Artificial night light alters nocturnal prey interception outcomes for morphologically variable spiders

Suet Wai Yuen [1] , **Timothy C Bonebrake** Corresp. [1]

[1] School of Biological Sciences, University of Hong Kong, Hong Kong, Hong Kong

Corresponding Author: Timothy C Bonebrake
Email address: tbone@hku.hk

Artificial night light has the potential to significantly alter visually-dependent species interactions. However, examples of disruptions of species interactions through changes in light remain rare and how artificial night light may alter predator prey relationships are particularly understudied. In this study, we examined whether artificial night light could impact prey attraction and interception in *Nephila pilipes* orb weaver spiders, conspicuous predators who make use of yellow color patterns to mimic floral resources and attract prey to their webs. We measured moth prey attraction and interception responses to treatments where we experimentally manipulated the color/contrast of spider individuals in the field (removed yellow markings) and also set up light manipulations. We found that lit webs had lower rates of moth interception than unlit webs. Spider color however had no clear impact on moth interception or attraction rates in lit nor unlit webs. The results show that night light can reduce prey interception for spiders. Additionally, this study highlights how environmental and morphological variation can complicate simple predictions of ecological light pollution's disruption of species interactions.

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7   Suet Wai Yuen[1], Timothy C. Bonebrake[1†]

10   [1]The School of Biological Sciences, The University of Hong Kong, Hong Kong

16   [†]Corresponding author

17   E-mail: tbone@hku.hk (TCB)

21 **Abstract**

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23 interactions. However, examples of disruptions of species interactions through changes in light

24 remain rare and how artificial night light may alter predator prey relationships are particularly

25 understudied. In this study, we examined whether artificial night light could impact prey

26 attraction and interception in *Nephila pilipes* orb weaver spiders, conspicuous predators who

27 make use of yellow color patterns to mimic floral resources and attract prey to their webs. We

28 measured moth prey attraction and interception responses to treatments where we experimentally

29 manipulated the color/contrast of spider individuals in the field (removed yellow markings) and

30 also set up light manipulations. We found that lit webs had lower rates of moth interception than

31 unlit webs. Spider color however had no clear impact on moth interception or attraction rates in

32 lit nor unlit webs. The results show that night light can reduce prey interception for spiders.

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34 complicate simple predictions of ecological light pollution's disruption of species interactions.

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Introduction

41

42 Artificial night light represents an emerging threat to biodiversity (Hölker et al., 2010). Studies

43 are increasingly demonstrating the widespread impacts of artificial light on species (Longcore &

44 Rich, 2004), ecological communities (Davies, Bennie & Gaston, 2012; Gaston et al., 2014) and

45 ecosystem functioning (Macgregor et al., 2017). One important consequence of light pollution

46 and artificial night light is a change in natural light landscapes and seascapes that could alter

47 species communication and interactions (Davies et al., 2013). Within species, visual

48 communication can be disrupted by ecological light pollution with consequences for mating

49 success and population dynamics (Firebaugh & Haynes, 2016). However, the prospect that

50 artificial light could disrupt visual cues, color perception and species interactions remains an

51 important subject for further empirical study (Delhey & Peters, 2017).

52   Predator-prey interactions in particular are potentially vulnerable to ecological light pollution.

53 Prey species often rely on specific light conditions for camouflage or crypsis where artificial

54 night light can render such species detectable by predators (Davies et al., 2104; Underwood,

55 Davies & Queirós, 2017). Light pollution can also impact prey behavior including vigilance

56 effectiveness (Yorzinski et al., 2015) and predator avoidance (Perkin et al., 2011). Similarly,

57 Minnaar et al. (2015) found that bats in lit areas consumed six times more moths than bats in

58 unlit areas, highlighting the importance of night light in attracting moths and dramatically

59 changing the dynamics of a long-evolved predator-prey relationship. Some spiders also appear to

60 take advantage of light attraction of prey species and preferentially choose web building sites

61   near light sources (Heiling, 1999), potentially explaining why some orb-weaver spiders have

62   successfully established within well-light urban areas (Lowe, Wilder & Hochuli, 2014).

63   Coloration in spiders is particularly important and recent studies have shown that nocturnal

64   spiders can use body markings as visual lures to attract prey (Tso et al., 2006; Chuang, Yang &

65   Tso, 2008; Fan, Yang & Tso, 2009; Zhang et al., 2015). Night vision is a challenge for nocturnal

66   species requiring visual systems that exploit moonlight, zodiacal light, airglow and starlight to

67   distinguish color and detect motion (Warrant, 2004; Cronin et al., 2014). Therefore, nocturnal

68   insects lured to spider coloration might be differentially attracted or deterred under artificial

69   night light.

70   To examine the potential of artificial night light in disrupting a visually driven predator-prey

71   relationship, we manipulated light conditions and spider body coloration in a field experiment of

72   the orb weaver spider, *Nephila pilipes*. The spider has a distinctive yellow body pattern that is

73   well known as a visual lure for nocturnal prey species (Tso, Lin & Yang, 2004; Fan, Yang &

74   Tso, 2009). We predicted that artificial light would decrease the effectiveness of the visual lure

75   and impact prey attraction outcomes for spiders.

76

77   **Materials and methods**

78   **Study sites and species**

79   *Nephila pilipes* are orb-weaver spiders commonly found in Hong Kong during the wet season

80   (March to November). The species exhibits conspicuous yellow patterns scattered over their

81   dorsal and ventral cephalothorax, abdomen and legs. *N. pilipes* hunt diurnally and nocturnally

82   and use these conspicuous color patterns to attract prey (Tso, Lin & Yang, 2004). Habitats

83   include semi-rural areas in Hong Kong where artificial night light sources from street lamps and

84   housing are common. Six sites were chosen due to their semi-rural characteristics including

85   outlying islands (Lamma Island and Lantau Island), country park forests (Tai Tam, Parker Hill

86   and Pak Tam Chung) and a rural village (So Kwun Wat). Sites were close to low-density

87   residential areas where active human disturbance was low relative to nearby urban areas.

88

89   **Experimental design**

90   In each site, we searched for adult female spiders in their webs. We chose four spider individuals

91   at each site and each adult was assigned randomly to one of four experimental set ups: (1) spider

92   web was lit by a lamp and yellow spider coloration was not painted away (lit control), (2) yellow

93   spider coloration was painted away by black paint (dark and painted), (3) both light and paint

94   were applied to the spider (lit and painted), and (4) no lamp was present and yellow coloration

95   remained (dark control). All setups within a site were located within 50m of each other. We used

96   1000W warm white LED light bulbs directed towards the web (approximately one meter from

97   the web) as a light source in lit setups, with paper tape wrapped over the surface to downward

98   adjust the light intensity. These bulbs have a similar emission spectrum as Hong Kong street

99   lamps (i.e. high pressure sodium lamps), characterized by peaks in wavelength between 450 and

100   600 nm (Elvidge & Keith, 2009). For spider color manipulations, we used black acrylic paint due

101   to its low toxicity and ease of removal (Tamiya Colour Acrylic Paint Mini Black X-1, diluted by

102   thinner of the same brand). We also applied the paint to black body parts of spiders in the yellow

103   coloration "controls" (setups 1 and 4) to exclude possible effects of ink. Spiders were gently

104   removed from their webs and cooled to an inactive state by an ice bath. After treating with paint,

105   they were carefully placed back on their webs for the commencement of the experiment.

106   We also recorded body length, the total length of cephalothorax and opisthosoma, of each

107   spider. Web size was measured as the average of web radii in eight cardinal directions, from web

108   hub to the outermost capture spiral following Tso et al. (2006). We measured light intensity by

109   placing a digital light meter (Dr. Meter LX-1330B) one meter from each of the webs.

110   We examined *N. pilipes* predation success through single-night videotaping of all

111   experimental spider webs. We recorded from between 7:00 p.m. and 8:00 p.m to the beginning

112   of sunrise (4:00 a.m. to 5:00 a.m.). We sampled each site once between Oct 2016 and Nov 2017.

113   All setups in each site were recorded on the same night simultaneously. We used high definition

114   car rearview cameras with infra-red emitters (Theera YRS0889) for the night video recording. *N.*

115   *pilipes* mostly builds webs under tree trunks, at a height of one to two meters. Cameras were

116   therefore placed on tripods approximately one meter from each web.

117   We examined prey responses to each treatment by focusing on moths in all video recordings.

118   Moths are a dominant nocturnal prey species of *N. pilipes* (Fan, Yang & Tso, 2009). Moths also

119   use a trichromatic visual system, possessing green, blue and ultra-violet light receptors (Briscoe

120   & Chittka, 2001). Based on a model of a hawkmoth visual system (Johnsen et al., 2006),

121   Chuang, Yang & Tso (2007) determined that the yellow stripes of *N. pilipes* were more

122   distinctive under moonlight than black markings. Specifically, the contrast of black body parts of

123   the spiders with vegetation backgrounds was remarkably smaller than those of yellow body parts

124   (Chuang, Yang & Tso, 2007). Yellow flowers are in fact a common moth food source such that

125   this coloration pattern might be particularly attractive to potential moth prey species (Johnsen et

126   al., 2006).

127

128   **Data analysis**

129   We focused on three variables for analysis; attraction (number of moths seen approaching the

130   web), interception (number of moths that physically hit the web, but not necessarily caught in the

131   web) and interception efficiency (number of moths intercepted divided by the number of moths

132   attracted). We used generalized linear mixed models to model the moth attraction and

133   interception data. We fit the models with a negative binomial distribution due to the nature of the

134   count data and the fact that the data were over-dispersed (Zuur et al., 2009). We included site as

135   a random effect and number of hours as an offset term. We modeled web size, color, light and

136   spider size as fixed effects and modeled all combinations and first order interactions. We log

137   transformed interception efficiency and used a linear mixed effects model with site as a random

138   effect and web size, spider size, color and light as fixed effects. For the linear mixed effects

139   models, we also examined all first order interactions. All models were run in R using packages

140   glmmADMB and nlme (Pinheiro et al., 2014; Skaug et al., 2014). For each set of generalized

141   linear mixed models and linear mixed effects models, we used model selection and chose the

142   model with the best AICc. For all models where delta AICc < 4, we used a model averaging to

143   determine relative variable importance (RVI) using package MuMIn (Barton, 2013).

144

145   **Results**

146   We recorded 163 hours during the course of the study period. In three cases the spider left and so

147   we were unable to collect data. Over the entire recording period we documented 5375 moths

148   attracted and 300 moths intercepted – but only ten moths remained in the web and were

149   consumed by the spider.

150   The best model for attraction included light, color, spider size and the interaction between

151   spider size and color (Table 1; light: estimate±se: -2.40±0.51, *P*<0.001; color: -13.1±2.91,

152   *P*<0.001; size: -0.18±0.45, *P*=0.69; size:color: 2.65±0.63, *P*<0.001). In sites with smaller

153   spiders, fewer moths flew near the webs (Fig. 1: for large spiders above 4.5cm, 31.9±6.1 [mean ±

154   standard error] moths attracted/hour and 14.1±4.7 for small spiders).

155   For interception, lit webs had lower interception rates (Fig. 2) and the best performing model

156   included only light as a variable (Table 1; light: estimate±se: -2.47±0.88, *P*=0.005). Seven

157   models performed equally well (Table 1), and of those models light (RVI=1.0) was the most

158   important followed by spider size (RVI=0.45) and color (RVI=0.24).

159   For interception efficiency, the best three models were light alone, size alone and light plus

160   size (Table 1; light alone: estimate±se: -0.43±0.25, *P*=0.10; size alone: -0.33±0.18, *P*=0.08; and

161   light+size: light: -0.54±0.26, *P*=0.05; size: -0.37±0.17, *P*=0.04). Of the five best performing

162   models (Table 1) light was the most important variable (RVI=0.61) followed by spider size

163   (RVI=0.47) and color (RVI=0.19). Light tended to diminish interception efficiency (especially

164   for webs with large spiders) and small spiders exhibited a higher efficiency (Fig. 3). For large

165   spiders, those that were unpainted (yellow) and in dark webs had a higher interception efficiency

166   than all other treatment combinations (Fig. 2).

167

168   **Discussion**

169   Prey attraction rates were affected by size, color, and light conditions but not in a consistent

170   manner (Fig. 1). We did however find a consistent and large effect of light in lowering prey

171   interception (~1 moth/hr; Fig. 2) comparable to the positive effect of yellow markings

172   documented in previous studies of *N. pilipes* (~1 moth/hr; Chuang, Yang & Tso (2007)). In this

173   study, we found no clear consequences of color for prey attraction or interception. Yet, spider

174   size and color exhibited an interactive effect for all attraction variables (Table 1) demonstrating

175   the complexity of the relationship between spider morphology and attraction outcomes. These

176   results together highlight 1) that light can reduce prey interception for spiders and 2) the role of

177   morphological and environmental variation in complicating and potentially obscuring important

178   but difficult-to-detect artificial night light effects on predator-prey interactions.

179   We found that interception rates were lower in lit webs than unlit webs. The lack of an effect

180   of color on interception suggests that the cause for this pattern is unlikely through changes in the

181   effectiveness of the visual lure. The presence of light will change the contrast of the web with its

182   background and could make the web more easily perceived and avoided by moth prey (Craig,

183   1988; Théry & Casas, 2009). While some spiders build webs near artificial light sources to take

184   advantage of attracted prey (Heiling, 1999), there might be a tradeoff in web detectability that

185   could offset increased prey availability near light. Further exploration into the costs and benefits

186   of locating webs near artificial night light would be productive in revealing the impacts of

187   ecological light pollution on urban spider populations.

188   For attraction, the light treatment alone did not consistently result in higher attraction rates.

189   While each site had all treatments on the same day to minimize time or site effects on the results,

190   the high variation in attraction may have obscured possible effects of light and morphology.

191   Light can have strongly contrasting effects on predator-prey interactions depending on the

192   habitat (Russ, Lučeničová & Klenke, 2017). Environmental conditions across sites and days, and

193   variable light intensity in particular (e.g. different moon phases), may have resulted in complex

194   patterns between the light treatment effects and prey attraction. We did find that, in general,

195   larger spiders had more moths attracted to their webs than smaller spiders (Fig. 1). The higher

196   attraction rate for large spiders could be a consequence of a bigger visual lure capable of

197   attracting more prey than smaller spiders (Hauber, 2002). Alternatively, spiders who select better

198   microhabitats with more prey may grow larger (Brown, 1981) such that the association is driven

199   by greater prey availability increasing spider size, not larger spiders attracting more prey. In any

200   case, the high heterogeneity of light landscapes across spatial scales in the environment (Swaddle

201 et al., 2015) along with other sources of microhabitat and temporal variation are important

202 considerations for the results of this study as well as ecological light pollution studies broadly.

203   Size and color likely have different effects at variable distances: small spiders may attract

204 fewer prey (or be located in sites with fewer prey) but they also tend to have a higher (but

205 variable) interception efficiency suggesting that their small size might be advantageous in

206 disguising their presence once moths are near the web. For large spiders, that the unlit and

207 unpainted (yellow markings intact) treatment had the highest interception efficiency could be

208 indicative of increased, effectiveness of the lure for large spiders in natural light conditions.

209 However, interception efficiencies across treatments were highly variable across treatments and

210 the mechanisms and effects are difficult to interpret. In addition to the importance of morphology

211 for prey attraction, the visual cues and coloration of *N. pilipes* may also attract their own

212 predators potentially (Fan, Yang & Tso, 2009; Meyer et al., 2013; Yeh et al., 2015). Artificial

213 night light effects on predator-prey relationships must then take into account multiple

214 morphological variables (e.g. color and size) as well as multiple consequences of those visual

215 cues (e.g. prey attraction and predator attraction).

216   Our results provide insights into the relationship between prey attraction and artificial night

217 light but this study may not be reflective of the entirety of night light impacts on this predator-

218 prey relationship. For example, the short time period covered for each web in this study could

219 miss crucial rare catches of large prey items which may have disproportionate positive impacts

220 on spider fitness (Venner & Casas, 2005). If light differentially affects or attracts large moths

221   (Wölfling et al., 2016) then the average overall interception rate may be less important than the

222   ability to catch large moths occasionally. The effects of artificial night light on predation rates

223   are rarely straightforward and will ultimately be the product of both negative and positive

224   impacts of light on predator and prey behavior (Grenis, Tjossem & Murphy, 2015).

225   Reduced feeding, mobility and possible increased predation are all potential consequences of

226   artificial night light for moths and these effects may result in trophic cascades within these novel

227   ecosystems (van Langevelde et al., 2017). This study highlights how night light can impact

228   species interactions but also that environmental and morphological variation can obscure simple

229   relationships between predator and prey. As artificial night light continues to dramatically alter

230   the environment (Davies et al., 2013), the conditions under which these predator-prey

231   relationships have evolved will also change resulting in the possible disruption of important

232   species interactions within ecosystems.

233

234   **Conclusion**

235   Our experiment demonstrates a clear reduction of prey interception in sites with artificial

236   night light for orb-weaver spiders in Hong Kong. The results also suggest that body size and

237   color might also influence prey interception outcomes for spiders but no clear patterns were

238   detected. Future research into the complex interactions between predator, prey, light and

239   morphology will aid in predictions and understanding of how anthropogenic changes in light are

240   likely to affect ecological communities and ecosystems.

241

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245

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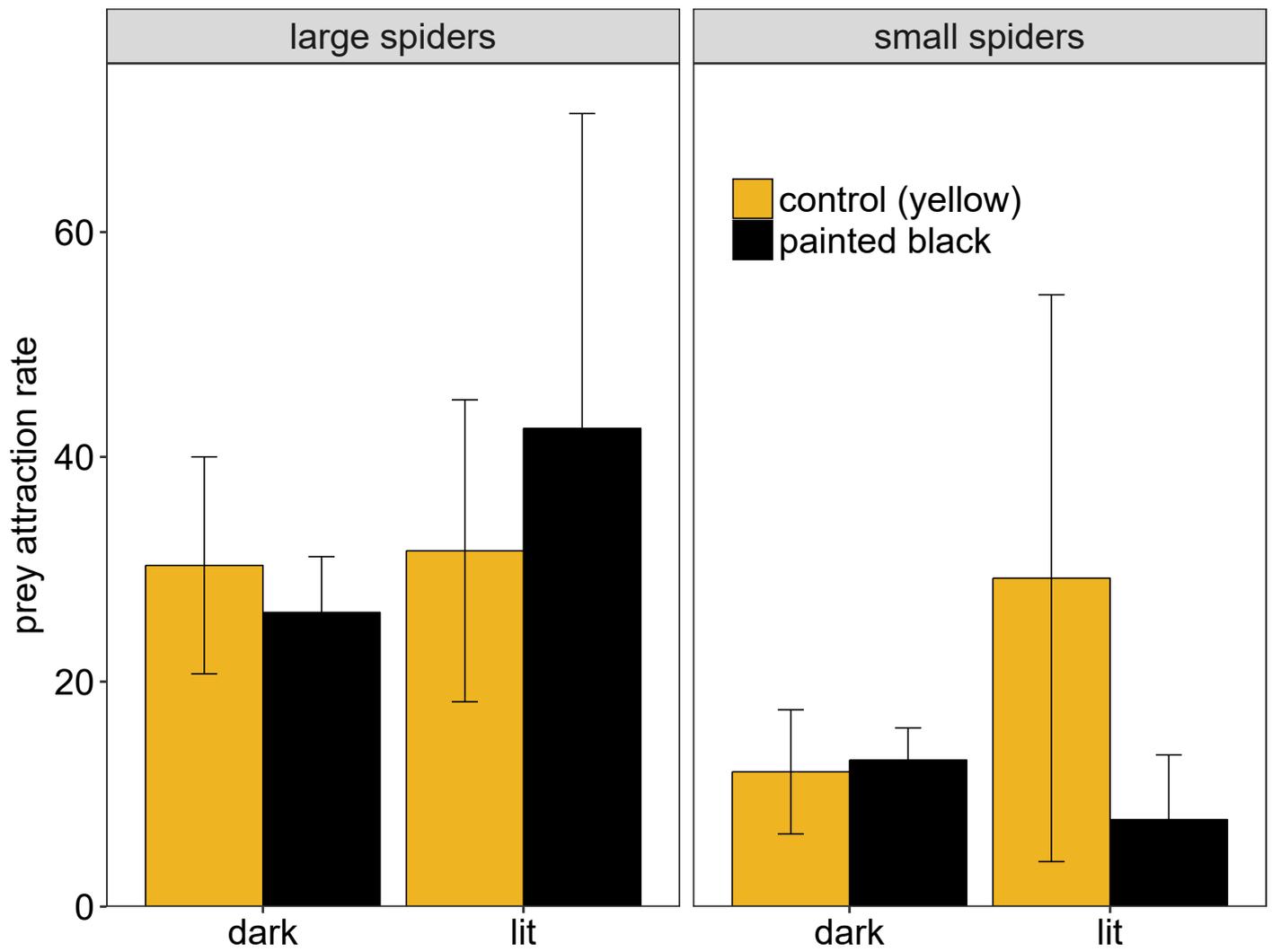
344

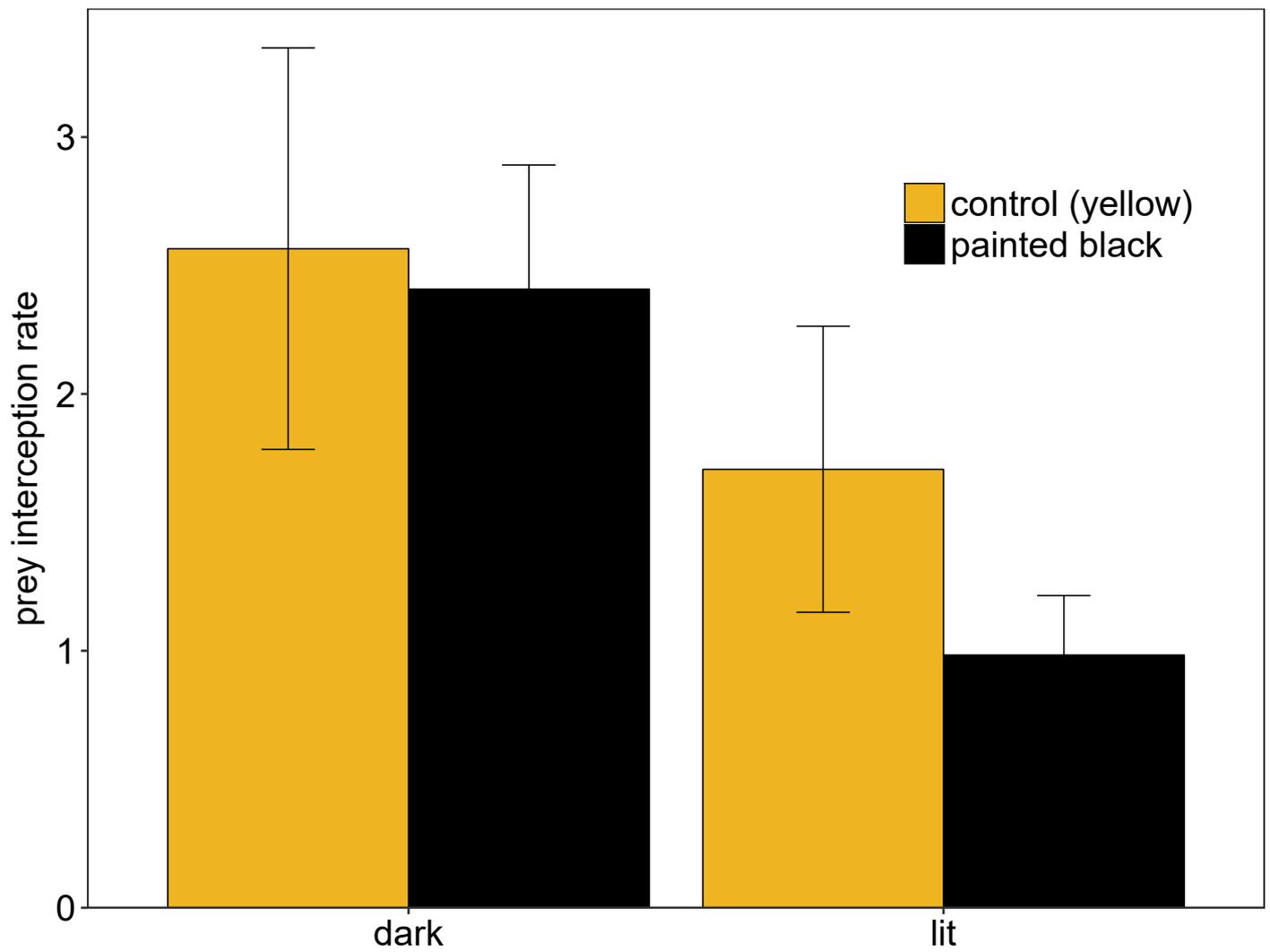
Model results for attraction, interception and interception efficiency.

We used generalized linear mixed models (GLMM) for attraction and interception and linear mixed effects models (LMM) for interception efficiency. Fixed effects include color, light, spider size (Size), and web size (Web). Roman"; co▯ �BG

Models	Log-likelihood	AIC$_c$	AIC$_c$ Delta	Akaike Weight
Moth attraction (GLMM)				
Color, Light, Size, Color:Size	-145.14	312.9	0.00	0.61
Moth interception (GLMM)				
Light	-95.47	201.4	0.00	0.31
Light, Size	-94.29	202.6	1.13	0.18
Color, Light, Size, Color:Size	-90.65	203.9	2.48	0.09
Light, Web	-95.18	204.4	2.92	0.07
Color, Light	-95.39	204.8	3.35	0.06
Light, Size, Web	-93.64	205.3	3.84	0.05
Color, Light, Size	-93.665	205.3	3.89	0.04
Interception efficiency (LMM)				
Light	-20.83	52.2	0.00	0.35
Size	-21.56	53.6	1.47	0.17
Light, Size	-19.90	53.8	1.65	0.15
Color	-22.17	54.8	2.68	0.09
Color, Size, Color:Size	-18.70	55.4	3.24	0.07

Prey attraction rates (number of moths/ hour) across color and light treatments.

Error bars indicate mean ± standard error. Spider size was broken down into categorical variable for visualization, where spiders of 4.5cm or below were identified as small.

Moth interception rate as a function of spider color and light.

Error bars indicate mean ± standard error.

Interception efficiency across color and light treatments.

Error bars indicate mean ± standard error. Spider size was broken down into categorical variable for visualization, where spiders of 4.5cm or below were identified as small.