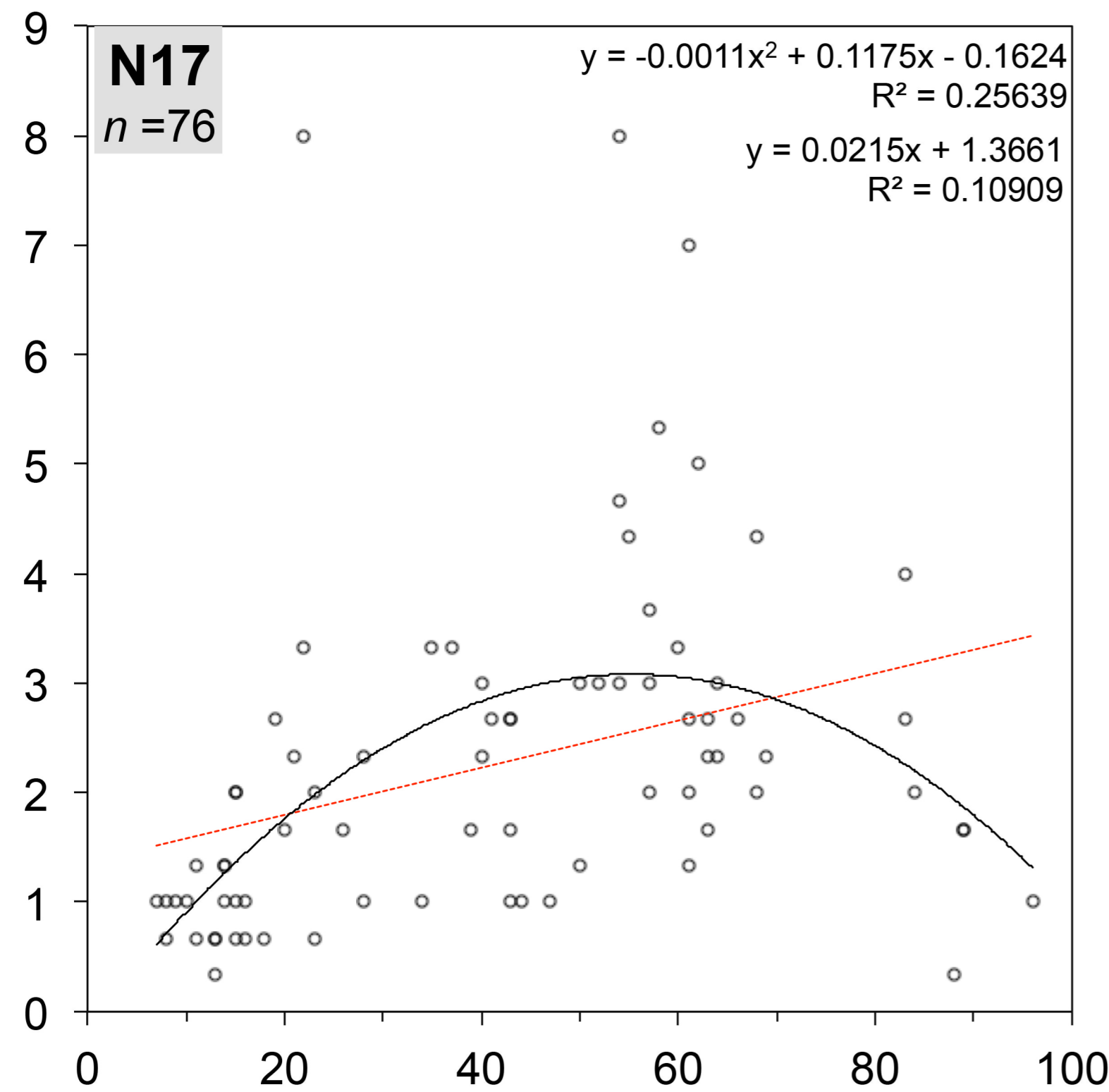
at least 5 m

30 cm

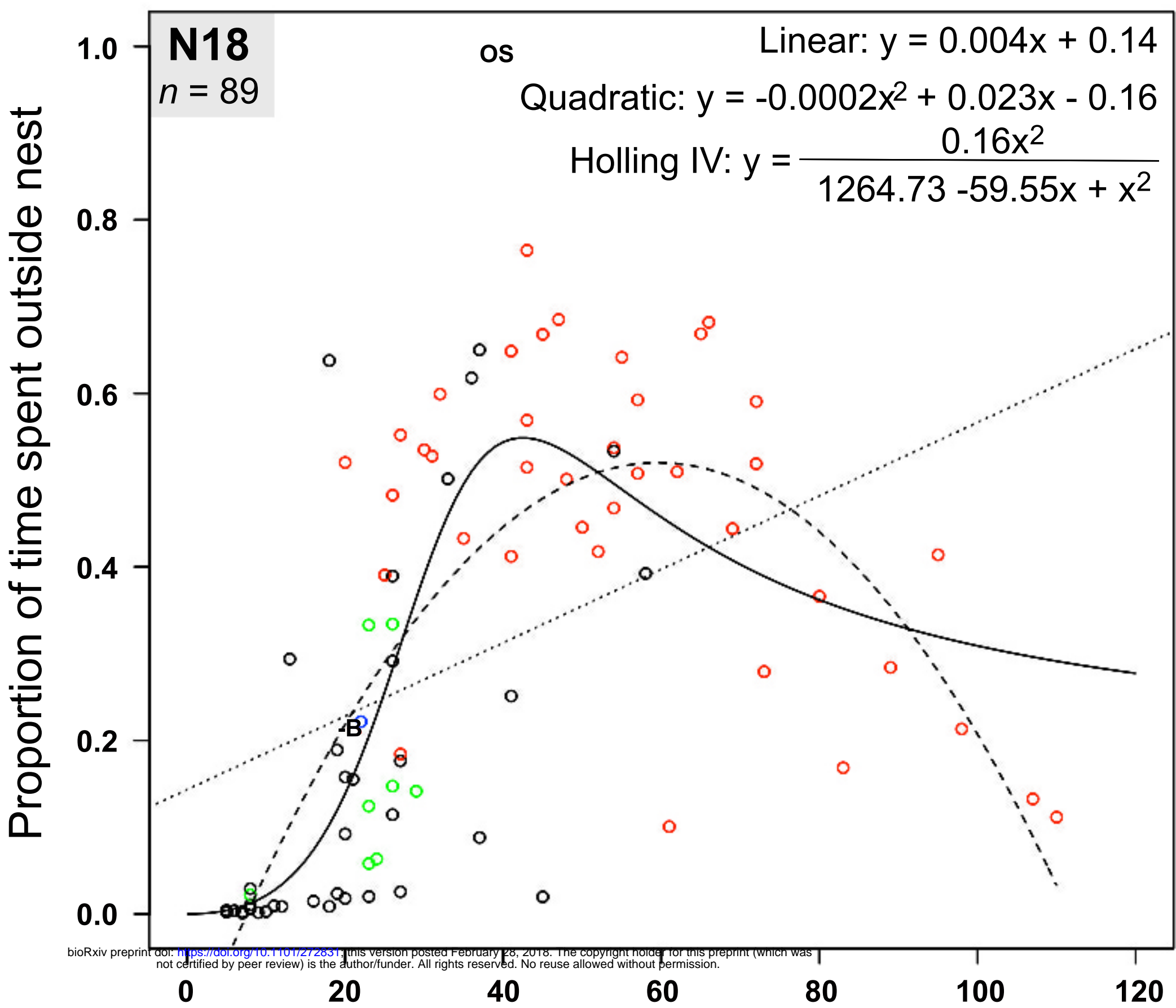
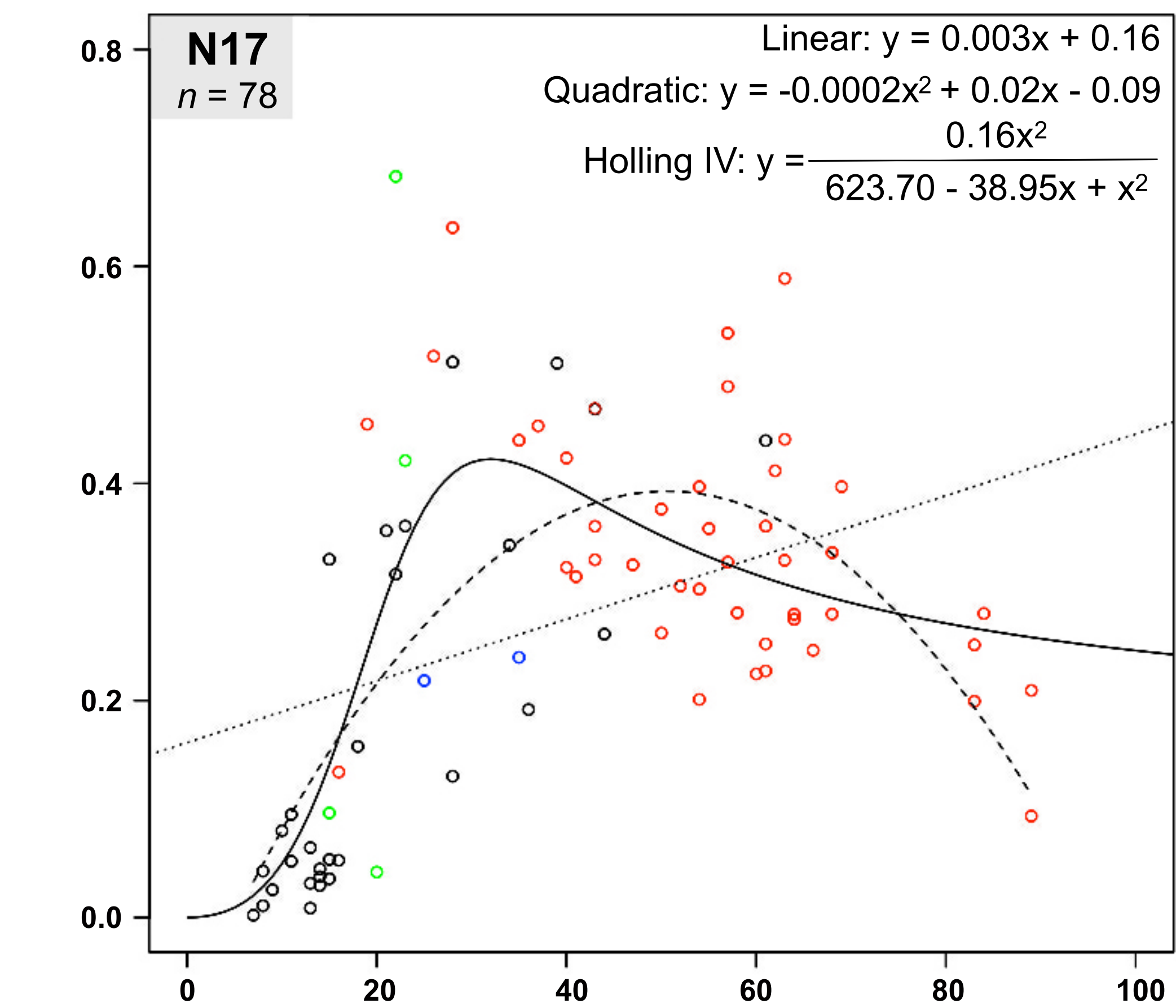




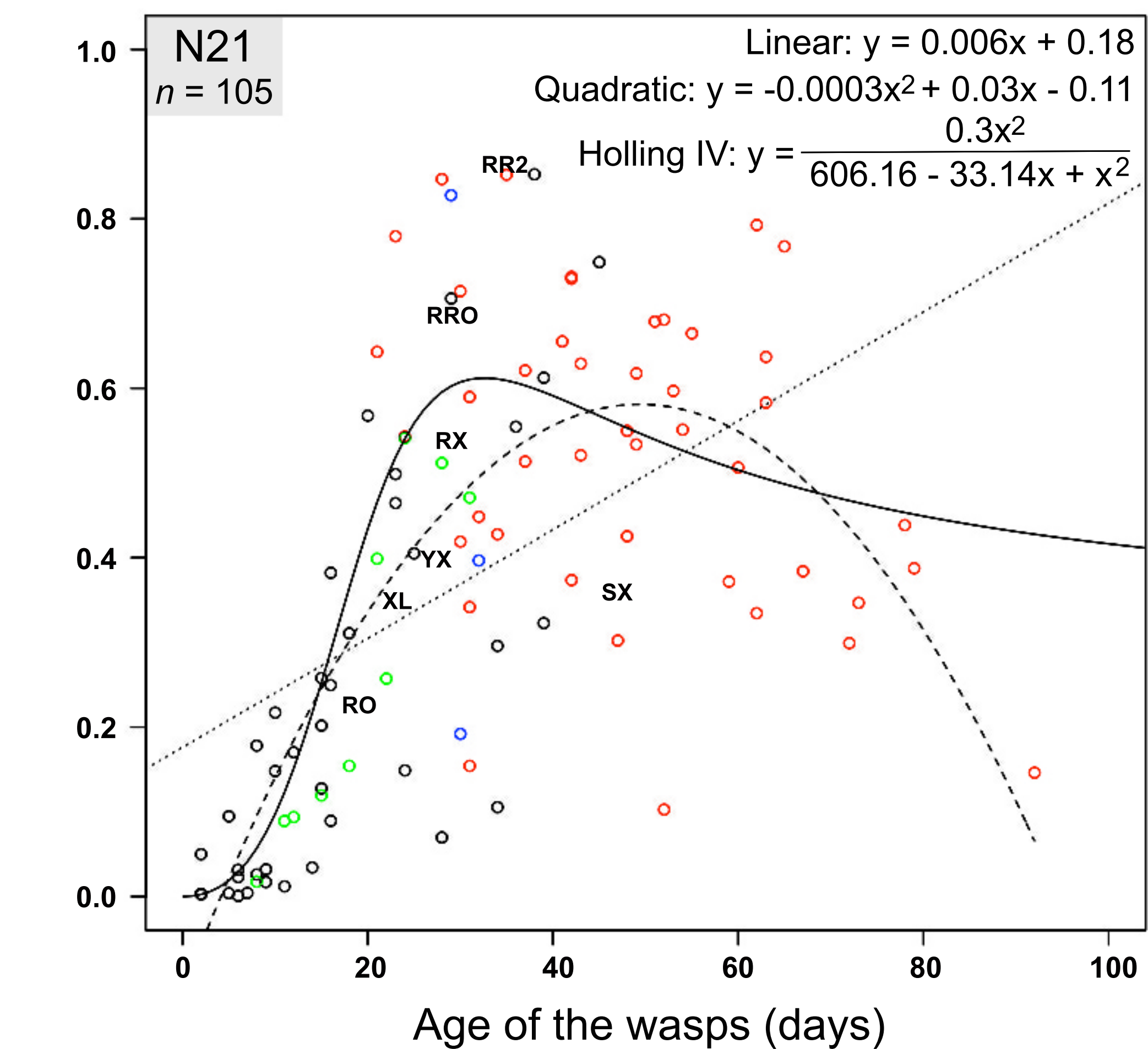
Mean number of trips taken daily

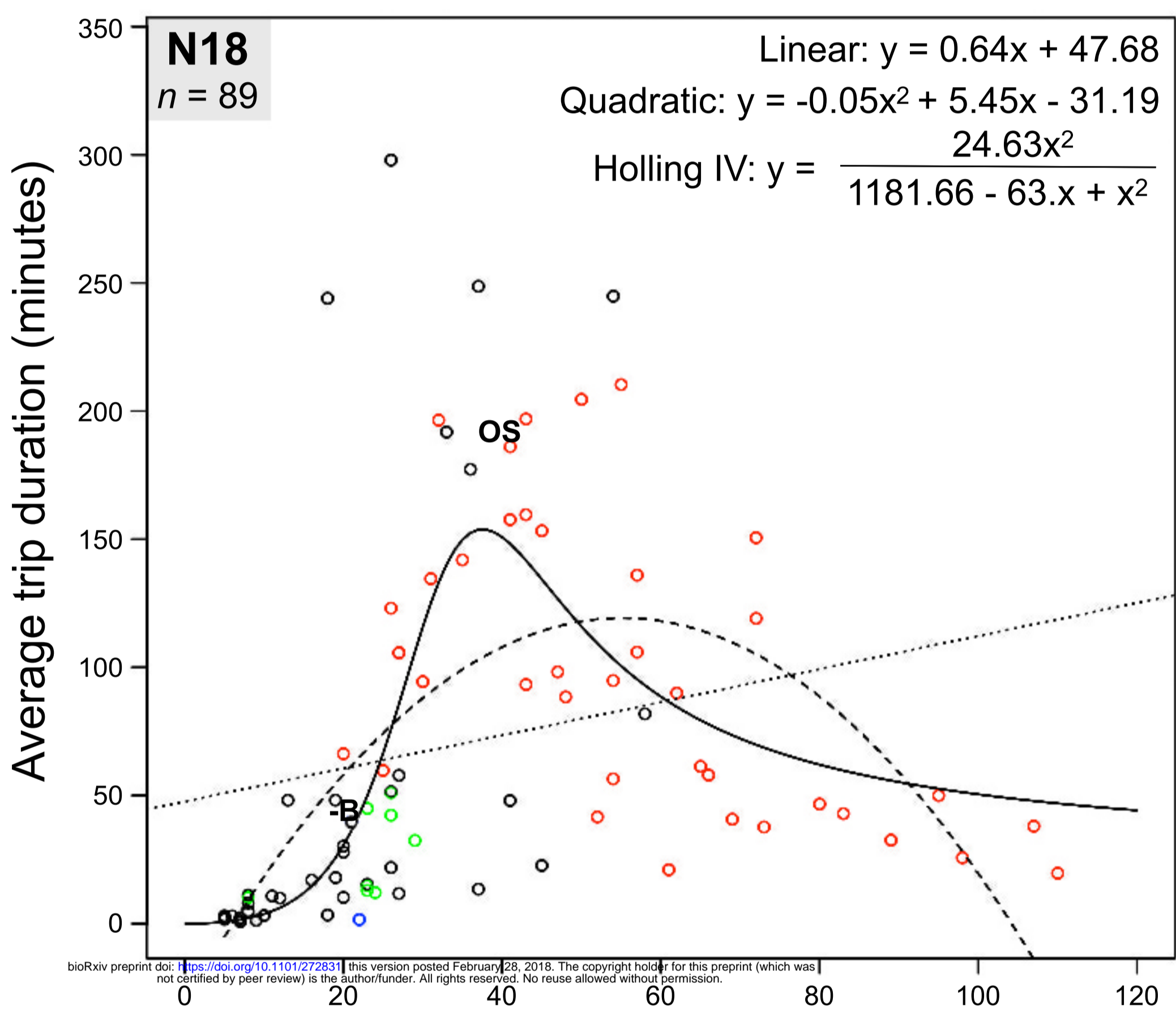
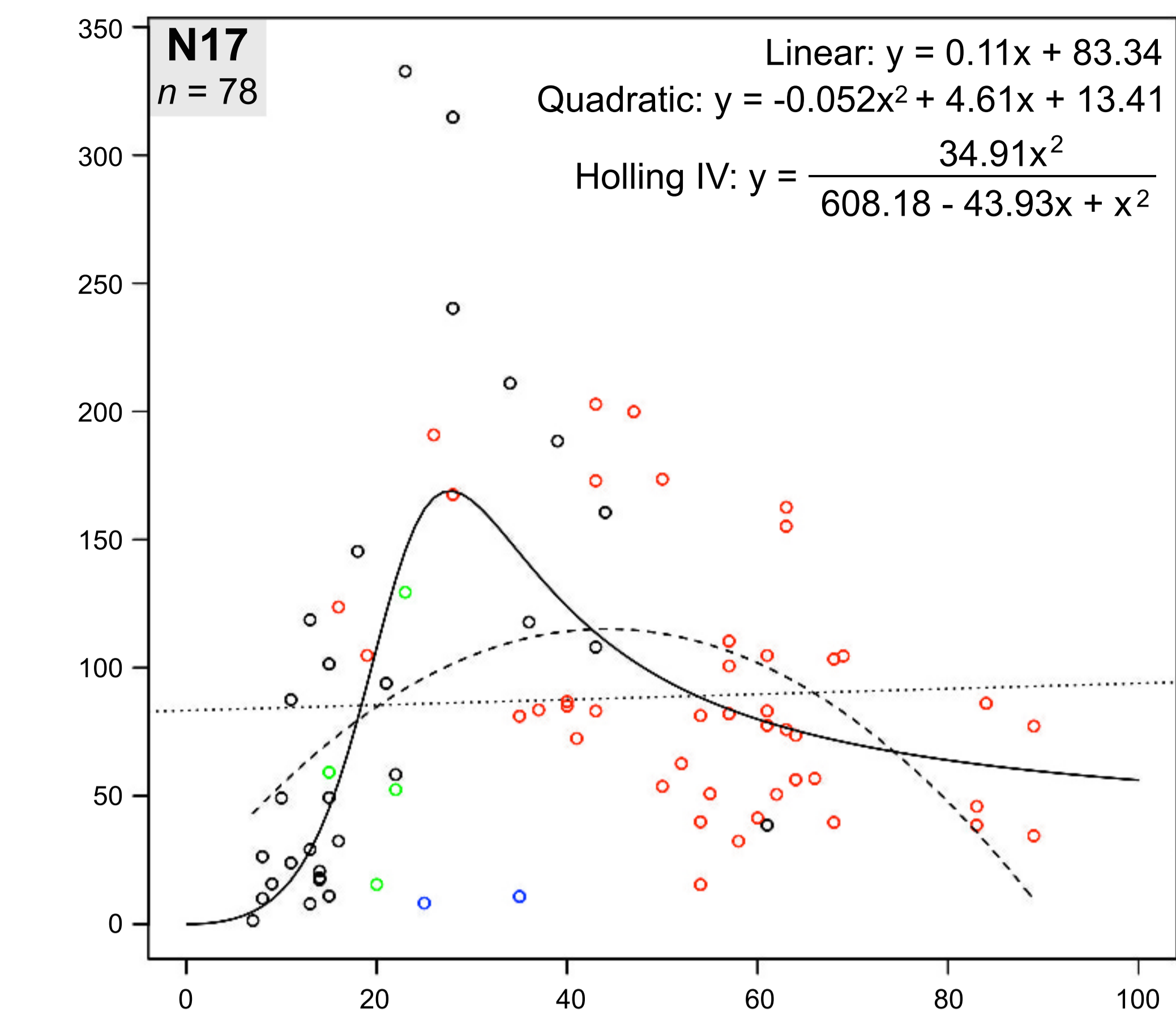


Age of the wasps (days)

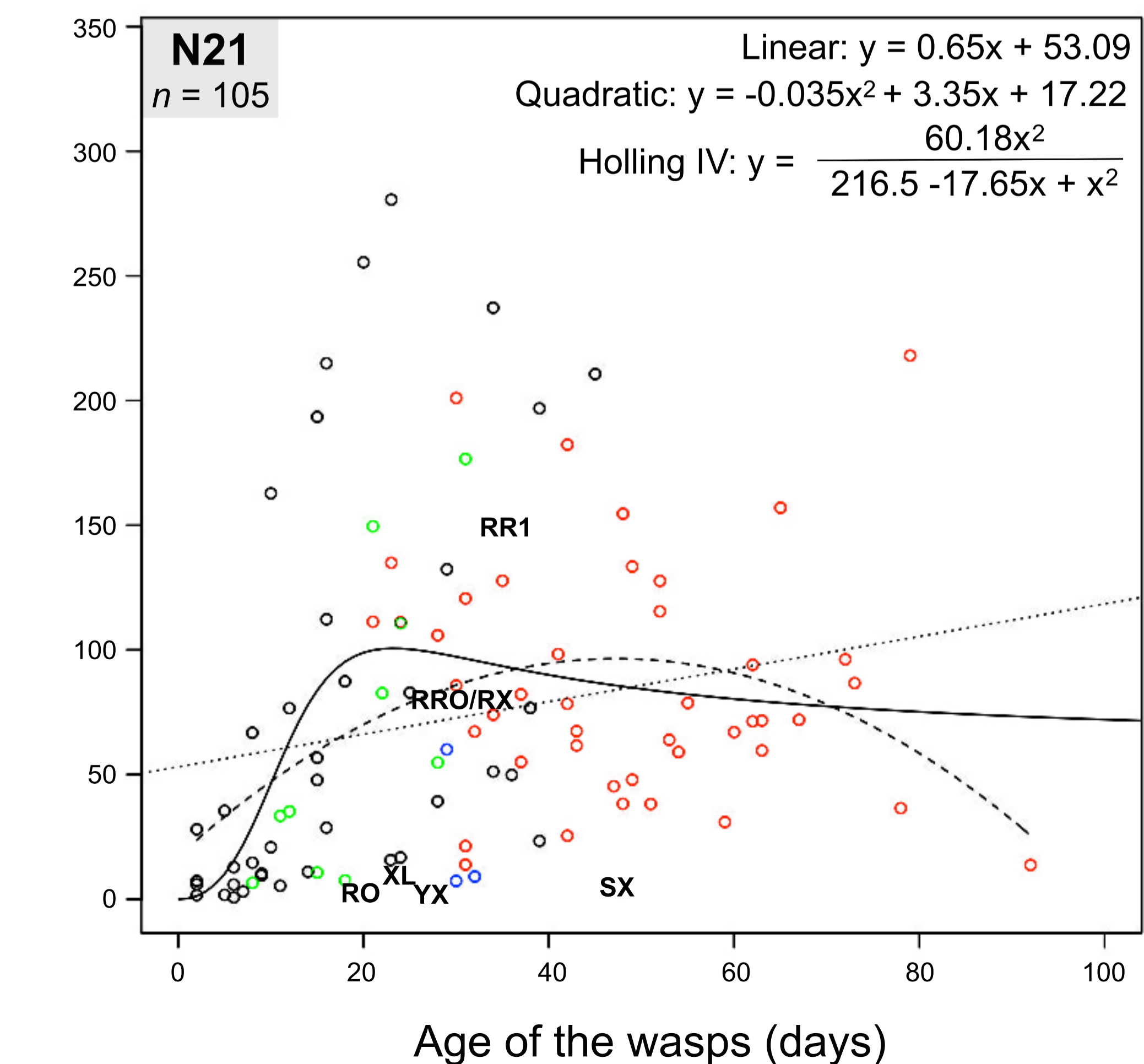


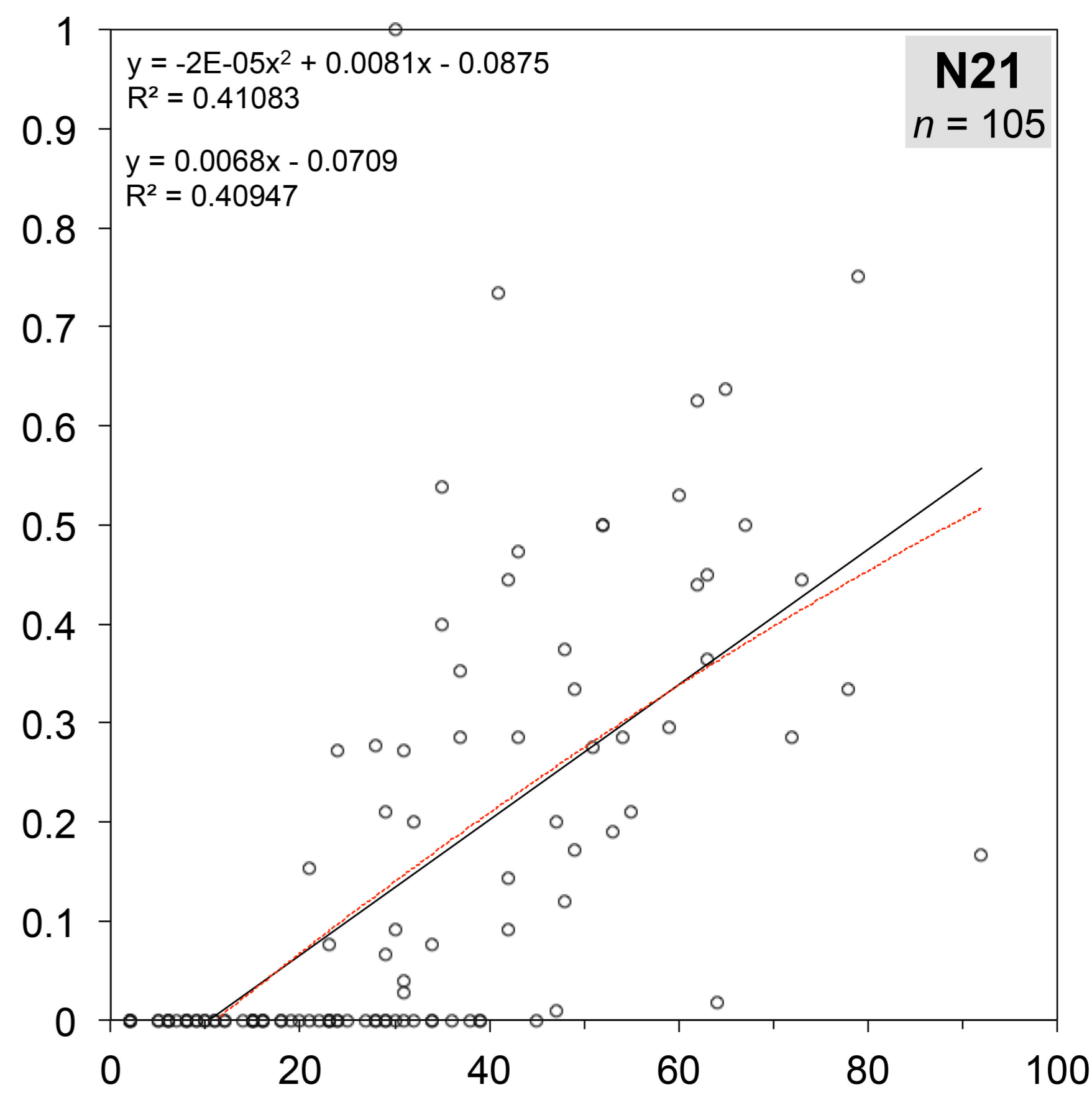
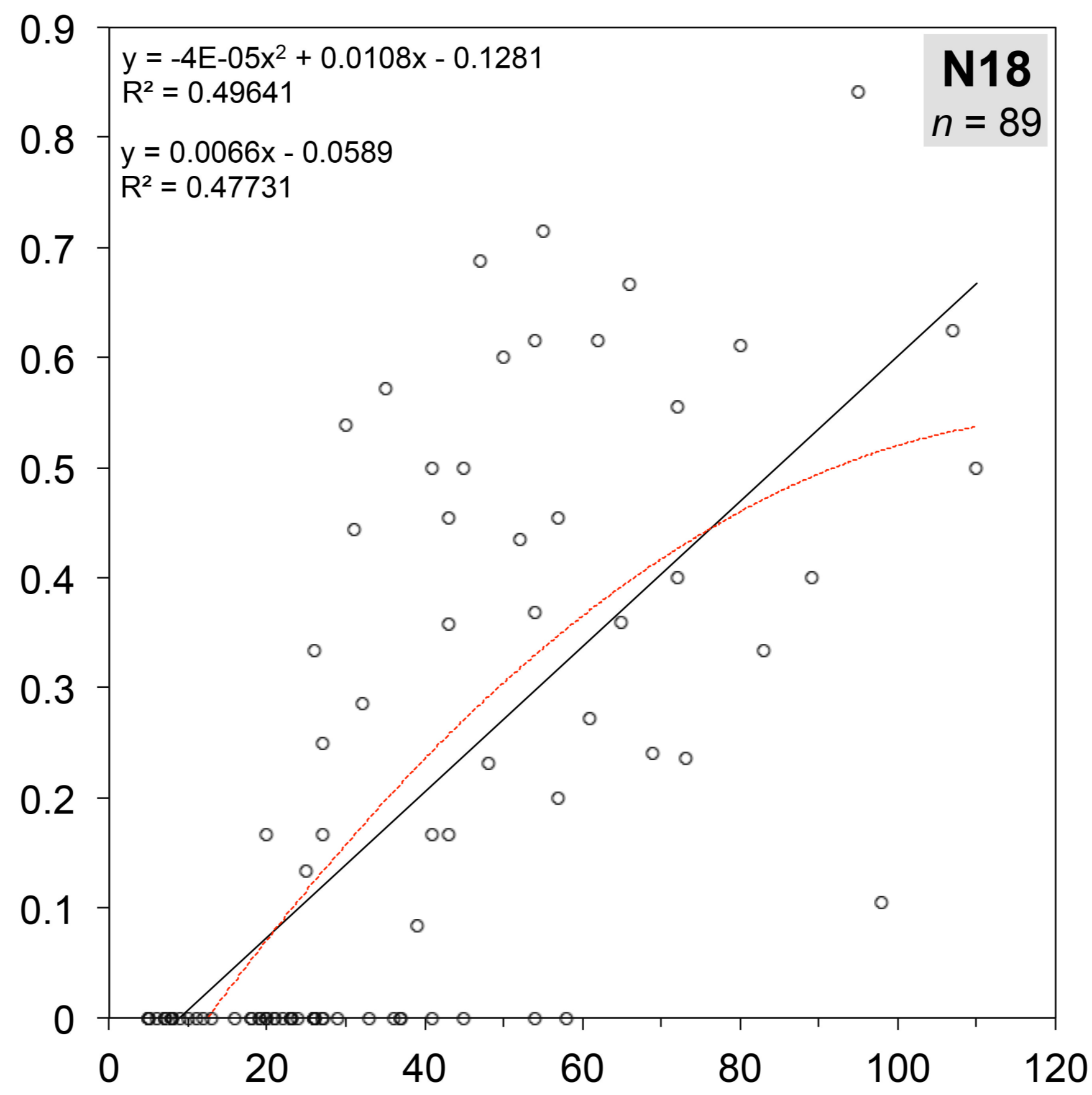
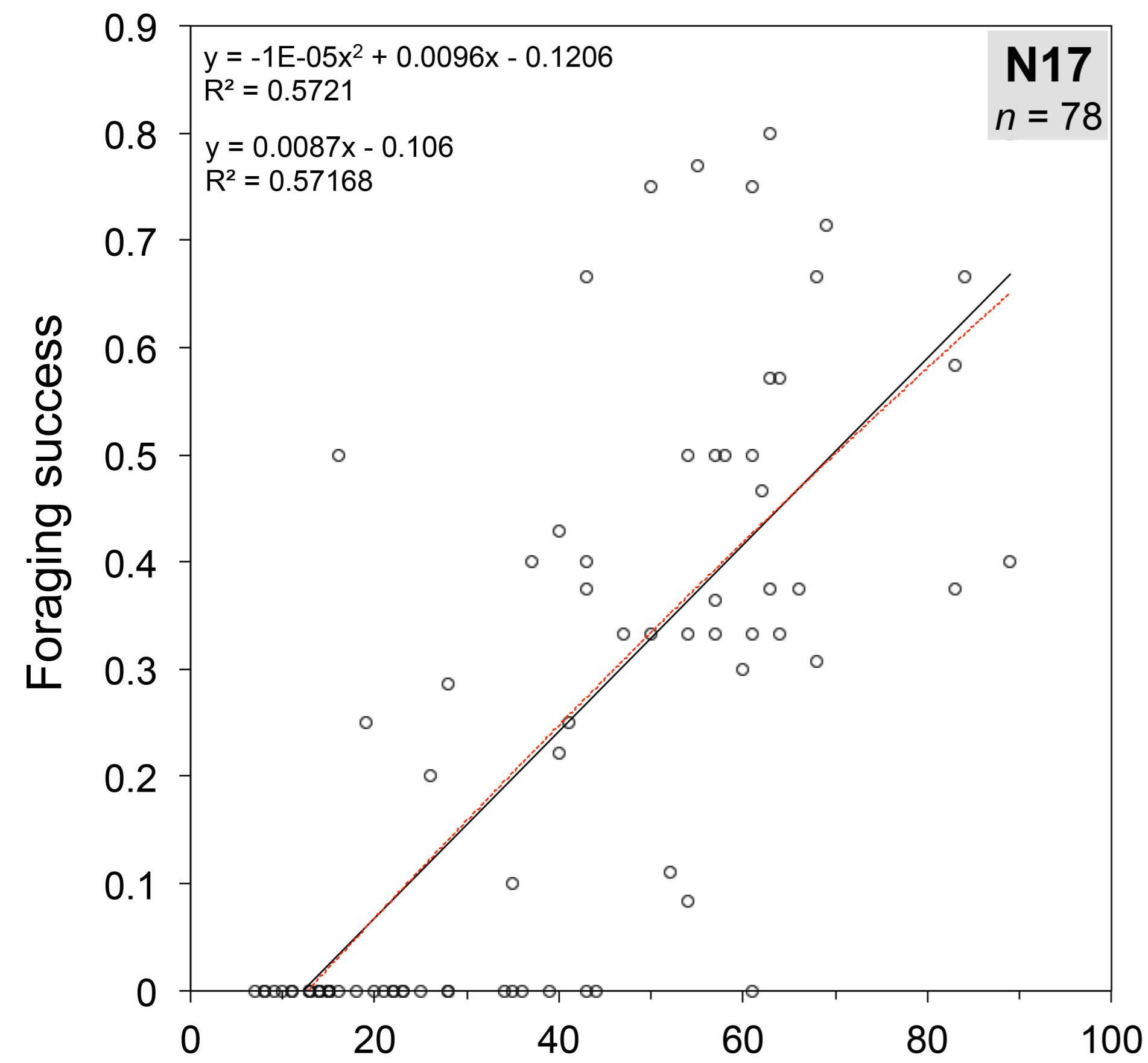
bioRxiv preprint doi: <https://doi.org/10.1101/272831>; this version posted February 28, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

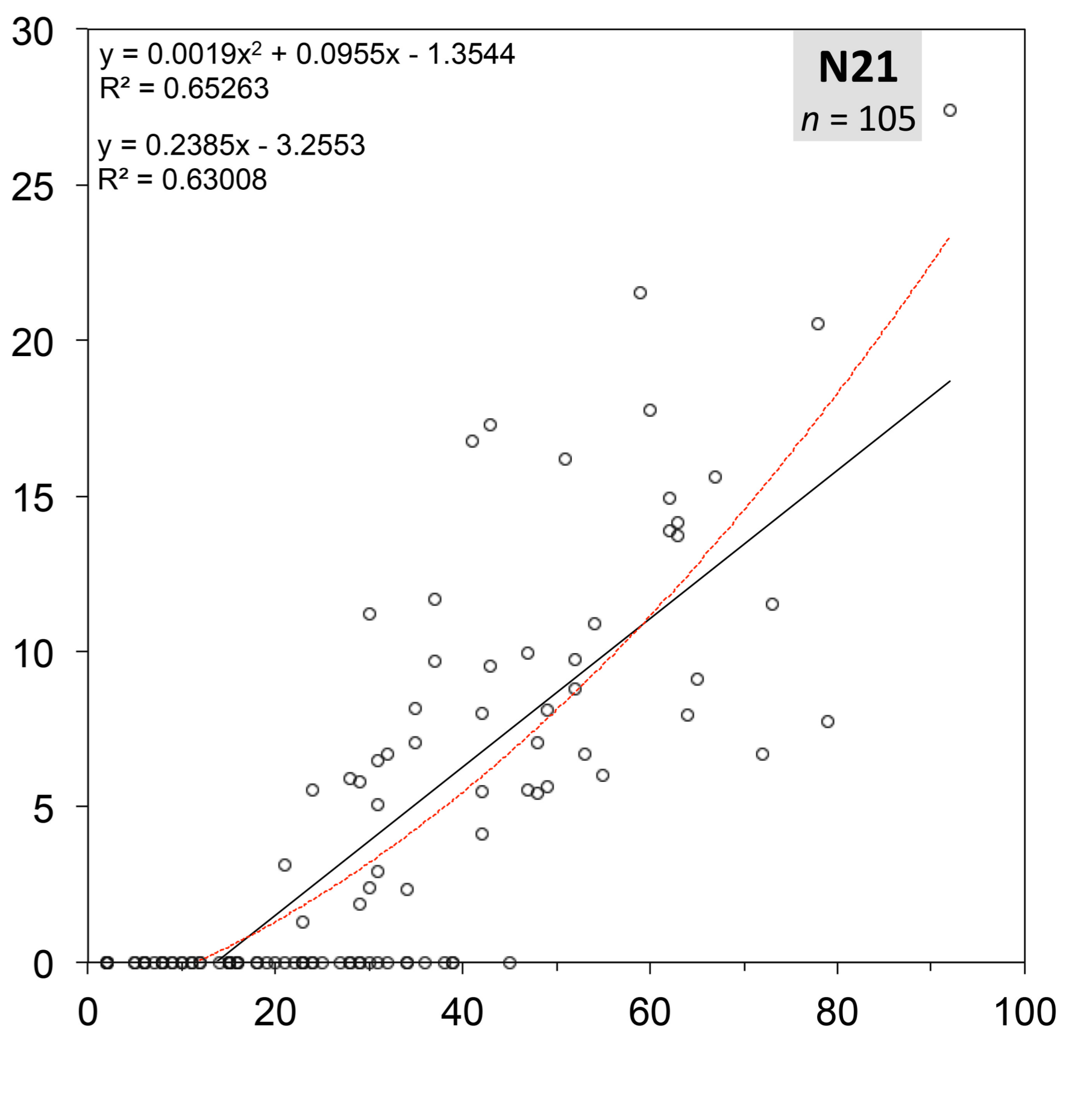
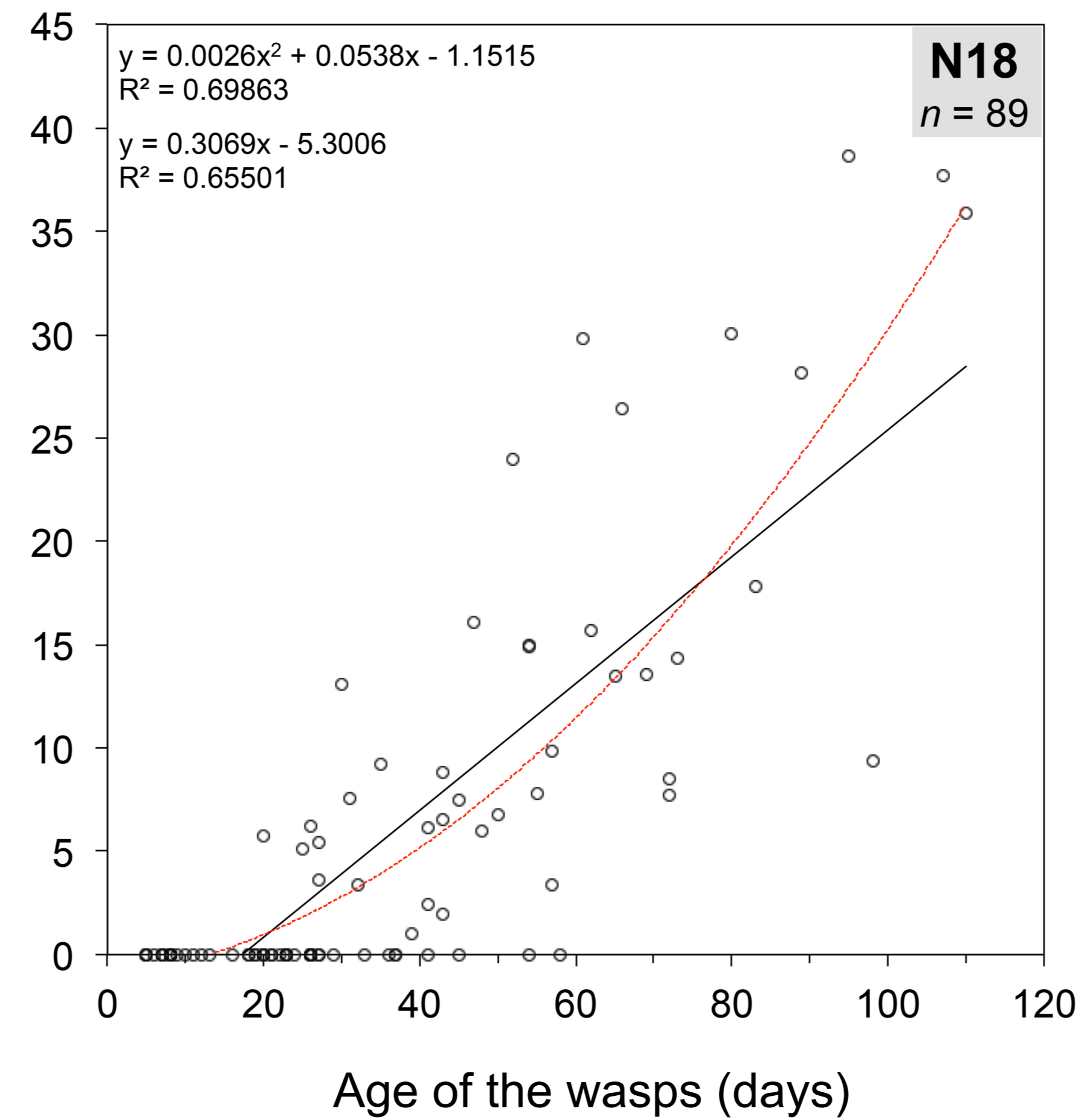
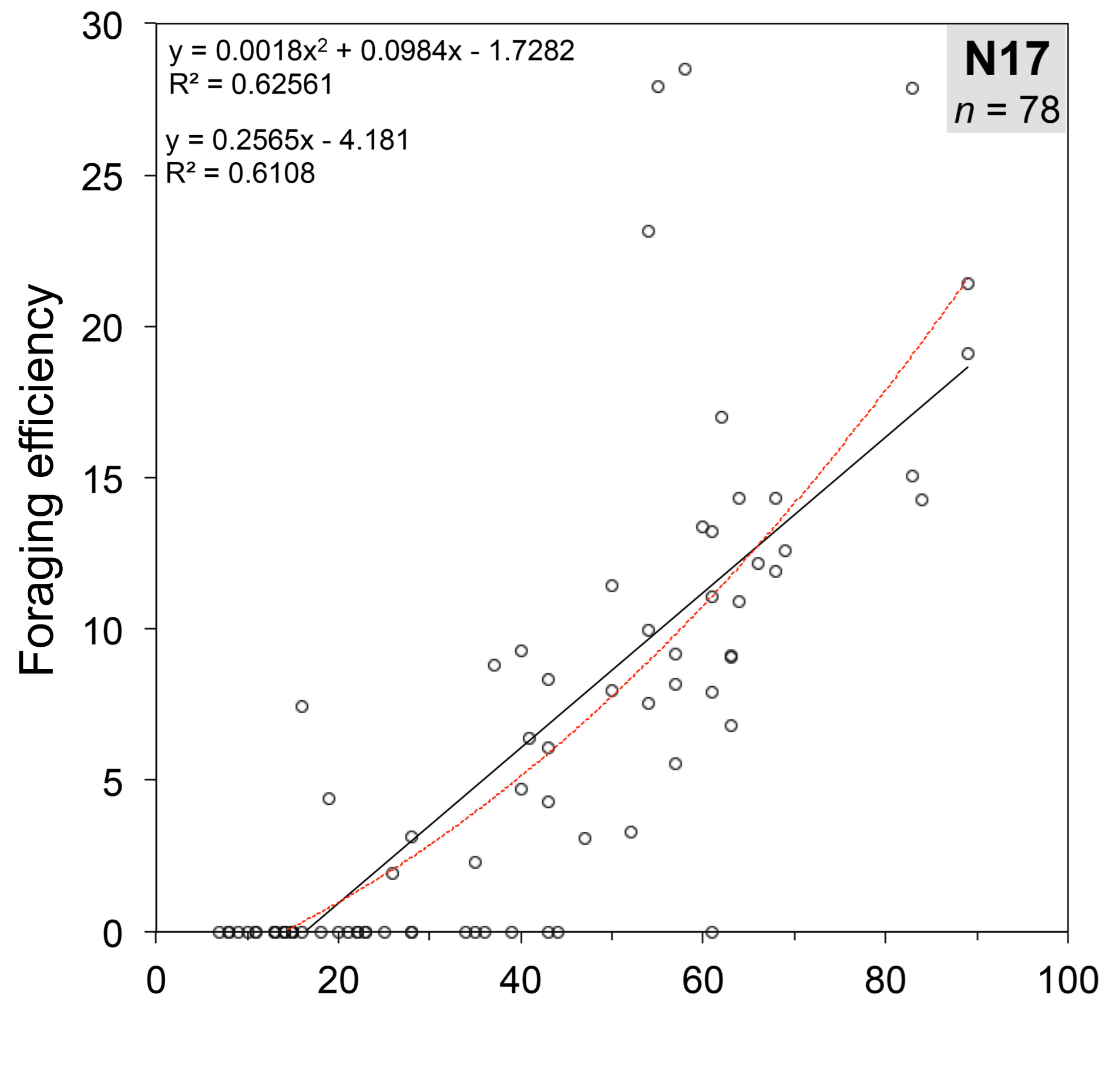




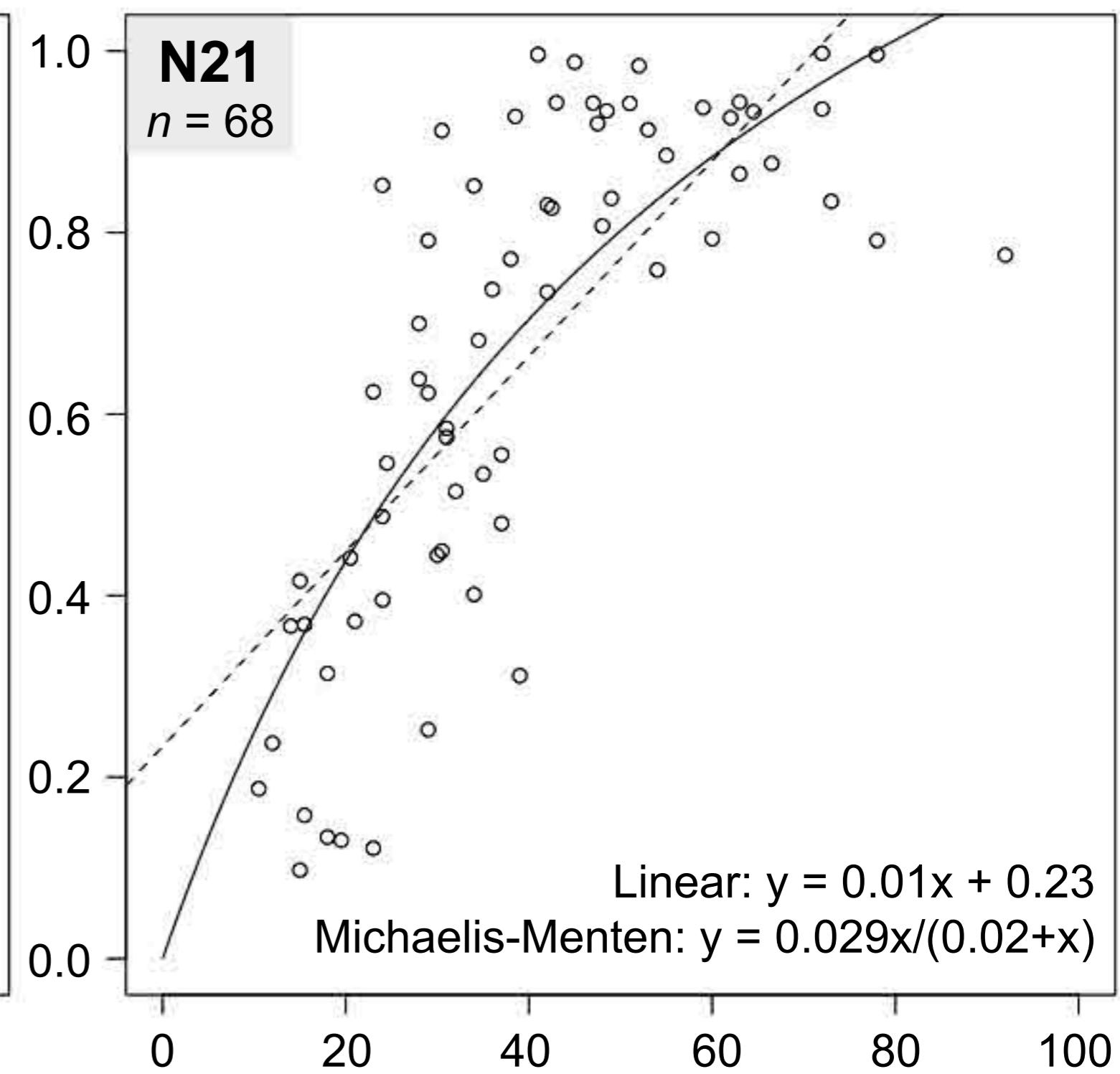
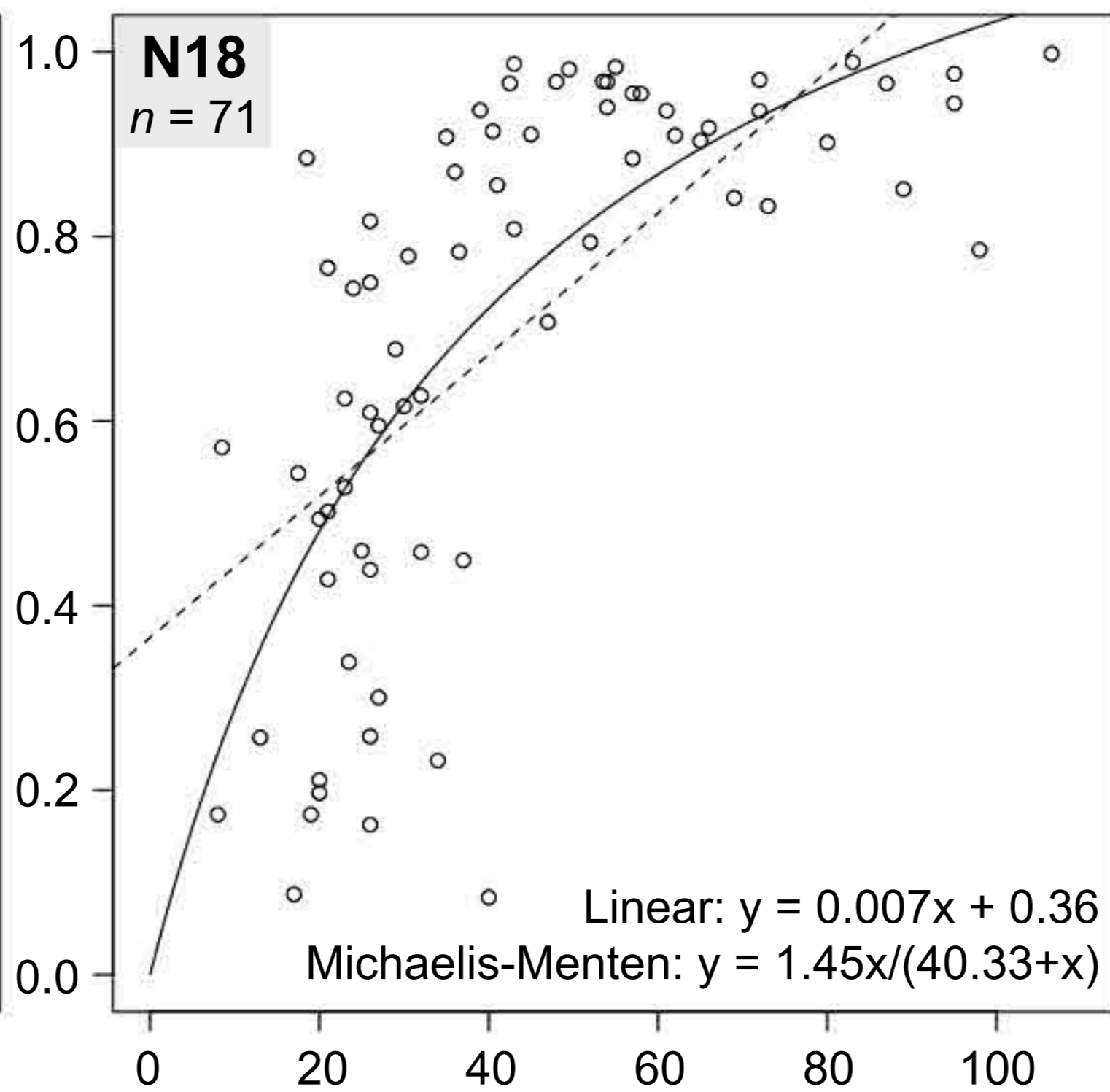
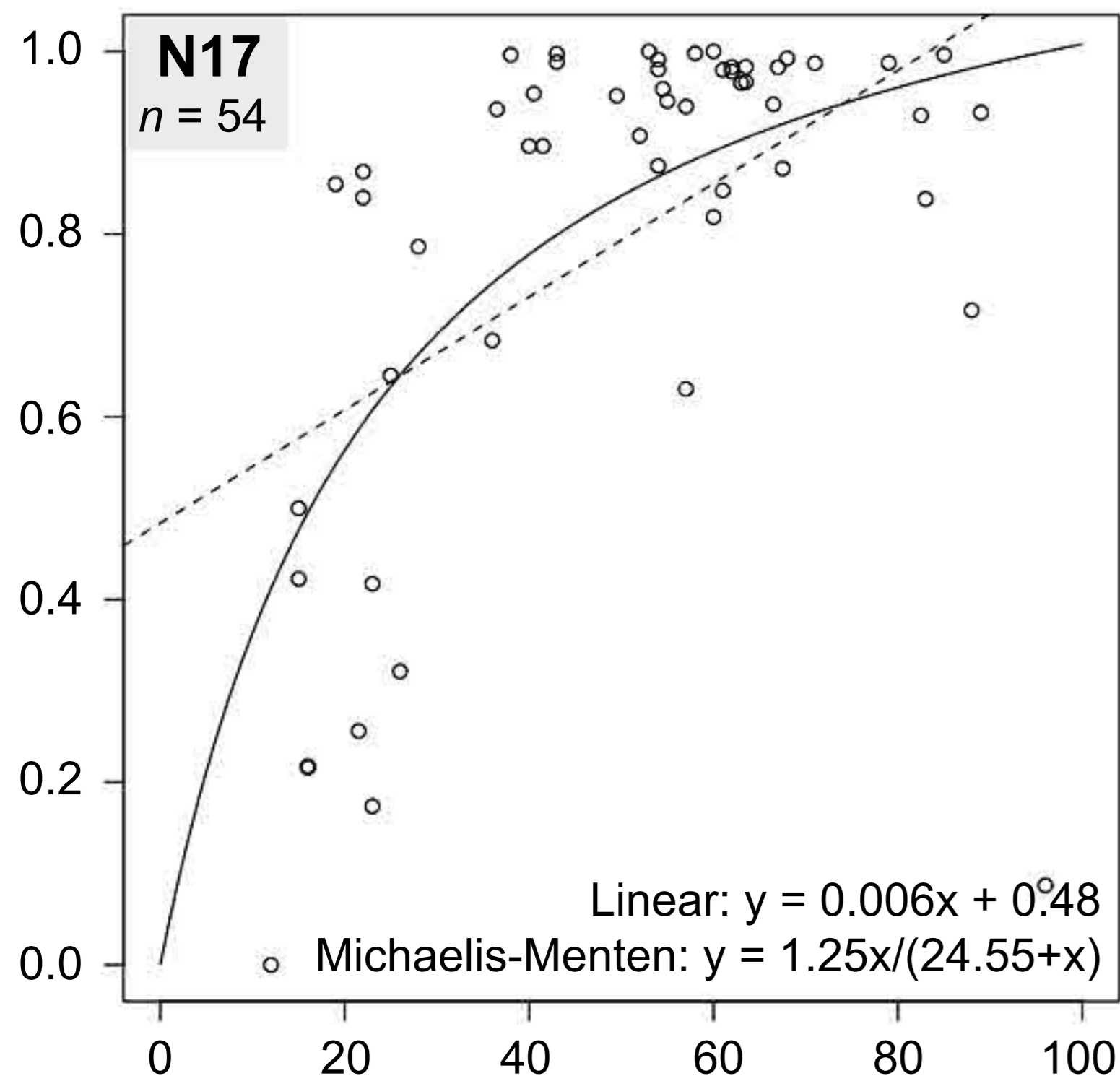
bioRxiv preprint doi: <https://doi.org/10.1101/272831>; this version posted February 28, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.





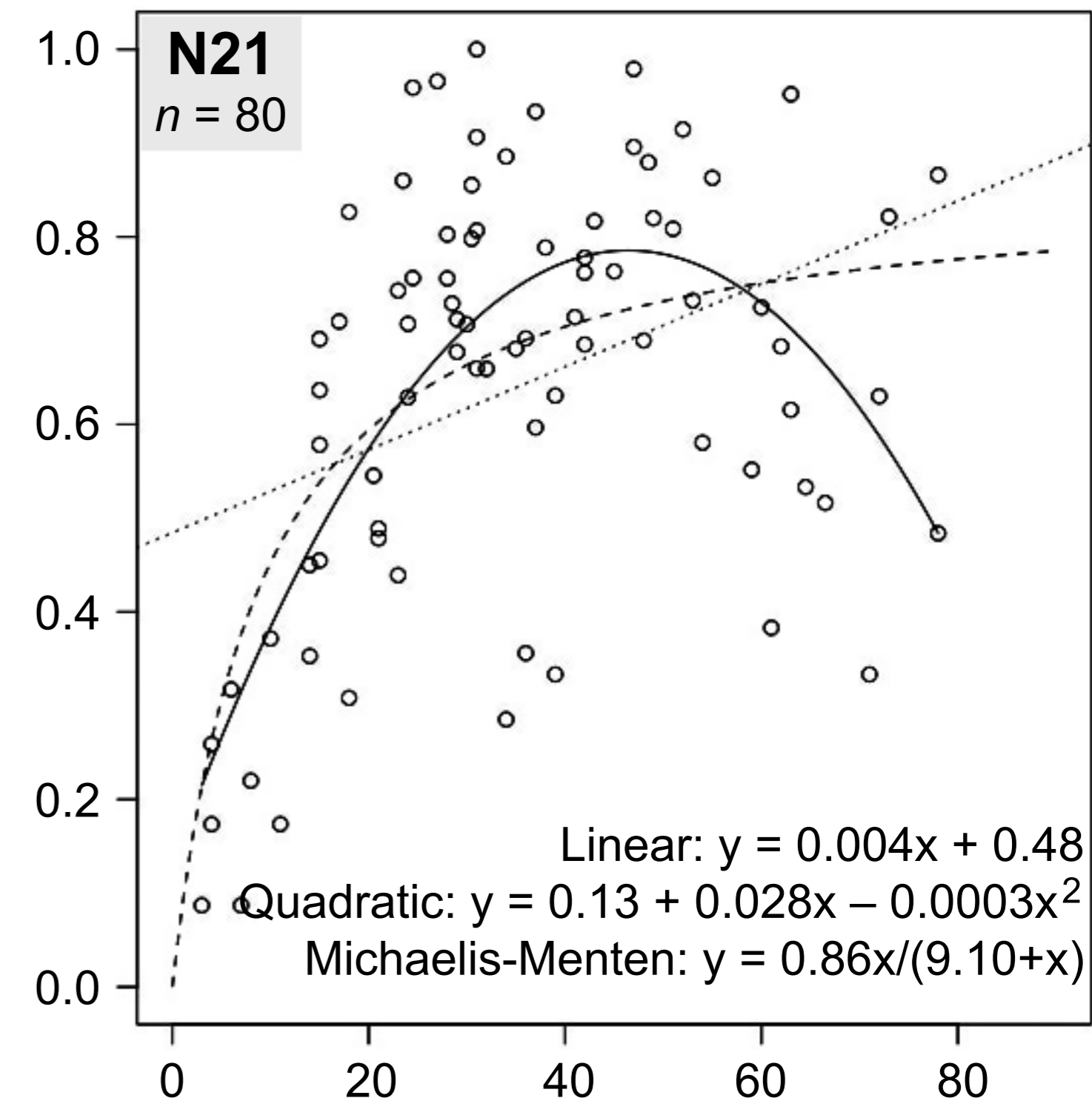
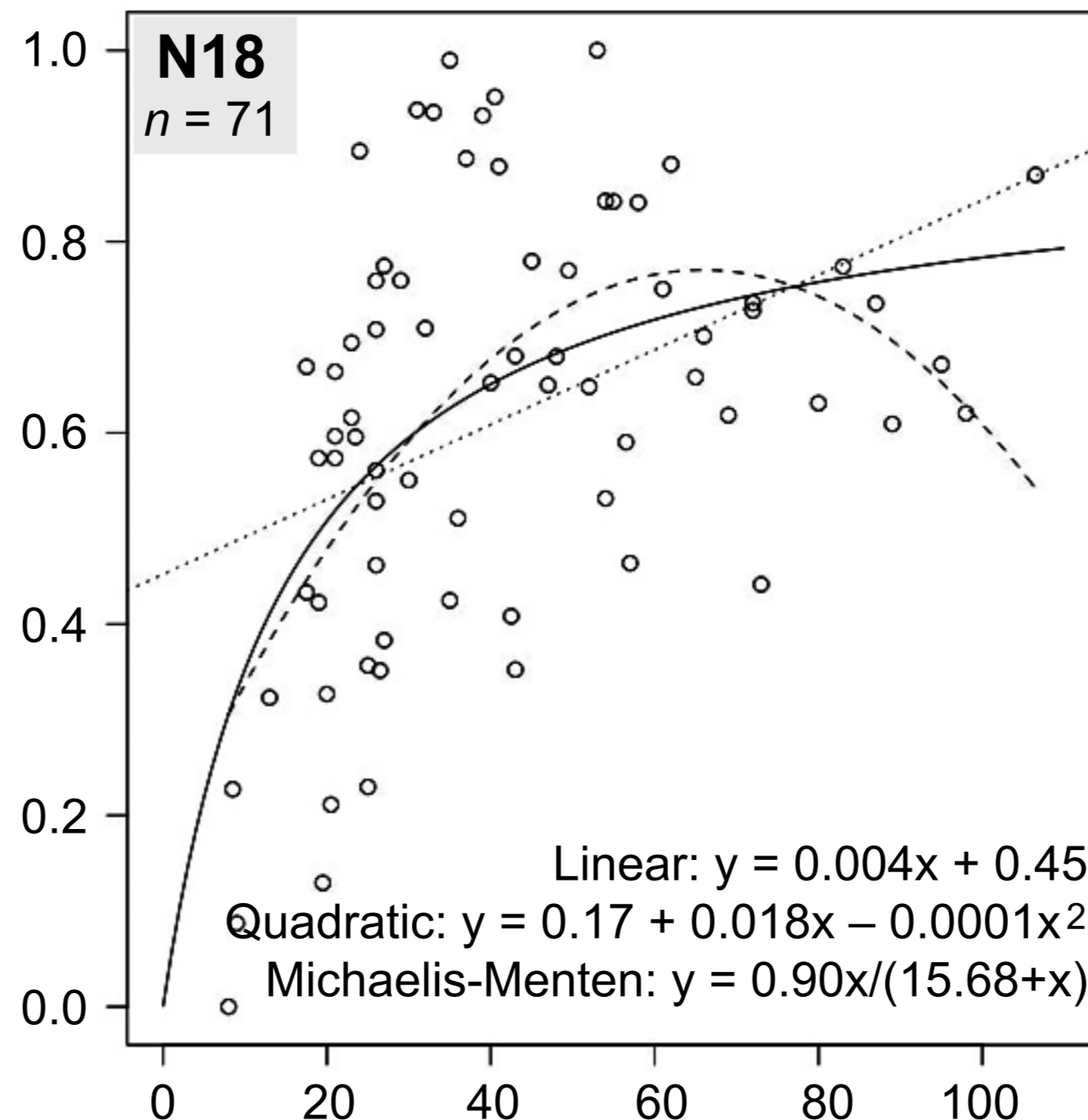
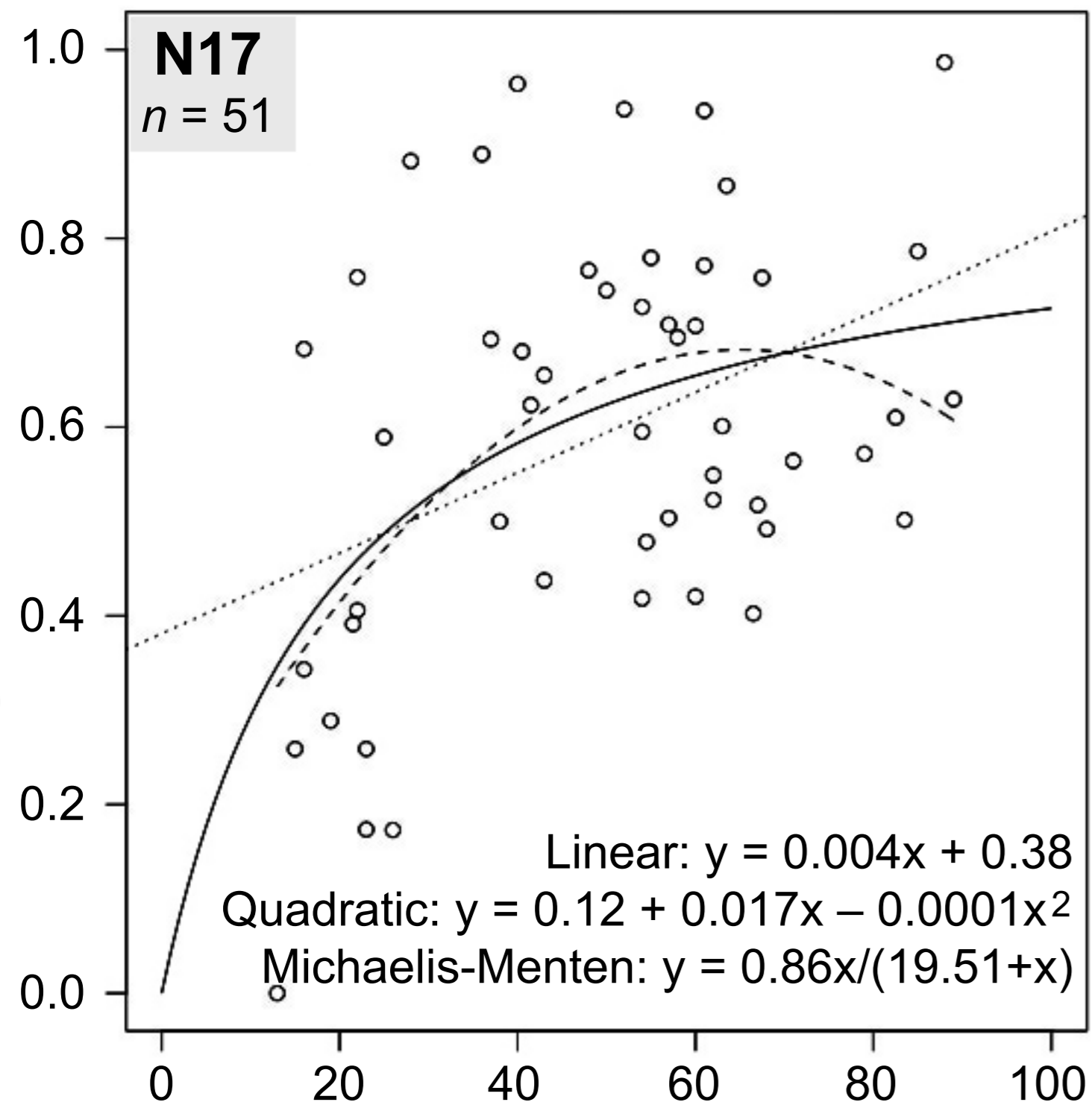


Average r of outbound trips



Age of the wasps (days)

Average r of inbound trips



Age of the wasps (days)