

1 **Effect of egg production dynamics on the functional response of parasitoids**

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21 **ABSTRACT**

22 Functional response describes the number of hosts attacked by a parasitoid in relation to  
23 host densities and plays an important role by connecting behavioral-level processes with  
24 community-level processes. Most functional response studies were carried out using simple  
25 experimental designs where the insects were confined to a plain and small arena with  
26 different host densities during a fixed period of time. With these designs, other factors that  
27 might affect the functional response of parasitoids were not analyzed, such as fecundity, age,  
28 and experience. We proposed a series of latent-variables Markovian models that comprised  
29 an integrated approach of functional response and egg production models to estimate the  
30 realized lifetime reproductive success of adult parasitoids. As a case study, we used the  
31 parasitoids *Anagyrus cachamai* and *A. lapachosus* (Hymenoptera: Encyrtidae), two  
32 candidate agents for neoclassical biocontrol of the Puerto Rican cactus pest mealybug,  
33 *Hypogeococcus* sp. (Hemiptera: Pseudococcidae). *Anagyrus cachamai* and *A. lapachosus*  
34 presented a type III functional response. However, the two parasitoids behaved differently:  
35 for *A. cachamai*, the number of parasitized hosts decreased with female age and depended  
36 on the number of mature eggs that were available for oviposition, whereas *A. lapachosus*  
37 host parasitism increased with female age and was modulated by its daily egg load and  
38 previous experience. The tested species were assessed according to their physiology and  
39 prior experience. We estimated the number of mature eggs after emergence, egg production  
40 on the first day, egg production rate, proportion of eggs resorbed, egg resorption threshold,  
41 and egg storage capacity. The methodology presented may have large applicability in pest  
42 control, invasive species management, and conservation biology, as it has the potential to  
43 increase our understanding of the reproductive biology of a wide variety of species, ultimately  
44 leading to improved management strategies.

45

## 46 **Introduction**

47 Functional response is one of the most commonly used mathematical frameworks to  
48 describe and estimate the number of hosts attacked by a parasitoid in relation to host  
49 densities [1,2], allowing the connection of behavioral-level processes with community-level  
50 processes. Identifying a parasitoid's response to changes in host-density is central to any  
51 description of parasitism because the number of hosts attacked determines development,  
52 reproduction, and survival of the parasitoid [3]. Applications of this mathematical framework  
53 are found in studies on pest control, invasive species management, and conservation biology  
54 [4].

55 Despite the abundance of functional response models [5], the most frequently used are  
56 Holling's type II and type III [1], describing a hyperbolic saturating curve and a sigmoid curve,  
57 respectively. Development of both functional response models requires only two parameters:  
58  $a$ , the attack rate, and  $H$ , handling time. The attack rate represents the efficiency of a  
59 parasitoid in locating hosts via different "areas of discovery" measured in various habitat  
60 complexities or experimental arena sizes, according to Rogers [6], or simply, efficiency in  
61 locating hosts, measured as the proportion of hosts found per time unit according to Holling  
62 [1]. Handling time,  $H$ , is the time that a parasitoid spends manipulating its hosts. According to  
63 Holling [1], its inverse is the asymptotic value of the functional response curve. Type III  
64 sigmoidal functional response curves represent situations where the parasitoid is assumed to  
65 switch between two or more host species as a result of host availability or learning [1,7], but  
66 can also represent an improved efficiency by learning even when only one host is present  
67 [8].

68 In simple terms, attack rate describes the space that a parasitoid seeks per unit of time,  
69 while handling time is associated with host processing. Functional response models assume  
70 continuous foraging by individuals, along with stationary behavioral and physiological

71 processes, when actually a plethora of biological processes are included under these two  
72 parameters [9,10]. Most parasitoid functional response studies are carried out using  
73 experimental designs where the insects are confined to a small arena with different host  
74 densities during a fixed time period ranging from 1 to 48 hours [11–16]. These experimental  
75 designs ignore factors related to parasitoid behavior that affect functional response, such as  
76 fecundity, age, and experience of the wasp [17–19]. Varone et al. [20], studying functional  
77 response throughout the entire female lifetime of the larval parasitoid *Campoletis grioti*  
78 Blanchard (Hymenoptera: Ichneumonidae), found that attack rate and handling time of the  
79 parasitoid varied throughout the female's lifespan, determined by the daily load of mature  
80 eggs.

81 Parasitoid wasps exhibit a wide spectrum of reproductive strategies that lead to  
82 variation in egg production dynamics. Egg load varies throughout the female's lifespan,  
83 responding to both individual physiological and environmental factors [21–25]. In this context,  
84 the number of eggs that a female lays during her lifetime is determined by the number of  
85 hosts that the female encounters, the number of mature eggs over the female's life span, and  
86 the behavior affecting the oviposition rate [26]. Since egg production is costly, selection  
87 should favor production strategies in which parasitoid females do not die before exhausting  
88 their egg complement (time limitation) or run out of eggs before all available hosts are used  
89 (egg limitation) [27]. Understanding ovarian dynamics is particularly relevant to describing the  
90 parasitoids' foraging behavior because the physiological status of the ovaries may determine,  
91 for example, the duration of the pre-reproductive period and the rate of oviposition.

92 Egg limitation is mediated by oviposition and ovarian production, which in turn is  
93 regulated by two processes: egg maturation and egg resorption [28]. Parasitoid longevity  
94 influences the extent to which parasitoid becomes time-limited. To maximize longevity in the  
95 field, many parasitoids require a carbohydrate source such as nectar, hemipteran honeydew,

96 or they might feed directly on their hosts [29,30]. However, the variability in nutrient income  
97 caused by the use of external stochastic sources of nutrients can entail great risks of  
98 starvation. Egg resorption acts as an insurance against stochasticity, but it is considered as a  
99 “last-resort” strategy given the relatively low energy content of an egg [31,32]. What  
100 distinguishes resorption from other sources of nutrients is its controllable nature, since the  
101 reserves contained in the eggs are made readily available to the female when they are most  
102 needed.

103 For over 80 years, researchers have proposed different models to determine if the  
104 realized lifetime reproductive success of adult female parasitoids was limited by the finite  
105 amount of time available to locate hosts that serve as oviposition sites [33–37], or by the  
106 finite supply of mature eggs [38,39]. Rosenheim [40], using models to explore how  
107 stochasticity influences the evolution of egg limitation in insects, found that both egg and time  
108 limitations are fundamental in shaping insect reproductive behavior and population dynamics.  
109 These results underscore the importance of developing models of insect reproduction and  
110 population dynamics that incorporate the constraints imposed by both egg and time  
111 limitation, rather than just one constraint or the other.

112 In this study, we proposed a series of latent-variables Markovian models that  
113 comprised an integrated approach of functional response and egg production models to  
114 estimate the realized lifetime reproductive success of adult parasitoids. As a case study, we  
115 used the parasitoids *Anagyrus cachamai* Triapitsyn, Logarzo & Aguirre and *A. lapachosus*  
116 Triapitsyn, Aguirre & Logarzo (Hymenoptera: Encyrtidae), promising candidates for the  
117 neoclassical biological control of the mealybug *Hypogeococcus* sp. (Hemiptera:  
118 Pseudococcidae), a pest of native cacti in Puerto Rico [41–43]. Both parasitoid species are  
119 synovigenic wasps that do not engage in host feeding, but each presents differences in their  
120 reproductive biology (egg load at birth, ovigeny index and sex ratio) [42]. Each parasitoid

121 species was evaluated employing a dynamic variant of the most common functional  
122 response models (e.g., [1,44]), which included population parameters related to the  
123 parasitoids' fecundity (egg resorption and daily egg load, limited by egg load capacity and  
124 daily egg production), and the age of the female parasitoid. Unlike the techniques used in  
125 previous classical methods, we worked on the entire parasitoid lifetime and incorporated  
126 physiological processes related to egg load into our evaluation of parasitism efficiency. This  
127 technique will provide a more accurate estimation between the two tested parasitoid species  
128 according to their physiology and prior experiences.

129

## 130 **Materials and Methods**

131 The studies were conducted at the Fundación para el Estudio de Especies Invasivas  
132 (FuEDEI), located in Hurlingham, Buenos Aires, Argentina, between January 2014 and  
133 December 2016. All experiments and insect rearing were carried out in environmental-  
134 controlled chambers ( $25 \pm 1^\circ\text{C}$ , 16:8 L:D, 60–80% RH). All observations were conducted  
135 under a dissecting microscope at 40X.

136

## 137 **Parasitoid rearing**

138 Laboratory experiments were conducted with colonies of *A. cachamai* and *A. lapachosus*  
139 reared at FuEDEI since 2014 following the methodology described in Aguirre et al. [42]. Each  
140 primary parasitoid species was reared on first instar nymphs of *Hypogeococcus* sp.  
141 "*Cactaceae* host-clade" [45], a congener but a different species from the mealybug pest of  
142 cacti in Puerto Rico [43]. Pure mealybug colonies were reared without parasitoids on clean  
143 potted plants of *Cleistocactus baumannii* (Lem.) Lem. (Cactaceae).

144 Colonies of *A. cachamai* and *A. lapachosus* were reared in separate rooms. Four  
145 mated females of each wasp species were placed in a plastic cage (2 L) with a 6 cm

146 diameter hole cut in the lid and covered with polyester gauze for ventilation. The cage  
147 contained a piece of *C. baumannii* (20-25 cm long) infested with about 100 nymphs of  
148 *Hypogeococcus* sp. “*Cactaceae host-clade*”. After 72 hours, the four female parasitoids were  
149 removed from the plastic cage, and the parasitoid-exposed nymphs were monitored every  
150 three days. After the first parasitoid pupa was detected, monitoring was conducted daily, and  
151 all parasitoid pupae found were transferred to a Petri dish (1.5 cm high x 5.5 cm diameter)  
152 covered with plastic food wrap to keep wasps from escaping after emergence. Using this  
153 process, the wasps’ age, feeding conditions, and mating were controlled. As the parasitoids  
154 emerged, they were placed in a new Petri dish of equal dimensions with a squashed drop of  
155 honey on the bottom, and covered with clear plastic food wrap, to be used either for rearing  
156 or experimental purposes. The age of the female parasitoids for the experiments was 24  
157 hours old; they were fed, mated, and had no previous oviposition experience. Throughout the  
158 paper, the mention of *Hypogeococcus* sp. nymphs exposed to female parasitoids refers to  
159 first instar nymphs of *Hypogeococcus* sp. “*Cactaceae host-clade*” on 20-25 cm long pieces of  
160 *C. baumannii*.

161

## 162 **Functional response experiments**

163 To estimate the functional response of the parasitoids *A. cachamai* and *A. lapachosus*, a  
164 constant daily density of non-parasitized *Hypogeococcus* sp. nymphs was exposed to a  
165 female parasitoid once she was 24 hours old and until her death [20]. The daily number of  
166 parasitized nymphs was estimated for each female by recording the number of emerged  
167 parasitoids relative to the number of nymphs offered. Six nymph densities were evaluated:  
168 10, 20, 40, 60, 80 and 110, with 5 replications per density, and a maximum error of 10% in  
169 the daily number of nymphs per density offered. The densities selected in this study were  
170 based on the results of a pilot test, where densities of 80 and 110 nymphs produced a

171 plateau in the curve of the number of nymphs attacked as a function of the host density  
172 offered.

173 The experiments were conducted in vented plastic cages similar to the one described  
174 above for parasitoid rearing. To ensure that the daily number of non-parasitized nymphs  
175 available to each wasp was constant, the cactus piece with the nymphs exposed to the wasp  
176 was removed every 24 hours from the experimental arena and replaced by another piece of  
177 cactus with an equal number of nymphs not previously exposed to a parasitoid. Each cactus  
178 piece with the parasitoid-exposed nymphs was held individually in a similar plastic cage. All  
179 exposed nymphs were checked every three days and the number of emerged parasitoids  
180 counted until all non-parasitized nymphs completed their development and all wasps had  
181 emerged from parasitized nymphs.

182

## 183 **Data analyses**

### 184 ***Description of models***

185 The outcome of the functional response experiments was analyzed with a series of latent-  
186 variables Markovian models that comprised an integrated approach of functional response  
187 and egg production models. Each model was summarized in a single equation that  
188 integrated two modules, one represented a functional response equation and another an  
189 equation of egg production:

$$190 \quad p(n,t) = \begin{cases} f(n), & \text{if } e(t) > f(n) \\ e(t), & \text{otherwise} \end{cases}$$

191 where  $f(n)$  represents the functional response equation,  $e(t)$  the egg production equation,  
192 and  $p(n,t)$  the model that describes the number of eggs laid by a wasp. If the number of  
193 eggs that a female has available is greater than the number of eggs that can be oviposited  
194 according to the functional response module, then the number of hosts attacked is predicted



195 by the functional response equation. If the females' egg load is less than the number of hosts  
196 available, she simply lays all the eggs she has. Using this basic structure, the proposed  
197 models are the combination of one of the six functional response equations of the functional  
198 response module with one of the eight egg production equations of the egg production  
199 module. This resulted in a matrix of 48 possible models, all of which were tested. Both  
200 modules are briefly described below.

201

#### 202 Functional response module

203 The six equations tested in the functional response module were based on type I, type II, and  
204 two type III generalized functional responses [1,8,44,46–48]. For each of the type III  
205 generalized functional response equations, an additional version where the female gains  
206 experience in the course of her life when interacting with the host was also proposed. See  
207 the appendix section in the supporting information for details on the six equations tested (S1  
208 File, Functional response module).

209

#### 210 Egg production module

211 Eight egg production equations were proposed and tested. The simplest equation considers  
212 that the female has unlimited egg production. The equation with the next level of complexity  
213 assumes that the female is strictly pro-ovigenic and therefore all of its oocytes are mature  
214 upon emergence. The remaining six equations describe the behavior of synovigenic females,  
215 meaning, females that emerge with few or no mature eggs but continue to mature eggs  
216 throughout their lifetime. The most complex synovigenic-based model includes parameters  
217 related to egg resorption and daily egg load, limited by egg load capacity and daily egg  
218 production. The eight egg production equations proposed for testing within the egg

219 production module are presented in the appendix section in supporting information (S1 File,  
220 Egg production module).

221

### 222 ***Model fitting and selection***

223 We used a fully Bayesian approach and the Metropolis-Hastings algorithm [49,50] in order to  
224 select the best explaining models (out of the 48 models proposed) and to calculate their  
225 parameters. Traditionally, statistical analysis of the functional response experiments is  
226 carried out by selecting the functional response model by a logistic regression thereby  
227 reducing the problem of differentiating between a hyperbolic curve (type II functional  
228 response) and a sigmoid curve (type III functional response). The use of a non-linear  
229 regression in a frequentist framework is then recommended to estimate the parameters of  
230 the curve [51]. Since this approach is not appropriate for selecting several models that  
231 compete with one another, Johnson and Omland [52] proposed the use of the Bayesian  
232 system. In this work, the selection of models and the estimation of parameter distribution  
233 were conducted in a Bayesian framework. The results of the analysis enabled us to infer with  
234 which models and parameters it is possible to explain the results of the laboratory  
235 experiments and their statistical distributions.

236 The Deviation Information Criterion (DIC) index was used as the decision rule for  
237 model selection [53]. The models that presented lower DIC were selected according to  
238 Gelman et al. [54], as a balance of the explanatory power (in terms of the likelihood function)  
239 and complexity (in terms of number of parameters). It is necessary to obtain DIC values that  
240 have a difference greater than 5 among the different models in order to select one model  
241 over other models. If DIC values among the different models are not greater than 5, then  
242 model averaging is required following Burnham and Anderson [55]. A total of 200,000  
243 iterations were used to fit the models; the first 100,000 were discarded as a “burn-in” for

244 model selection, and the remaining iterations were used to calculate the parameters of each  
245 model and the information indexes. The *a priori* distribution of the parameters of the  
246 functional response curves were normal distributions with a mean of 0 and a variance equal  
247 to 100, or uniform distributions defined between the minimum and the maximum value that  
248 each parameter can obtain. In some parameters, such as handling time ( $H$ ), attack rate of  
249 the female when she emerges ( $b$ ), the number of mature eggs when a female emerges ( $h_0$ ),  
250 egg resorption threshold ( $u$ ), and egg storage capacity ( $C$ ), the values were restricted to be  
251 positive, since negative values would not make biological sense. Since the variables  
252 obtained (number of parasitized hosts) are discrete and bounded, the binomial likelihood  
253 function was used [54]. Finally, fitness of each of the selected models to the data of the  
254 experiments was calculated by using the generalized coefficient of determination (GCD) for  
255 binary data, according to Cox and Snell [56] and Magee [57].

256       The analyses were carried out by using a Parasitoid-Egg model version 0.02 [58] for  
257 the parasitoid model, and PyMC version 2.3.7 for Monte Carlo methods [59] for parameter  
258 calculation and fitting.

259

## 260 **Results**

261 From the 48 models proposed to explain the pattern observed in the functional response  
262 experiments conducted with the parasitoids *A. cachamai* and *A. lapachosus* (Figs 1 and 2),  
263 four models were selected for each species (S1 Table). In both encyrtid species, the  
264 difference observed in the DIC values of the selected models was lower than 5;  
265 consequently, it was not possible to select a unique model for each species. *Anagyrus*  
266 *cachamai* and *A. lapachosus* females presented a type III functional response, but they used  
267 different strategies to exploit their host, *Hypogeococcus* sp. nymphs. On the other hand,

268 although both species are synovigenic, females showed differences in their pattern of egg  
269 production though their lifetime.

270

271

272 **Fig 1. Observed functional response of *Anagyrus cachamai* females at different ages**

273 **(days) of their lifespan (1-11 days) represented as the total number of nymphs**

274 **parasitized relative to the total number of *Hypogeococcus* sp. nymphs offered.** Six

275 nymph densities were evaluated: 10, 20, 40, 60, 80 and 110, with 5 replications per density,

276 and a maximum error of 10% in the number of nymphs per density offered.

277

278

279 **Fig 2. Observed functional response of *Anagyrus lapachosus* females at different ages**

280 **(days) of their lifespan (1-12 days) represented as the total number of nymphs**

281 **parasitized relative to the total number of *Hypogeococcus* sp. nymphs offered.** Six

282 nymph densities were evaluated: 10, 20, 40, 60, 80 and 110, with 5 replications per density,

283 and a maximum error of 10% in the number of nymphs per density offered.

284

285 The following models were selected for the parasitoid *A. cachamai*:  $C5$  (DIC =

286 1933.43),  $E5$  (DIC = 1932.39),  $C7$  (DIC = 1933.38) and  $E7$  (DIC = 1935.21) (S1 Table); and

287 their explanatory power in terms of GCD was  $GCD_{C5} = 0.85$ ,  $GCD_{E5} = 0.85$ ,  $GCD_{C7} = 0.85$ , and

288  $GCD_{E7} = 0.86$ , respectively. The four integrated models selected comprised between 8-9

289 parameters. When the components of the four selected models were analyzed in terms of

290 functional response, two type III functional response equations were selected (Table 1, Fig

291 3A and 3B). In those models where equation C of the functional response module was

292 selected, the attack rate increased linearly with the number of hosts offered. Emerged female

293 attack rate was  $0.073 \pm 0.015 \text{ days}^{-1}$  ( $b$ ), the attack rate change was  $0.003 \pm 0.000 \text{ days}^{-1}$  ( $a$ ),  
294 and the handling time was  $0.005 \pm 0.001 \text{ days}$  ( $H$ ). In the models where the equation  $E$  of  
295 the functional response module was selected, the attack rate changed with host densities as  
296  $an^s$ , where  $a = 0.018 \pm 0.005 \text{ days}^{-1}$ ,  $s = 1.676 \pm 0.063$  and  $H = 0.005 \pm 0.001 \text{ days}$ . In  
297 reference to the egg production module, two equations were selected; equation 5 and  
298 equation 7. *Anagyrus cachamai* females emerged with  $56 \pm 2$  mature eggs ( $e$ ), and lived on  
299 average  $4 \pm 2$  days (range 2-11 days). During the first day of life, a female produced  $8 \pm 1$   
300 eggs ( $h_0$ ), and the daily egg production rate was  $0.972 \pm 0.036$  ( $g$ ). Eggs that were not used  
301 on day  $t$ , were resorbed on day  $t + 1$ , providing the number of accumulated eggs from one  
302 day to another was greater than  $19 \pm 1$  eggs ( $u$ ). When resorption existed, the proportion of  
303 eggs resorbed was  $0.677 \pm 0.045$ . In equation 7, females also presented an egg storage  
304 capacity of  $58 \pm 2$  eggs ( $C$ ). The four integrated models selected are detailed in S2 Table and  
305 represented in S1-S4 Figs.

306 **Table 1. A posteriori mean  $\pm$  standard deviation of the species-specific parameters of the selected models for two**  
 307 **parasitoids, *Anagyrus cachamai* and *A. lapachosus*, attacking *Hypogeococcus* sp.** The values presented are the result of  
 308 weighing the models selected for *A. cachamai* and *A. lapachosus* females (see the supporting information for details on the models  
 309 selected: S1-S3 Tables).

	Functional response module parameters								
	Without female experience						With female experience		
	FR III (attack rate increased linearly with the available host number [46,47])			FR III (the attack rate changed with host densities as $\alpha n^s$ [44])			FR III (attack rate increased linearly with the available host number [46,47])		
	Attack rate after emergence at $n=0$ ( $b$ )	Attack rate change ( $a$ )	Handling time ( $H$ )	Attack rate change ( $a$ )	Exponent $s$ ( $1+q$ )	Handling time ( $H$ )	Attack rate after emergence at $n=0$ ( $b$ )	Attack rate change ( $a$ )	Handling time ( $H$ )
<i>A. cachamai</i>	0.073 $\pm$ 0.015 $d^{-1}$	0.003 $\pm$ 0.000 $d^{-1}$	0.005 $\pm$ 0.001 $d$	0.018 $\pm$ 0.005 $d^{-1}$	1.676 $\pm$ 0.063 $d^{-1}$	0.005 $\pm$ 0.001 $d$	-	-	-
<i>A. lapachosus</i>	-	-	-	-	-	-	0.109 $\pm$ 0.010 $d^{-1}$	0.001 $\pm$ 0.000 $d^{-1}$	0.004 $\pm$ 0.001 $d$
	Egg production module parameters								
	No. mature eggs after emergence ( $e$ )	Egg prod. on the first day ( $h_0$ )	Egg production rate ( $g$ )	Proportion of eggs resorbed ( $r$ )	Egg resorption threshold ( $u$ )	Egg storage capacity ( $C$ )			
<i>A. cachamai</i>	56 $\pm$ 2	8 $\pm$ 1	0.972 $\pm$ 0.036	0.677 $\pm$ 0.045	19 $\pm$ 1	58 $\pm$ 2			
<i>A. lapachosus</i>	57 $\pm$ 2	11 $\pm$ 1	1.330 $\pm$ 0.024	0.935 $\pm$ 0.028	15 $\pm$ 1	59 $\pm$ 2			

310 Parameters reported for the egg production term are averaged considering all the iterations with the functional response type III  
 311 without female experience in the case of the species *A. cachamai* or with experience for *A. lapachosus*. On the other hand, the  
 312 functional response parameters were not mixed because the values and their behavior were slightly different depending on the kind  
 313 of model selected. Physical units of the calculated parameters:  $d$  is days, parameters without units are dimensionless.

314 **Fig 3. Estimated type III functional response of *Anagyrus cachamai* females at**  
315 **different ages (days) of their lifespan (1-11 days) considering limited egg production.**

316 (A) Equation C of functional response module; the attack rate increases linearly with the  
317 number of hosts available [46,47]; (B) Equation E of functional response module; the attack  
318 rate changes with host densities as  $an^s$  [44].

319

320 The models selected for the species *A. lapachosus* were  $D4$  (DIC = 2974.66),  $D5$  (DIC  
321 = 2973.60),  $D6$  (DIC = 2976.63), and  $D7$  (DIC = 2975.19); and their explanatory power in  
322 terms of GCD was  $GCD_{D4} = 0.86$ ,  $GCD_{D5} = 0.86$ ,  $GCD_{D6} = 0.86$ , and  $GCD_{D7} = 0.86$ ,  
323 respectively. The number of parameters of the four models selected ranged between 7-9. For  
324 the functional response module, equation  $D$  was selected which assumes that the female  
325 has a type III functional response and that the efficiency increases linearly with the number of  
326 hosts offered during the females' life. This meant a daily increase in the attack rate of *A.*  
327 *lapachosus* females (Table 1, Fig 4). Emerging female attack rate was  $0.109 \pm 0.010$  days<sup>-1</sup>  
328 ( $b$ ), the daily attack rate change was  $0.001 \pm 0.000$  days<sup>-1</sup> ( $a$ ), and the handling time was  
329  $0.004 \pm 0.001$  days ( $H$ ). Regarding the egg production module, four egg production  
330 equations were selected: 4, 5, 6 and 7. *Anagyrus lapachosus* females lived on average  $5 \pm 3$   
331 days (range 2-12 days), and emerged with  $57 \pm 2$  mature eggs ( $e$ ). After emerging, a female  
332 produced  $11 \pm 1$  eggs ( $h_0$ ) and the daily egg production rate was  $1.330 \pm 0.024$  ( $g$ ). Eggs  
333 that were not used on day  $t$ , were resorbed the next day in a proportion of  $0.935 \pm 0.028$  ( $r$ ).  
334 In the case of equations 5 and 7, for resorption to exist, the number of remaining eggs from  
335 one day to another had to exceed a threshold of  $15 \pm 1$  eggs ( $u$ ). Finally, just for equations 6  
336 and 7, females presented a maximum egg storage capacity of  $59 \pm 2$  eggs ( $C$ ). The models  
337  $D4$ ,  $D5$ ,  $D6$ , and  $D7$  are detailed in S3 Table and represented in S5-S8 Figs.

338

339 **Fig 4. Estimated type III functional response of *Anagyrus lapachosus* females at**  
340 **different ages (days) of their lifespan (1-12 days) considering limited egg production**  
341 **and female experience.** In equation  $D$  of the functional response module, the female gains  
342 experience throughout her life by interacting with the hosts, this is reflected in a daily  
343 increase in her attack rate.

344

345

## 346 **Discussion**

347 We proposed a series of latent-variables Markovian models that comprised an integrated  
348 approach of functional response and egg production models to study the realized lifetime  
349 reproductive success of adult parasitoids. With this approach, insight was gained about the  
350 reproductive biology dynamics of two parasitoid species being considered as biological  
351 control agents of a cactus mealybug pest. The number of hosts parasitized by *A. cachamai*  
352 decreased with female age and depended on the number of mature eggs that were available  
353 for oviposition (Fig 3A and 3B), while host parasitism by *A. lapachosus* increased with female  
354 age and was modulated by its daily egg load and previous experience (Fig 4).

355 According to Vinson [60], parasitoid females show distinct oviposition behaviors,  
356 consisting of host location and evaluation, ovipositor insertion, host acceptance, oviposition,  
357 and host marking (chemical or mechanical to avoid superparasitism). Although host finding  
358 and attack cycle are inborn, experience gained during the oviposition process may result in  
359 an improvement in the skill of the females to locate and parasitize their host [61]. However, a  
360 parasitoids' "motivation" is another element that is important in describing a parasitoids'  
361 oviposition behavior, and may be influenced by factors such as the onset of hunger, egg  
362 load, presence of competitors and predators, as well as environmental changes [60]. This  
363 concept is assigned to the category of hidden or latent variables, which cannot be measured  
364 directly but only by its correlation with observable behavior [62]. With the models we



365 developed, we explained the oviposition behavior of *A. cachamai* and *A. lapachosus* against  
366 variations in host densities in more detail than with the commonly used classical functional  
367 response models [1,63]. Furthermore, by studying both species throughout their adult lives,  
368 we were able to analyze how age and previous experience with the host influenced their  
369 reproductive success.

370 Both species *A. cachamai* and *A. lapachosus* were determined to have a type III  
371 functional response. Holling [64] suggested that type III functional responses could be a  
372 consequence of parasitoid learning, however, his formulations of this behavior were not  
373 permanent. At low host densities, Holling's model assumed that the contact of the parasitoid  
374 with the host would be so rare that the parasitoid could not develop a "search image" for the  
375 host. If host density increased, the frequency of contacts would rise and the parasitoid could  
376 become more responsive to the specific stimuli of the host. However, if the parasitoid does  
377 not encounter the host for a prolonged period of time, everything learned will be forgotten.  
378 The increased foraging behavior exhibited by females after parasitizing the first host may be  
379 due to a process known as associative learning [60]. Associative learning is identified as a  
380 females' perception of chemical traces (semiochemicals) and/or physical stimuli of the host  
381 (visual or mechanical) after a full oviposition experience, and the parasitoid's subsequent  
382 ability to find, recognize and accept (or reject) other hosts [65]. When a female is rewarded  
383 after a full oviposition experience, it learns that its foraging behavior in response to certain  
384 plant odors or host cues leads to finding a suitable host. Females of *A. cachamai* were "fast  
385 learners" after a single oviposition experience, although their response faded at 24 hours (Fig  
386 3A and 3B). In contrast, females of *A. lapachosus* were "slow learners", but they developed a  
387 long-term memory, since they showed an increase in their daily attack rate (Fig 4). Learning  
388 abilities and memory retention vary among parasitoid species and comes at a physiological  
389 cost [66,67]. The different learning skills observed between *A. cachamai* and *A. lapachosus*  
390 females may be the result of their dissimilar reproductive strategies [67].

391 Thanks to the use of Markovian models combined with Bayesian statistics, it was  
392 possible to make an accurate description of the ovigeny strategy of *A. cachamai* and *A.*  
393 *lapachosus*. The number of mature eggs after emergence, egg production on the first day,  
394 egg production rate, the proportion of eggs resorbed, egg resorption threshold, and egg  
395 storage capacity was estimated for both species. The selected models confirmed that *A.*  
396 *cachamai* and *A. lapachosus* are synovigenic, coinciding with the results obtained by Aguirre  
397 et al. [42]. Our models indicated that *A. cachamai* females emerged with  $56 \pm 2$  mature eggs  
398 and that their storage capacity was  $58 \pm 2$  eggs, and that *A. lapachosus* females emerged  
399 with  $57 \pm 2$  eggs and their storage capacity was  $59 \pm 2$  eggs. Therefore, both species  
400 emerged with their maximum egg storage capacity.

401 Synovigenic parasitoids possess a variety of adaptations that reduce the risk of egg  
402 limitation and extend their lifespan (variable egg production rates, host acceptance or  
403 rejection, superparasitism of hosts, adjustable clutch size, egg resorption, host feeding) [25].  
404 The egg production rate ( $g$ ) of *A. cachamai* females decreased with increasing female age  
405 while the egg production rate for *A. lapachosus* increased with increasing female age. To the  
406 best of our knowledge, there are few studies that provide information about how egg  
407 production is affected by female age. In addition, most of the available information is for  
408 experimental designs where females received an excess of hosts. For example, Manzano et  
409 al. [68] reported that the egg production rate of *Cosmocomoidea annulicornis* (Ogloblin)  
410 (Hymenoptera: Mymaridae) females is affected by age. The lowest egg load observed is  
411 when the females are 1 and 12 hours old and the highest when females are 4, 5, and 8 hours  
412 old. [69]. On the other hand, in the egg parasitoid *Anagrus virlai* Triapitsyn (Mymaridae), the  
413 number of parasitized eggs decreases as females age, and wasps experience a double egg  
414 maturation process [30]. Palottini [62], using a similar experimental design and statistical  
415 analysis to the one we employed, found that the egg production rate of *Gonatocerus* sp.  
416 “clado 1” (Mymaridae) aff. *tuberculifemur* is 0.78, meaning that the egg production rate

417 decreases with female age. We also determined that both species needed time to replenish  
418 their egg supply when the oviposition rate was high (S1-S8 Figs). *Anagyrus lapachosus*  
419 females had a lower egg resorption threshold ( $u$ ) than *A. cachamai* females but shared the  
420 same egg storage capacity ( $C$ ). Egg resorption by parasitoids may be a mechanism to  
421 remove unviable eggs [70] or to recycle nutrients [71]. Most likely, *A. cachamai* and *A.*  
422 *lapachosus* females experience egg resorption when host densities are too low or unsuitable  
423 to provide adequate oviposition opportunities.

424 Our data provide evidence that the risk of egg limitation was higher for *A. cachamai*  
425 females than *A. lapachosus*, since egg maturation declined with *A. cachamai* female age.  
426 *Anagyrus lapachosus* females presented two biological traits that gave them “flexibility” over  
427 *A. cachamai* females during the oviposition process: 1) increased egg production rate ( $g$ )  
428 with increasing female age; 2) female gain in experience over the course of her life when  
429 interacting with the host.

430 Functional response experiments are usually carried out for a short amount of time (1-  
431 48 hours), ignoring that the wasp presents non-foraging behaviors until it is ready to begin  
432 host foraging (e.g. maturing or resorbing eggs, resting, grooming, exploring the experimental  
433 arena, etc.) [5]. The problem of non-foraging behaviors during functional response  
434 experiments can be addressed with the explicit inclusion of non-foraging mechanisms into  
435 the functional response models. Likewise, experimental trials should be of sufficient duration  
436 so that egg production, resting, and other normal non-foraging behaviors are expressed  
437 during the trial. This approach has the potential to fully address the problem arising from the  
438 expression of non-foraging behavior by parasitoids during functional response experiments,  
439 but it may result in complicated models that are challenging to fit to data and are difficult to  
440 interpret. In this work, thanks to the use of Markovian models combined with Bayesian  
441 statistics, it was possible to deal with non-foraging behavior when measuring a parasitoids’  
442 functional response.

443

## 444 **Conclusions**

445 The presented methodology has broad application and the potential to increase  
446 understanding of the reproductive biology of a wide variety of parasitoid species. From an  
447 applied perspective, our developed models have implications for the use of parasitoids as  
448 biological control agents. Unlike classical functional response methodology, we assessed  
449 candidate species according to their physiology and prior experiences. Using this  
450 methodological approach to predict the success of parasitoids as control agents will increase  
451 the amount of information obtained from the studied potential biological control species  
452 leading to more effective and safe agent selection.

453

454

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664  
665

## 666 **Supporting information**

667 **S1 Fig. Observed functional response of the parasitoid *Anagyrus cachamai* attacking**  
668 ***Hypogeococcus sp.* nymphs.** (A-K) Solid line indicates the mean estimation of functional  
669 response for model C5 at different ages of female lifespan (1-11 days), grey line indicates its  
670 credibility interval, and dashed line indicates the *a posteriori* credibility interval for individual  
671 measurements. Dark circles are the observed number of emerged parasitoids; (L) estimated  
672 functional response for model C5 from day 1 to11.

673 **S2 Fig. Observed functional response of the parasitoid *Anagyrus cachamai* attacking**  
674 ***Hypogeococcus sp.* nymphs.** (A-K) Solid line indicates the mean estimation of functional  
675 response for model C7 at different ages of female lifespan (1-11 days), grey line indicates its  
676 credibility interval, and dashed line indicates the *a posteriori* credibility interval for individual

677 measurements. Dark circles are the observed number of emerged parasitoids; (L) estimated  
678 functional response for model *C7* from day 1 to11.

679 **S3 Fig. Observed functional response of the parasitoid *Anagyrus cachamai* attacking**  
680 ***Hypogeococcus sp. nymphs.*** (A-K) Solid line indicates the mean estimation of functional  
681 response for model *E5* at different ages of female lifespan (1-11 days), grey line indicates its  
682 credibility interval, and dashed line indicates the *a posteriori* credibility interval for individual  
683 measurements. Dark circles are the observed number of emerged parasitoids; (L) estimated  
684 functional response for model *E5* from day 1 to11.

685 **S4 Fig. Observed functional response of the parasitoid *Anagyrus cachamai* attacking**  
686 ***Hypogeococcus sp. nymphs.*** (A-K) Solid line indicates the mean estimation of functional  
687 response for model *E7* at different ages of female lifespan (1-11 days), grey line indicates its  
688 credibility interval, and dashed line indicates the *a posteriori* credibility interval for individual  
689 measurements. Dark circles are the observed number of emerged parasitoids; (L) estimated  
690 functional response for model *E7* from day 1 to11.

691 **S5 Fig. Observed functional response of the parasitoid *Anagyrus lapachosus***  
692 **attacking *Hypogeococcus sp. nymphs.*** (A-L) Solid line indicates the mean estimation of  
693 functional response for model *D4* at different ages of female lifespan (1-12 days), grey line  
694 indicates its credibility interval, and dashed line indicates the *a posteriori* credibility interval  
695 for individual measurements. Dark circles are the observed number of emerged parasitoids;  
696 (M) estimated functional response for model *D4* from day 1 to12.

697 **S6 Fig. Observed functional response of the parasitoid *Anagyrus lapachosus***  
698 **attacking *Hypogeococcus sp. nymphs.*** (A-L) Solid line indicates the mean estimation of  
699 functional response for model *D5* at different ages of female lifespan (1-12 days), grey line  
700 indicates its credibility interval, and dashed line indicates the *a posteriori* credibility interval  
701 for individual measurements. Dark circles are the observed number of emerged parasitoids;  
702 (M) estimated functional response for model *D5* from day 1 to12.

703 **S7 Fig. Observed functional response of the parasitoid *Anagyrus lapachosus***  
704 **attacking *Hypogeococcus sp. nymphs*.** (A-L) Solid line indicates the mean estimation of  
705 functional response for model *D6* at different ages of female lifespan (1-12 days), grey line  
706 indicates its credibility interval, and dashed line indicates the *a posteriori* credibility interval  
707 for individual measurements. Dark circles are the observed number of emerged parasitoids;  
708 (M) estimated functional response for model *D6* from day 1 to12.

709 **S8 Fig. Observed functional response of the parasitoid *Anagyrus lapachosus***  
710 **attacking *Hypogeococcus sp. nymphs*.** (A-L) Solid line indicates the mean estimation of  
711 functional response for model *D7* at different ages of female lifespan (1-12 days), grey line  
712 indicates its credibility interval, and dashed line indicates the *a posteriori* credibility interval  
713 for individual measurements. Dark circles are the observed number of emerged parasitoids;  
714 (M) estimated functional response for model *D7* from day 1 to12.

715 **S1 Table. Deviance information criterion (DIC) of the 48 tested models.**

716 **S2 Table. Parameters of the selected models for the parasitoid species *Anagyrus***  
717 ***cachamai*.**

718 **S3 Table. Parameters of the selected models for the parasitoid species *Anagyrus***  
719 ***lapachosus*.**

720 **S1 File. Appendix.**

721

722

## 723 **Author Contributions**

724 **Conceptualization:** María Aguirre, Guillermo Logarzo, Octavio Bruzzone.

725 **Data curation:** María Aguirre, Guillermo Logarzo, Serguei Triapitsyn, Octavio Bruzzone.

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727 **Investigation:** María Aguirre, Guillermo Logarzo, Octavio Bruzzone.

728 **Methodology:** María Aguirre, Guillermo Logarzo, Octavio Bruzzone.

- 729 **Project administration:** Guillermo Logarzo, Hilda Diaz-Soltero, Stephen Hight.
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- 732 **Supervision:** Guillermo Logarzo, Octavio Bruzzone.
- 733 **Validation:** María Aguirre, Guillermo Logarzo, Octavio Bruzzone.
- 734 **Visualization:** María Aguirre, Guillermo Logarzo, Serguei Triapitsyn, Hilda Diaz-Soltero, Stephen
- 735 Hight, Octavio Bruzzone.
- 736 **Writing – Original Draft Preparation:** María Aguirre, Guillermo Logarzo, Serguei Triapitsyn, Hilda
- 737 Diaz-Soltero, Stephen Hight, Octavio Bruzzone.
- 738 **Writing – Review & Editing:** María Aguirre, Guillermo Logarzo, Serguei Triapitsyn, Hilda Diaz-
- 739 Soltero, Stephen Hight, Octavio Bruzzone.
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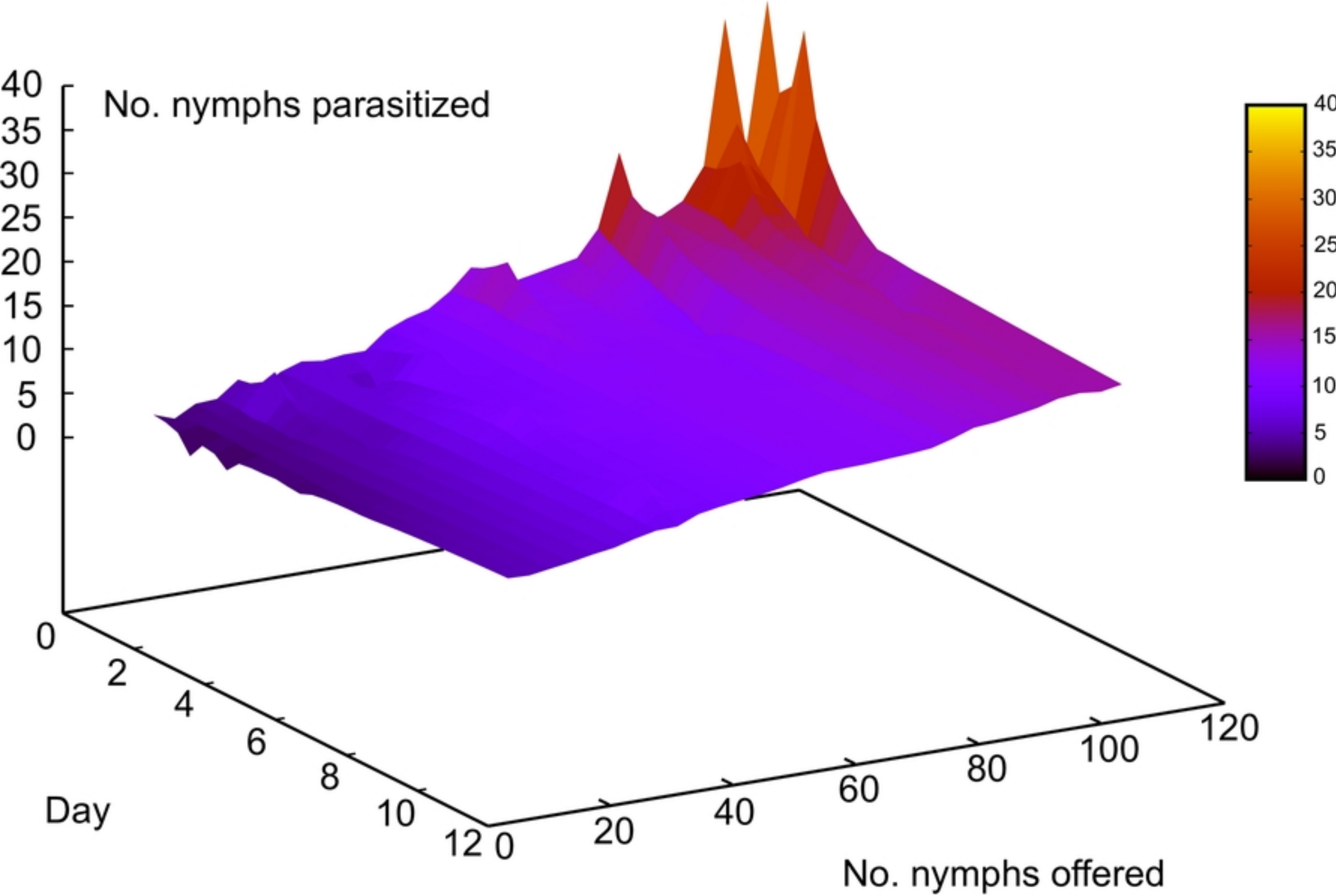


Fig 1



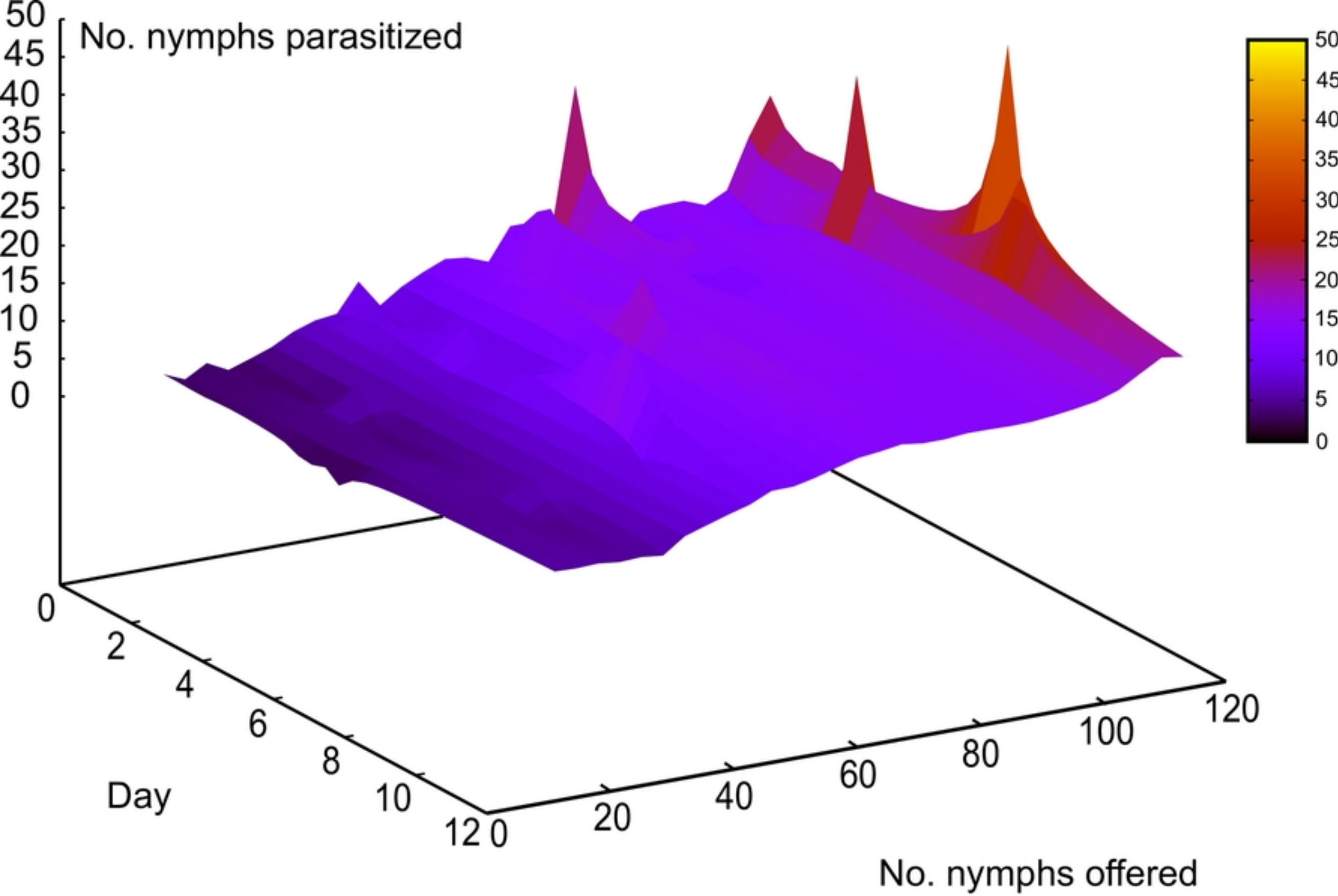


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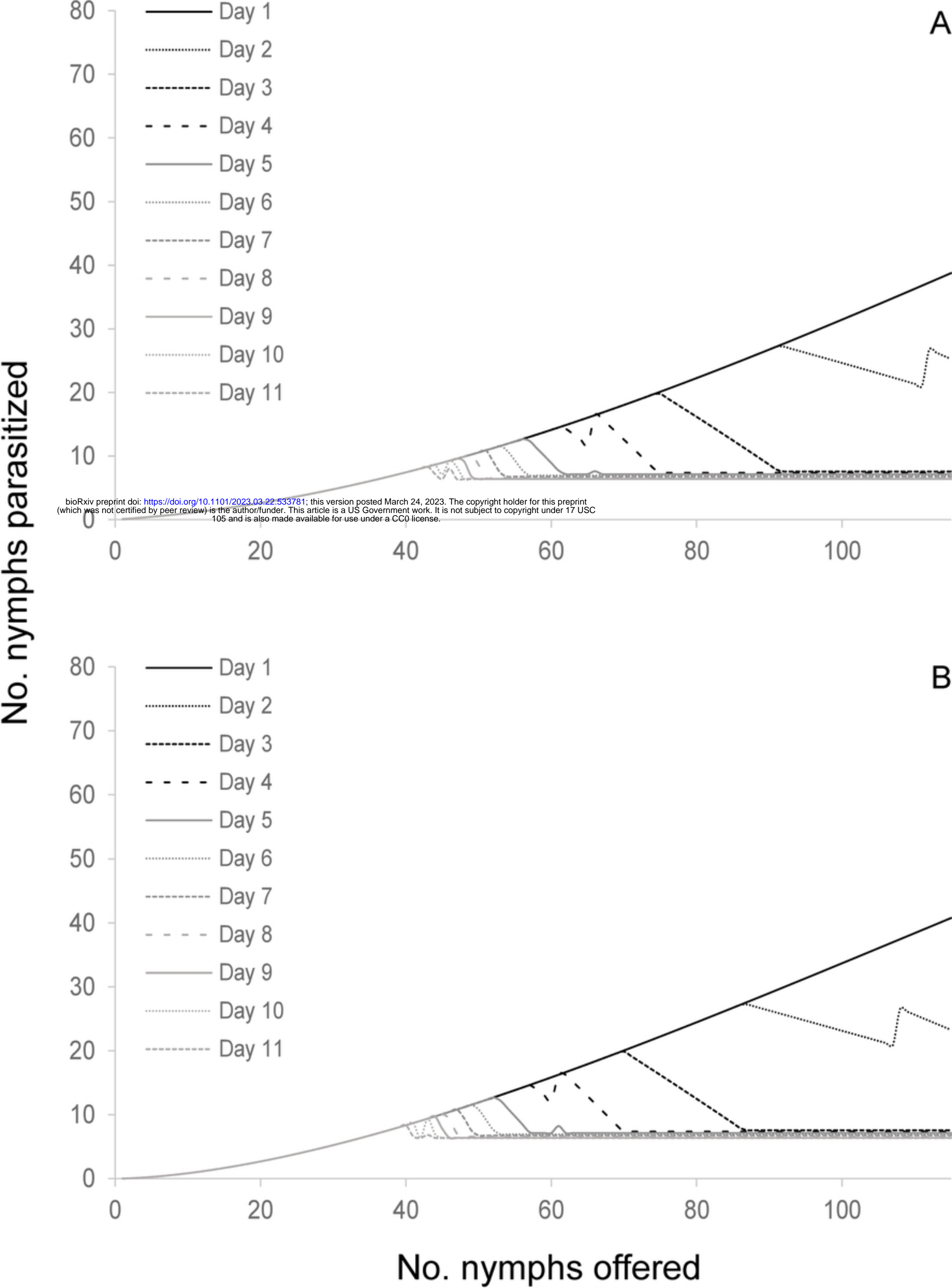


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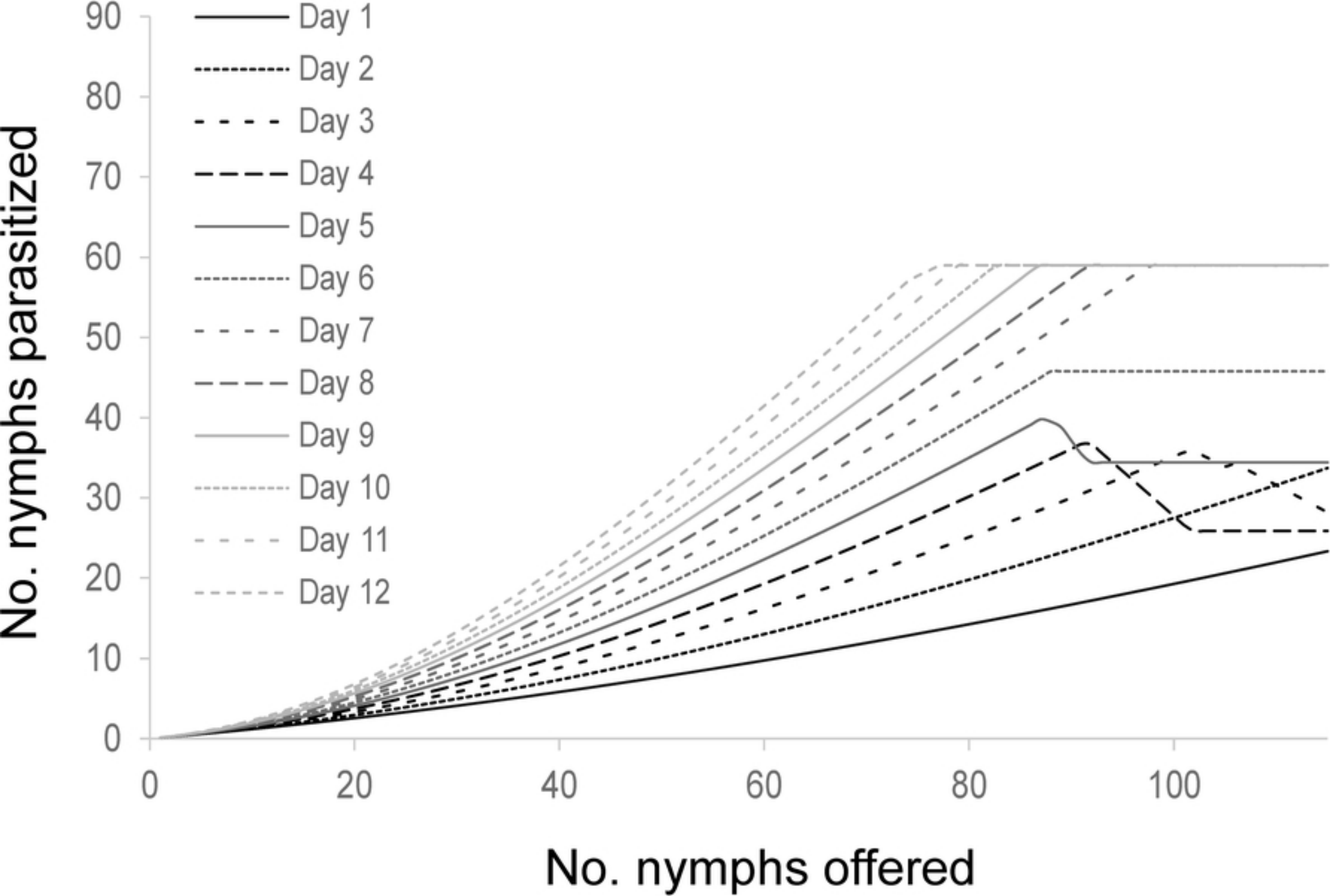
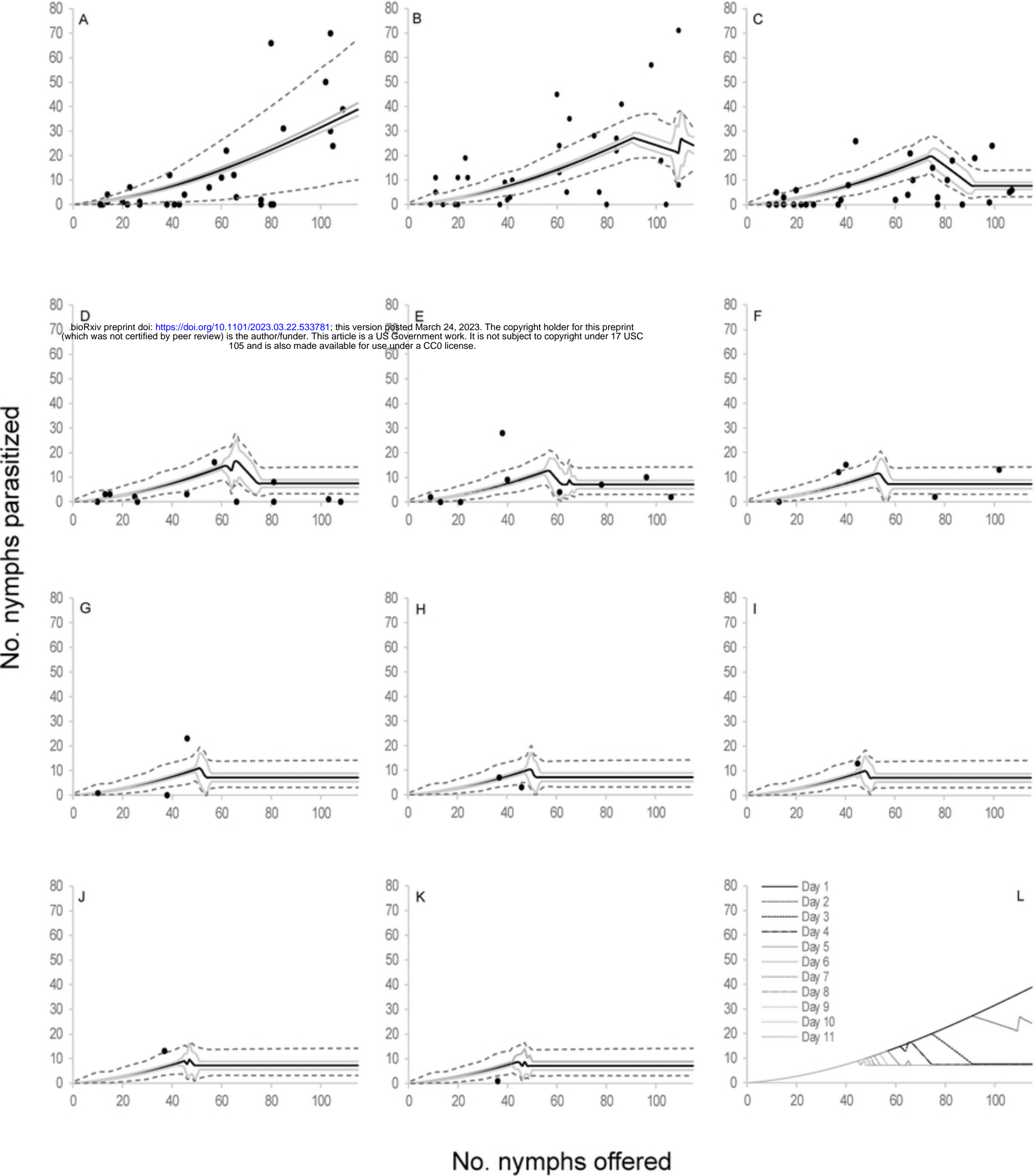
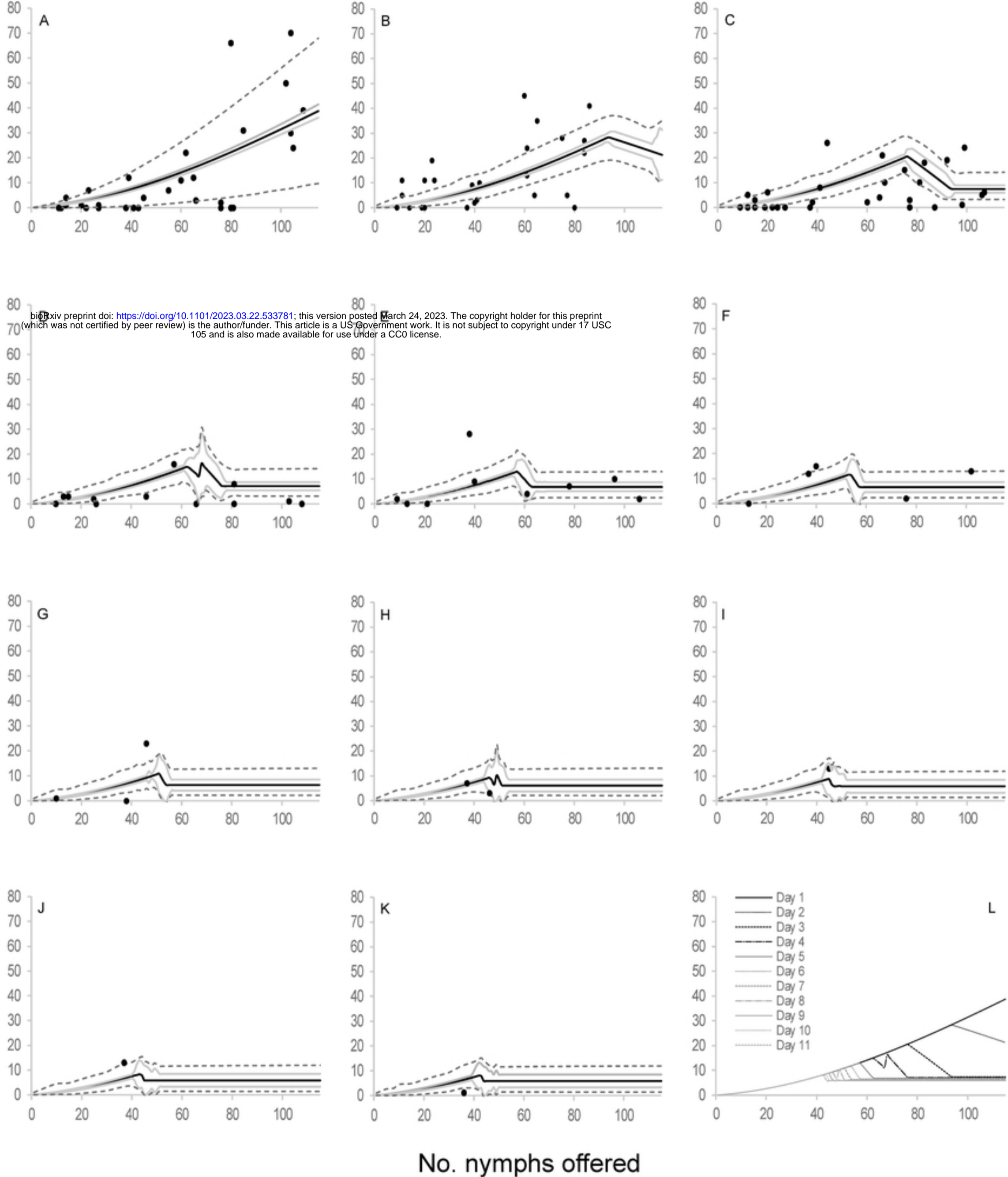


Fig 4

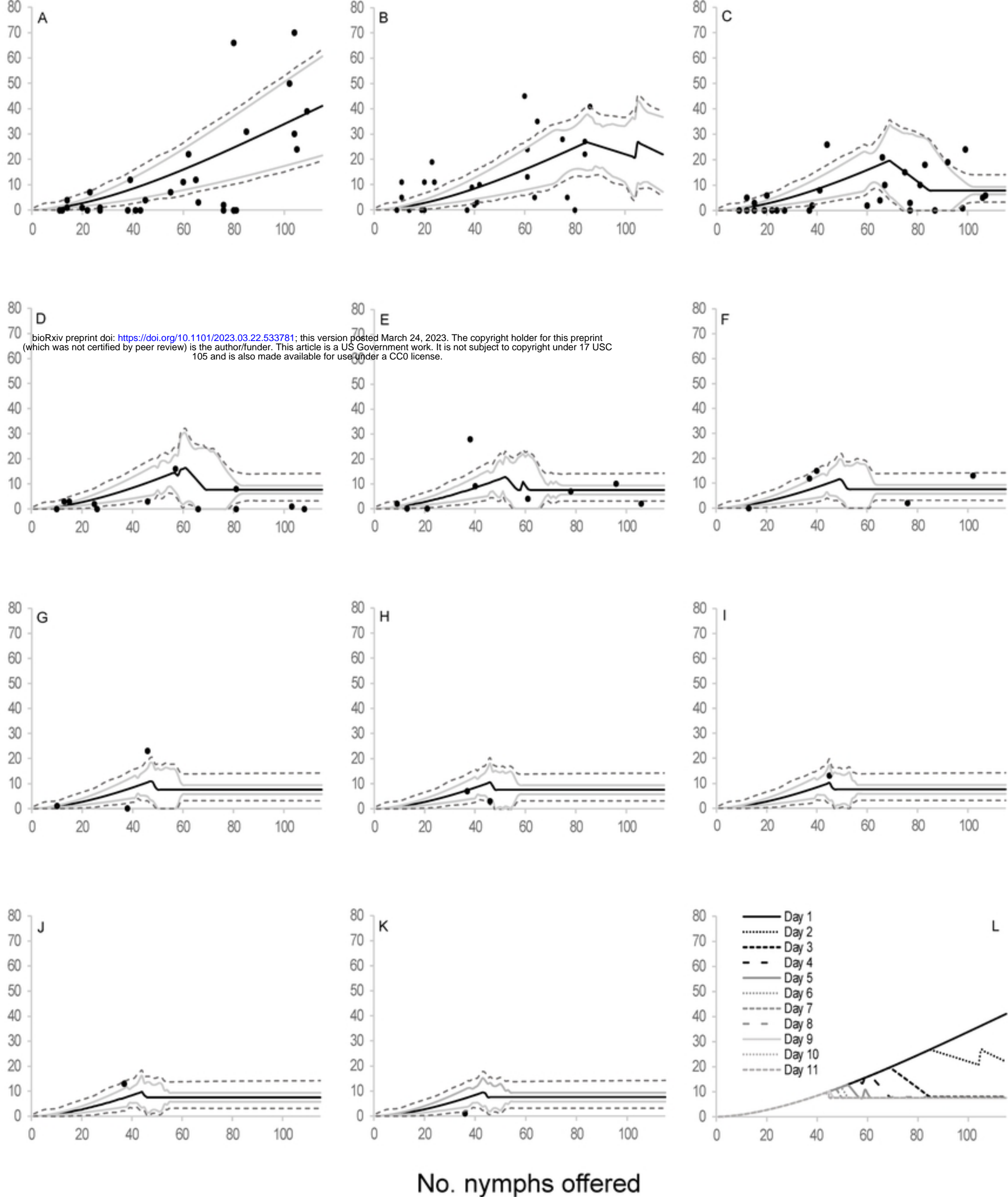


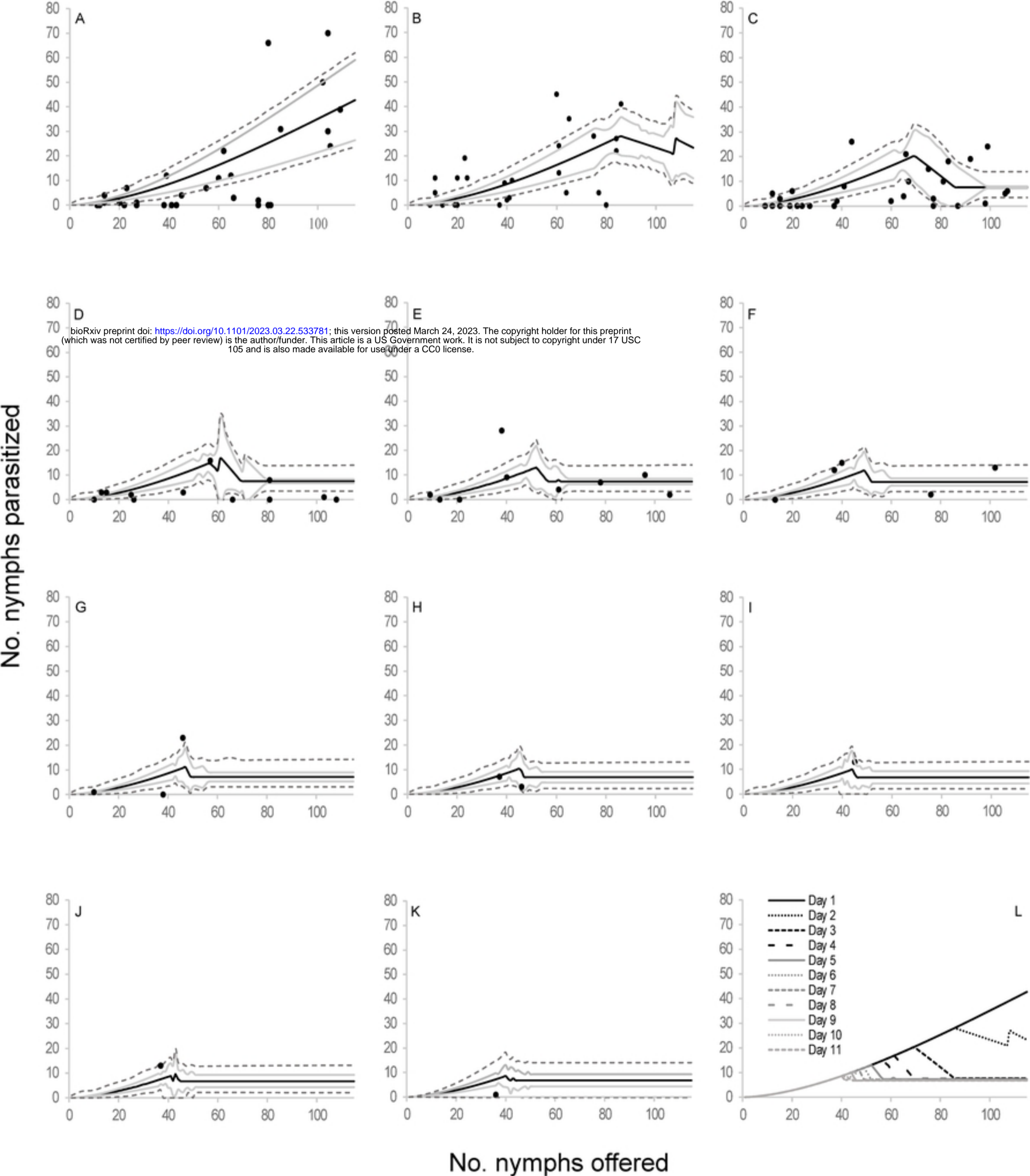
S1 Fig

No. nymphs parasitized



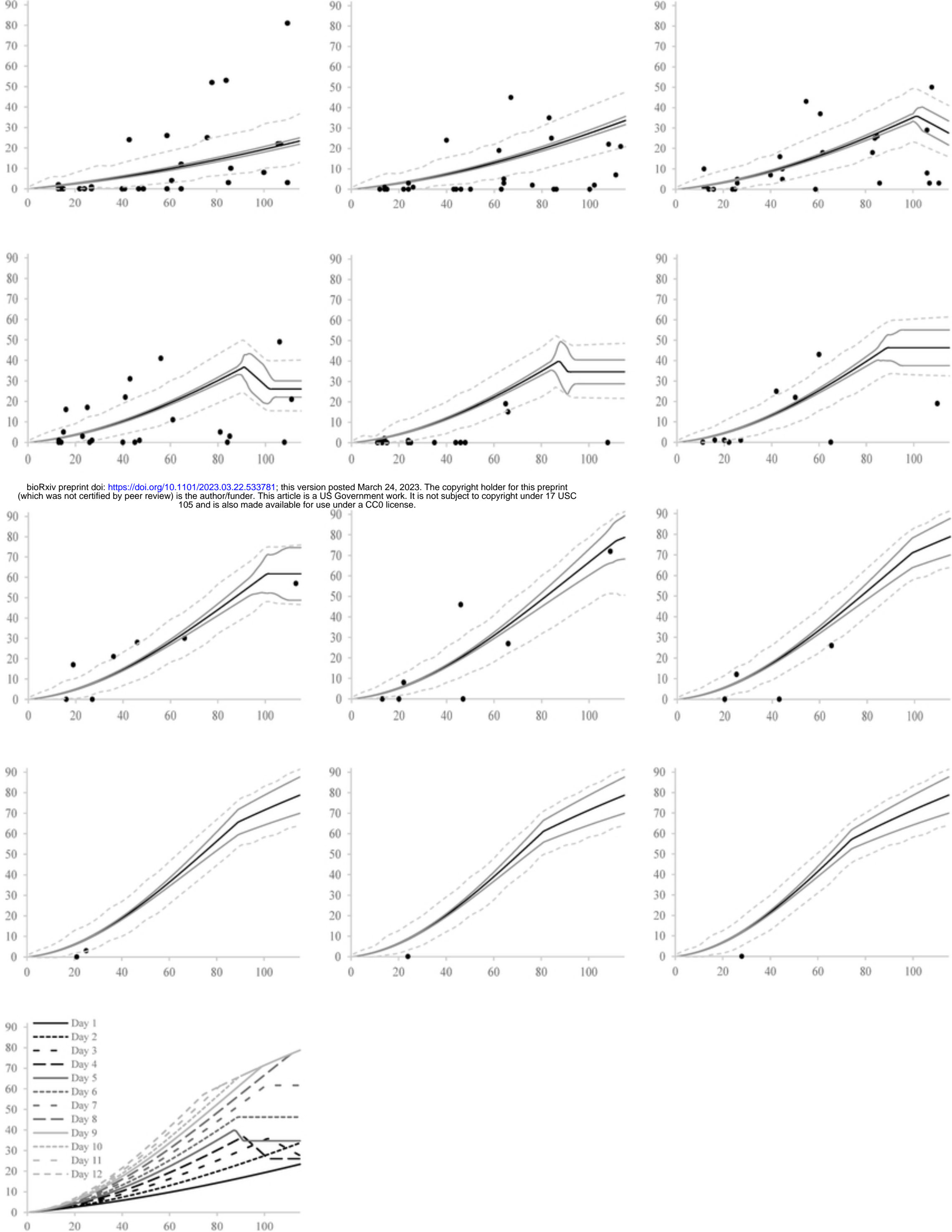
S2 Fig





S4 Fig

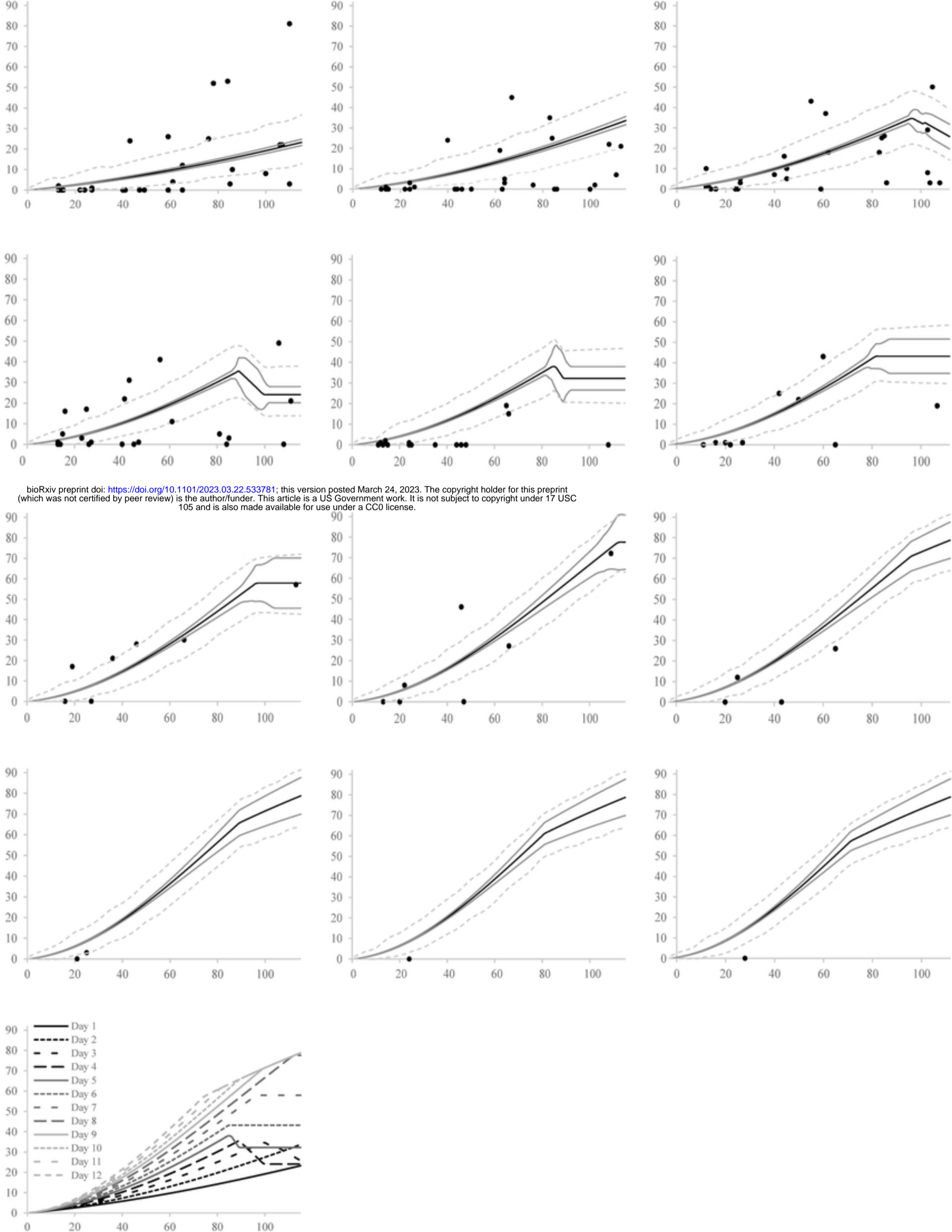
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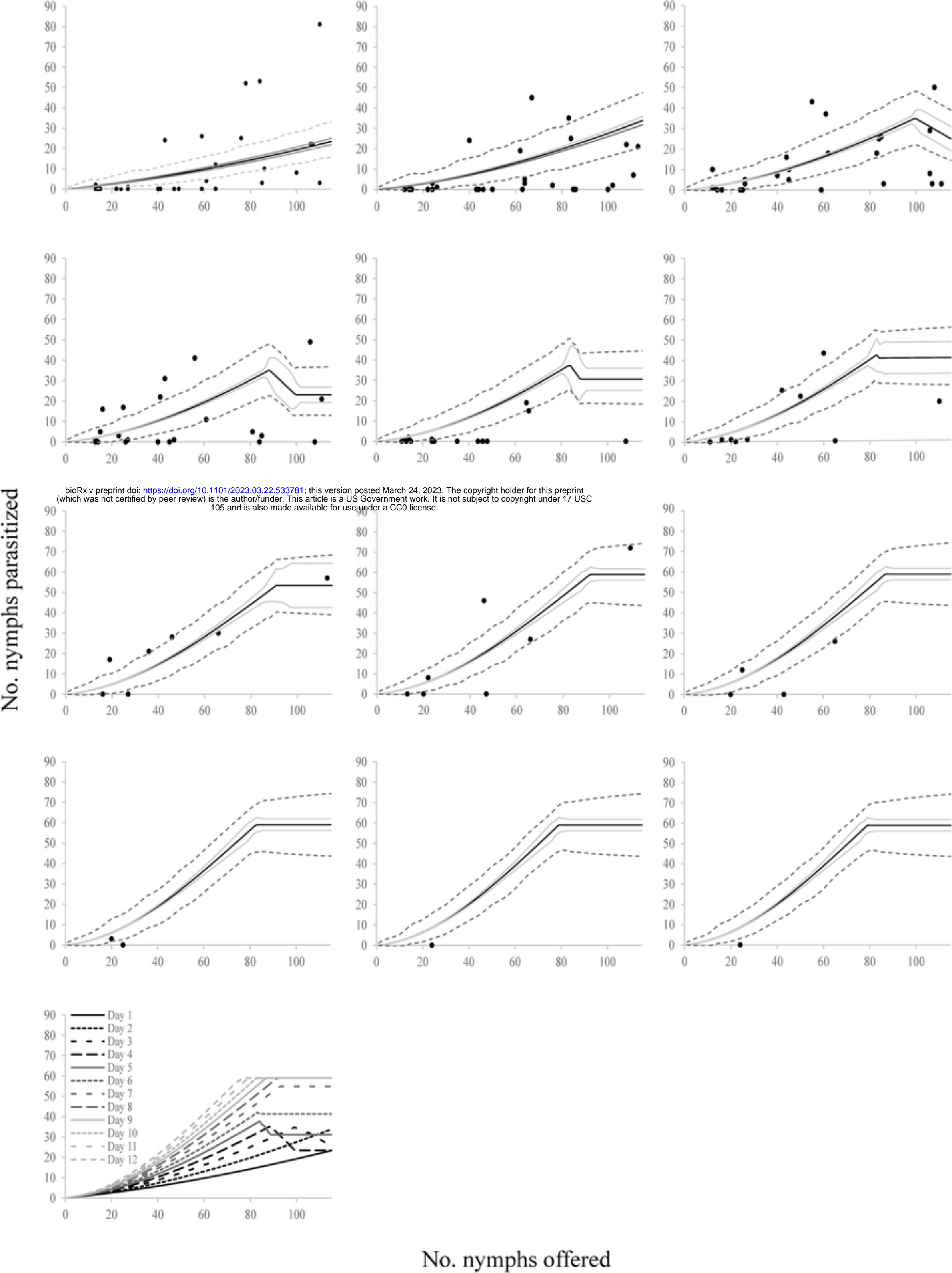
No. nymphs offered

S5 Fig

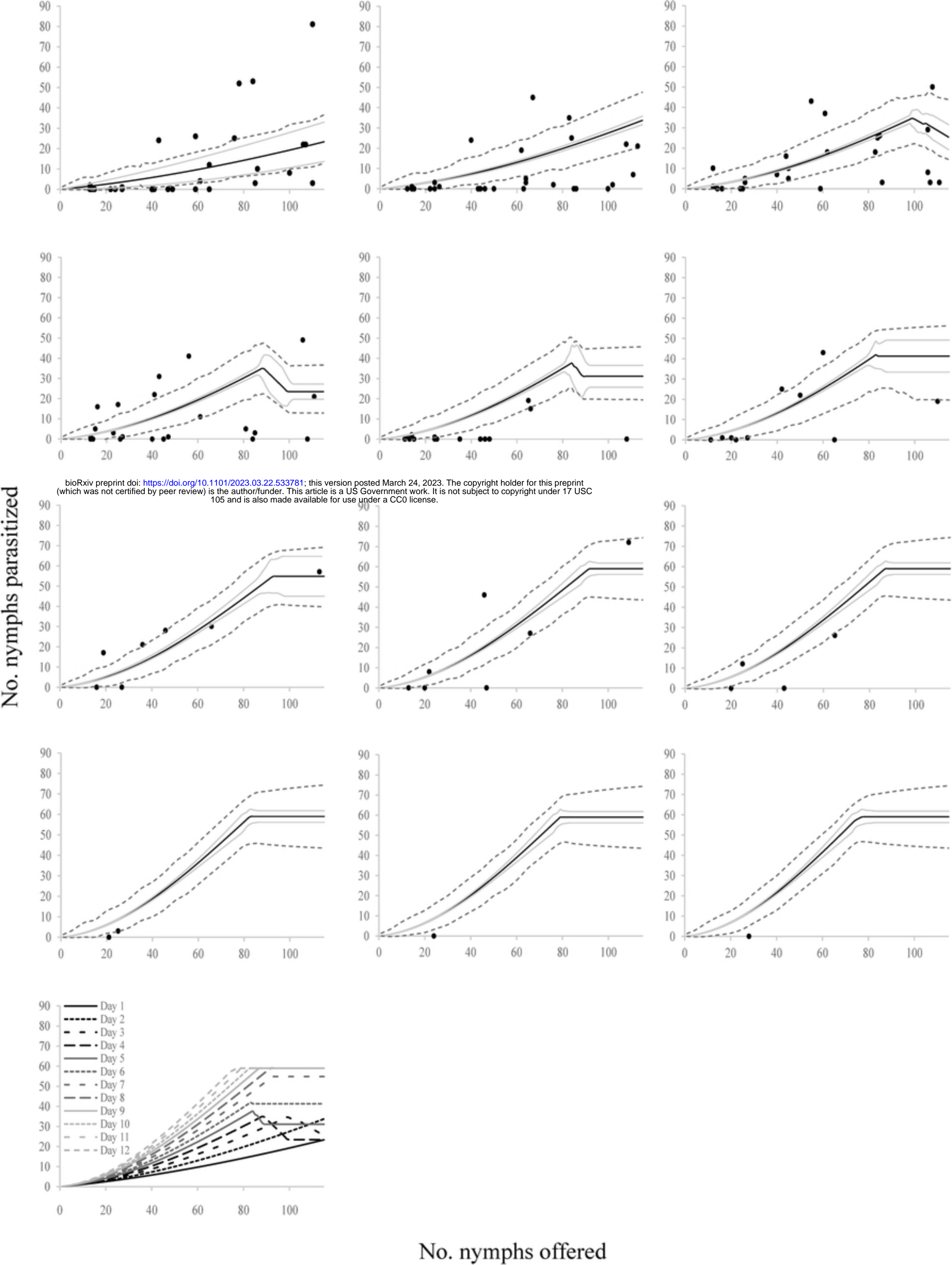




No. nymphs offered



S7 Fig



S8 Fig