Camera-trapping estimates of the relative population density of *Sympetrum* dragonflies: Application to multihabitat users in agricultural landscapes

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Although camera trapping has been effectively used for wildlife monitoring, its application to multihabitat insects (i.e., insects requiring terrestrial and aquatic ecosystems) is limited. Among such insects, perching dragonflies of the genus *Sympetrum* (darter dragonflies) are agroenvironmental indicators that substantially contribute to agricultural biodiversity. To examine whether custom-developed camera traps for perching dragonflies can be used to assess the relative population density of darter dragonflies, camera trapping, a line-transect survey of mature adult dragonflies, and a line-transect survey of exuviae were conducted for three years in rice paddy fields in Japan. The detection frequency of camera traps in autumn was significantly correlated with the density index of mature adults recorded during the transect surveys in the same season for both *Sympetrum infuscatum* and other darter species. In analyses of camera-detection frequency in autumn and exuviae in early summer, a significant correlation was observed between the camera-detection frequency of mature adults and the exuviae-density index in the following year for *S. infuscatum;* however, a similar correlation was not observed for other darter species. These results suggest that terrestrial camera trapping has the potential to be effective for monitoring the relative density of multihabitat users such as *S. infuscatum*, which shows frequent perching behavior and relatively short-distance dispersal.

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Abstract

29 Although camera trapping has been effectively used for wildlife monitoring, its application to
30 multihabitat insects (i.e., insects requiring terrestrial and aquatic ecosystems) is limited. Among
31 such insects, perching dragonflies of the genus *Sympetrum* (darter dragonflies) are
32 agroenvironmental indicators that substantially contribute to agricultural biodiversity. To
33 examine whether custom-developed camera traps for perching dragonflies can be used to assess
34 the relative population density of darter dragonflies, camera trapping, a line-transect survey of
35 mature adult dragonflies, and a line-transect survey of exuviae were conducted for three years in
36 rice paddy fields in Japan. The detection frequency of camera traps in autumn was significantly
37 correlated with the density index of mature adults recorded during the transect surveys in the

38 same season for both *Sympetrum infuscatum* and other darter species. In analyses of camera-
39 detection frequency in autumn and exuviae in early summer, a significant correlation was
40 observed between the camera-detection frequency of mature adults and the exuviae-density
41 index in the following year for *S. infuscatum;* however, a similar correlation was not observed
42 for other darter species. These results suggest that terrestrial camera trapping has the potential to
43 be effective for monitoring the relative density of multihabitat users such as *S. infuscatum*, which
44 shows frequent perching behavior and relatively short-distance dispersal.
45

Introduction

47 Technologies for automated and efficient monitoring of biodiversity are becoming increasingly
48 important (Bush et al., 2017). Camera trapping has drawn increasing attention as a relatively
49 reliable, non-intensive, non-invasive, and inexpensive tool (Bilodeau et al., 2022; Delisle et al.,
50 2021).
51 Although farming is typically assumed to harm wildlife inhabiting natural habitats, semi-natural
52 agricultural landscapes with a long history of cultivation typically play an important role in
53 biodiversity conservation (Kadoya and Washitani, 2011; Queiroz et al., 2014). Notably,
54 multihabitat users, which require multiple habitats to complete their life cycles, are critical
55 components of biodiversity in agricultural landscapes (Batary et al., 2020; Kadoya et al. 2009;
56 Kadoya and Washitani, 2011). Multiple ecosystems maintained by natural processes and
57 anthropogenic activities with spatial and temporal heterogeneities have benefited from such
58 organisms (Batary et al., 2020; Kadoya and Washitani, 2011; Yoshioka et al., 2017). Notably,
59 wetland animals such as birds, frogs, dragonflies, and other aquatic insects, which use both
60 terrestrial and aquatic habitats, are expected to be critical components of biodiversity in historical
61 rice cultivation zones, where wet rice paddy systems provide an alternative to natural wet
62 habitats (Kadoya et al., 2009; Kadoya and Washitani, 2011; Katayama et al., 2019).
63 However, few studies have evaluated the use of camera trapping to monitor multihabitat users
64 other than mammals, particularly for small and ectothermic organisms such as insects (Delisle et
65 al., 2021), though some smart image-based classification systems have been developed for pests
66 or flower-visiting insects (e.g., Bjerge et al., 2022). In general, camera trapping can be more
67 easily applied to terrestrial ecosystems than to aquatic ecosystems owing to optical and physical
68 issues and the associated increases in cost (Bilodeau et al., 2022). If terrestrial camera traps can
69 indicate the dynamics of multihabitat users not only at the terrestrial life stage but also at the
70 stage depending on the aquatic environment, they can enhance the effectiveness of camera
71 trapping. This will be helpful in biodiversity monitoring and conservation in agricultural
72 landscapes.
73 Darter dragonflies (*Sympetrum* spp.) can be considered suitable candidates for exploring the
74 potential of camera trapping. They are typical multihabitat users and are known as biodiversity
75 indicators of rice-dominated landscapes in Japan (Inoue and Tani, 2010; Sprague, 2003; AFFRC,
76 NIAES, and NIAS, 2012b; Tanaka, 2016). In spring, larvae typically grow in aquatic habitats,

77   including water-irrigated rice paddy fields. Immature adults emerge in early summer, leave
78   paddies, and stay in cooler habitats, such as forests or mountainous areas, during the summer.
79   They then return to autumn paddies and oviposit as mature adults (Corbet, 1999; Sugimura et al.,
80   1999; Watanabe et al., 2005). Mature adults have red bodies and are a familiar autumn feature in
81   Japan known as *akatombo*, meaning "red dragonfly" (Inoue and Tani, 2010). However,
82   comparisons of the current and past numbers of observed individuals at some locations and
83   questionnaire surveys of odonatologists suggest that the population has rapidly declined in some
84   regions (Jinguji and Ueda, 2015; Nakanishi et al., 2020a,b; Ueda and Jinguji, 2013). Mature
85   adults exhibit a characteristic perching behavior on natural or artificial rod-like materials.
86   Yoshioka et al. (2020) developed a camera-trapping system to automatically detect individuals
87   perching on sticks using inexpensive and energy-saving light sensors. Although Yoshioka et al.
88   (2020) revealed that camera traps set for two days at a research institute could detect perching
89   darter dragonflies with considerable accuracy, it remains unclear whether they can be used to
90   quantitatively assess and monitor the population status of dragonflies in agricultural landscapes.
91   In this study, we explored the effectiveness of camera trapping as a tool for assessing and
92   monitoring the population dynamics of darter dragonflies as indicators of multihabitat users in
93   agricultural landscapes. Using camera traps developed for perching darter dragonflies (Yoshioka
94   et al., 2020), two key questions were examined: 1) whether camera trapping is as effective as the
95   classical survey method (i.e., a line-transect survey) for assessing the relative population density
96   of mature adult darter dragonflies and 2) whether the relative population density of mature adult
97   dragonflies, as determined by camera trapping, indicates the relative population density of
98   exuviae of emerging adult darter dragonflies (determined by aquatic environments). If these are
99   true, we can expect a greater contribution from camera trapping to the monitoring of multihabitat
100   users such as darter dragonflies.

101

Materials & Methods

Study area

104   The study was conducted in a farmland area in eastern Fukushima Prefecture, northeastern Japan
105   (Fig. 1). The area is characterized by typical agricultural landscapes, including rice paddy fields,
106   secondary forests, and woodlands. The area was enclosed within the following four sets of
107   coordinates: (37°47′N, 140°34′E), (37°47′N, 140°59′E), (37°30′N, 140°59′E), and (37°30′N,
108   140°34′E). The annual mean temperature and annual precipitation during 1991–2020 obtained
109   from the Fukushima Local Meteorological Observatory were 13.4 °C and 1207.0 mm,
110   respectively (Japan Meteorological Agency, 2022). The study area was a part of the area targeted
111   by a three-year survey of biodiversity in paddy fields where rice farming was restarted after the
112   lifting of the evacuation order following the Fukushima Daiichi Nuclear Power Plant accident in
113   2011 (National Institute of Informatics, 2022). The study area included six study plots

114 (Harimichi, Imada, Kanaya, Mimigai, Sakata, and Sugaya), each of approximately 0.7–1.2 ha
115 comprising one or a few rice paddy fields (Fig. S1). We were granted verbal permission for
116 conducting the research on each of the farmer's private fields. The farmers were not represented
117 by an organization, but were in a cooperative relationship with the Fukushima Agricultural
118 Technology Centre. Rice farming in Kanaya, Mimigai, Sakata, and Sugaya was suspended
119 during the evacuation and restarted between 2014 and 2018; however, rice farming continued
120 without interruption in Harimichi and Imada. The camera-trapping and dragonfly adult surveys
121 in the autumn of 2018 were not conducted in the Imada plot. Additionally, the target rice paddy
122 fields in Kanaya were changed to neighboring rice paddy fields in 2019 (Fig. S1) because the
123 farmers intended to change farming methods.

Camera-trapping system for darter dragonfly detection

125 Yoshioka et al. (2020) developed the original camera trap system based on the following
126 principles. A perching dragonfly changes the resistance value of an upper light sensor at the tip
127 of a rod-shaped detector relative to a bottom light sensor, changes the difference in signals
128 between the sensors over a certain period, and activates a connected camera to a certain extent,
129 thereby triggering a picture to be taken of the tip of the detector. In addition, if an image is
130 captured, an additional picture is not taken unless the change in the relative signal values
131 between sensors is restored because of dragonfly takeoff. In a previous study, a change of 5%
132 and waiting period of 10 s (8 s for camera rebooting and an additional 2 s for image capture)
133 could adequately detect perching darter dragonflies.
134 The camera trap used in this study comprised a detector section, processor section, and a
135 connected commercial digital camera (TLC 200; Brinno, Inc.). Two CDS cells with a dark
136 resistance of 1 MΩ were used as light sensors in the detector section. The upper cell was then
137 covered with an LED silicone cap. The bottom of each cell was colored black using a permanent
138 marker. These cells were connected to a microprocessor via USB cables. An acrylic pipe (outer
139 diameter: 10 mm; inner diameter: 7 mm; length: 500 mm) was used to enclose the cells. The top
140 of the pipe was surrounded by a 150-mm-wide masking tape as a transmission diffuser and 20-
141 mm-wide black vinyl tape and was capped with a 0.5-mm-thick polyethylene terephthalate plate
142 using an adhesive.
143 In the processor section, an 8-bit PIC microcontroller (Microchip Technology Inc.) was used as
144 the main microprocessor. Signal values of 0–1023 were obtained, which were processed to
145 determine the presence or absence of a perching dragonfly based on the resistance values for
146 each CDS cell in the detector section, which decreased with increasing illumination intensity.
147 More details about the algorithm and materials used in the camera trap can be found in Yoshioka
148 et al. (2020).
149 During the study, the exterior of the processor section was modified to make it easier to check
150 the status of the traps and (re)boot them. Thus, three versions of the camera trap with different
151 exterior materials for the processor section were used (Fig. S2). Version 1 was characterized by a
152 processor section enclosed in a gray polyvinyl chloride (PVC) pipe to prevent rainwater intrusion

153   (Fig. S2a). Two silicone caps, penetrated by the detector section, were inserted at the top of the
154   PVC pipe. The enclosed microprocessor and its switch were attached. Investigators could not see
155   or touch the microprocessor without removing the PVC pipe, which made it difficult to handle
156   the camera trap. Version 2 (Fig. S2b) included a transparent PVC pipe surrounding the
157   microprocessor and microprocessor switch, which was separated from the microprocessor and
158   enclosed in a PVC pipe with a larger diameter below the PVC pipe enclosing the microprocessor
159   and connected to the microprocessor via cables. Investigators could visually check the LED light
160   on the microprocessor (which blinked if it worked correctly). The switch in the separate larger-
161   diameter pipe could be handled relatively easily. However, the part connecting the
162   microprocessor to the switch was vulnerable to corrosion owing to moisture during long-term
163   use. In version 3 (Fig. S2c), the microprocessor and its switch were enclosed in a translucent 400
164   mL polypropylene bottle for salad dressing (MT-TORIMATSU Inc.). The bottle was attached
165   upside down to the PVC pipe with a detector. Cables connected the processor and detector parts
166   through the bottle spout. Investigators could quickly check and handle the processor. Preliminary
167   experiments revealed that the microprocessor was adequately waterproof. In addition, versions 1
168   and 2 used three AA nickel hydride batteries for the processor, whereas version 3 used three
169   AAA nickel hydride batteries. In the survey, the PVC pipe with the detector part was attached to
170   a tripod or woodpile to adjust the height of the camera trap (approximately 2 m), regardless of
171   the camera trap version.
172

173   Darter dragonfly survey using camera traps

174   A camera-trapping survey was conducted from 2018 to 2020 in the study plots. For each year in
175   each plot, three camera traps were set up from the end of August to early September, and data
176   were collected from the end of October to early November (Table S1). To cover a large area
177   within a plot without disturbing farming, three camera traps were located on the levees of the
178   paddy fields so that they were as far from each other as possible within the plot (Fig. S1).
179   Although the traps were removed at the end of the study season every year, the levees where trap
180   were set were consistent across years, and each trap location in each plot was assigned a location
181   ID. When the trap location was changed at the field level, as in the case of Kanaya, a new
182   location ID was assigned. Different versions of the camera trap were equally allocated to each
183   plot, to the maximum extent possible. Every year, the detector parts of each version were
184   randomly allocated to plots and locations to minimize the effects of individual camera traps.
185   Each camera trap was inspected during early October. We manually intercepted the top of the
186   detector and checked it for successful autodetection. In addition, after the transect surveys or
187   typhoon events, the camera traps were briefly checked to ensure that they did not fall or run out
188   of battery power. When necessary, the traps were reset by rebooting camera traps, exchanging
189   batteries, and exchanging camera traps.
190   All pictures automatically captured by the camera traps and recorded in SD memory cards in the
191   cameras were visually checked, and those correctly capturing darter dragonflies were recorded as

192 darter dragonfly detection events (hereinafter, the frequency of these events is called "camera-
193 detection frequency"). If two pictures were captured within 5 s, the former was removed from
194 the analyses to avoid overestimating dragonfly detection following Yoshioka et al. (2020).
195 Because the signal to wake up the camera was sent a few seconds before the signal to capture a
196 picture, an extra picture was obtained if the camera was already active.
197 *S. infuscatum* (noshime-tombo, in Japanese) was recorded based on its characteristic dark spot on
198 the tip of each wing; this species can be easily distinguished from other darter species (Yoshioka
199 et al., 2020). Because the identification of other darter dragonflies at the species level was
200 difficult owing to low image resolution, they were pooled in subsequent analyses. Most other
201 darter dragonflies were likely the autumn darter *S. frequens* because this species was dominant
202 based on a transect survey, and we did not directly observe darter dragonflies other than *S.*
203 *frequens* and *S. infuscatum* perching on the camera traps during the survey season. These two
204 species are typical darter dragonflies reproducing at rice paddy fields in Japan (Jinguji, et al.,
205 2019) and are considered suitable as biodiversity indicator species of paddy fields (AFFRC,
206 NIAES, and NIAS, 2012b). Both males and females of these species are known to exhibit
207 perching behavior (Miyakawa 1994; Watanabe et al. 2004), while males do not clearly exhibit
208 territorial behavior (Taguchi and Watanabe, 1986; Sugimura et al., 1999; Watanabe et al., 2004).
209 In addition, mark-recapture studies have shown that the recapture rates of these species are
210 generally quite low (Taguchi and Watanabe 1986; Watanabe et al., 2004; Fukui, 2012) and it is
211 considered unlikely for a particular individual to stay perched at the same point for more than a
212 day (Fukui, 2012).
213 Owing to external factors, such as adverse weather and unanticipated internal factors, the period
214 for which the camera traps worked effectively varied. To standardize the dragonfly detection
215 frequency among camera traps, the occasion index (i.e., the period during which each camera
216 trap effectively worked each year) was also required. To calculate this value, the dates on which
217 pictures were taken were obtained; history of camera trap setting, resetting, and collection were
218 checked; and periods starting with the camera trap (re)setting and ending with the last picture
219 before resetting (or successfully capturing a picture through an operation check at the end of the
220 survey) were extracted. "Last pictures" included pictures with an appropriate view of the tip of
221 the detector, regardless of the presence of a dragonfly (pictures captured from a fallen camera
222 were invalid because such traps were considered ineffective). Although the exact date when
223 camera traps became ineffective could not be determined, the date of the last picture before
224 resetting is typically used in camera trap monitoring (Fukasawa et al., 2016). In this study,
225 autodetection (irrespective of whether the dragonflies were correctly detected) typically occurred
226 daily when the camera trap was active (Yoshioka et al., 2020). Second, the length of each period
227 was calculated as the difference between the date of (re)setting the camera trap and the last date
228 when a picture was captured before reset or the date of camera trap collection. Finally, the length
229 of each segment was summed as the number of occasions per camera trap per year. Thus, the
230 occasion index at the location in the year can be formulated as follows:
231

232 $$occasion = \sum_{i=1} \left(d^{last}_i - d^{set}_i \right)$$

233

234 where d^{last}_i is the date of the last picture in the i-th segment and d^{set}_i is the date of the (re)setup of
235 the camera trap.
236 For example, consider the case in which a camera trap was set up on September 5, reset in
237 response to a technical issue identified on September 19, and collected on October 31 with
238 depleted batteries. The last picture before September 19 was captured on September 11, and the
239 last picture before October 31 was captured on October 30. In this case, the occasion index for
240 the trap was (September 11 – September 5) + (October 30 – September 19) = 6 + 41 = 47. If a
241 camera trap remained active without any issues, the number of days between the date of setup
242 and the date of collection corresponded to the occasion index.

243

244 Transect survey of adult darter dragonflies in autumn

245 A line-transect survey was conducted as a classical method for measuring the relative population
246 density of adult dragonflies (Bouwman et al., 2009; Pearce-Higgins and Chandler, 2020). This
247 survey was conducted in the autumn of 2018, 2019, and 2020. Each study plot was surveyed
248 twice (once each in September and October) from 9:30 to 17:00 h on days with mild wind and no
249 measurable precipitation. According to the number of paddy fields in the plots, 8–16 line
250 transects of 10 × 2 m were set along the levees of the rice paddy fields in each plot. Four line
251 transects per rice field were set, except for the Mimigai plot, which had one large rice paddy
252 field. During the line-transect survey, the investigator slowly (about 0.15 m/s) walked in one
253 direction while searching for dragonflies within the line transect, and the number and species of
254 darter dragonflies were recorded for each transect. When relatively small and inconspicuous
255 individuals, such as females of *S. kunckeli* (maiko-akane in Japanese) or *S. eroticum* (foot-tipped
256 darter), were observed, a sweeping net of 50 cm in diameter was used to capture and evaluate
257 them. For each year and plot, the adult-density index by line transects for *S. infuscatum* was
258 obtained for analysis as follows:

259

260 *adult-density index by line transects* $= \left(\frac{n_{inf1}}{n_t} + \frac{n_{inf2}}{n_t} \right) / 2,$

261

262 where n_{inf1} and n_{inf2} are the total numbers of observed *S. infuscatum* in the first and second
263 surveys, respectively, and n_t corresponds to the total number of line transects in the plot per
264 survey. In the same way, the adult-density index by line transects of other darter dragonflies (i.e.,
265 darter dragonflies other than *S. infuscatum*) was calculated.

266

267 ## Transect survey of exuviae of darter dragonflies in early summer

268 Population growth of darter dragonflies may be related to the quality of the local aquatic
269 environment rather than to the abundance of adults with high mobility that oviposit at poor-
270 quality aquatic sites (Raebel et al., 2010). Therefore, sampling exuviae of emerged adults is a
271 highly effective method for surveying viable populations of dragonflies and the quality of local
272 aquatic environments, although it has some disadvantages, such as low detectability
273 (Pearce-Higgins and Chandler, 2020). This method has been recommended for surveys of darter
274 dragonfly densities in rice paddy fields in Japan (Baba et al., 2019; Mitamura et al., 2013;
275 Nakanishi et al., 2022). In this study, Mitamura et al. (unpublished data) collected a part of the
276 dataset to survey the biodiversity in rice paddies after the Fukushima nuclear disaster. The data
277 set for darter exuviae was obtained following a sampling protocol based on a survey and
278 evaluation manual for indicator animals of functional agrobiodiversity compiled by the national
279 government of Japan (AFFRC, NIAES, and NIAS, 2012a; Mitamura et al., 2013). In this survey,
280 four 10 m line transects per rice field were set along the levees of the rice paddy fields in each
281 plot. The investigators visited each plot twice a year during the daytime, from late June to early
282 July in 2018–2020. During the line-transect survey, an investigator walked slowly in one
283 direction while searching for and collecting exuviae of dragonflies on rice plants up to the third
284 row of rice hills from the edge of the levees (corresponding to a width of approximately 1 m).
285 The collected exuviae were identified to the species level in the laboratory. The number of
286 exuviae in the two surveys was summed for each transect in each year (hereinafter, "exuviae-
287 density index by line transects"). This index was expected to show the relative density of the
288 exuviae rather than the absolute density.
289

290 ## Statistical analyses

291 To examine whether the camera-detection frequency of adult darter dragonflies reflected the
292 adult-density index by line transects, a generalized linear mixed model (GLMM) with a negative
293 binomial error distribution was constructed. In the GLMM, the camera-detection frequency of *S.*
294 *infuscatum* (n = 51) was the response variable, adult-density index by line transects of *S.*
295 *infuscatum* was the explanatory variable, and the log of the occasion index was the offset term.
296 The year, study plot, location ID of a trap nested within a study plot, and trap version were
297 included as random effects. The adult-density index by line transects of *S. infuscatum*, was log-
298 transformed before the GLMM to obtain a more likely relationship between the density of
299 dragonflies and the camera-detection frequency as suggested by Yoshioka et al. (2020). That is, a
300 larger abundance of dragonflies would not always correspond to a higher camera-detection
301 frequency when the number of camera traps is smaller than the abundance of dragonflies because
302 only a small portion of individuals can occupy the detector in a short term. Therefore, log
303 transform to reduce the weight of larger values of the adult-density index by line transects was
304 desirable to obtain a more proportionate relationship with camera-detection frequency. Because
305 the data of *S. infuscatum* included zero values, 0.5 was added before log transformation (i.e.,

306 log(adult-density index by line transects of *S. infuscatum* + 0.5)) following the recommendation
307 of Yamamura (1999). Similarly, the effect of the adult-density index of other darter dragonflies
308 on their camera-detection frequency was examined.
309 In addition, relationships between exuviae surveyed in early summer, as an indicator of the
310 quality of the local aquatic environment, and adult darter dragonflies detected by camera traps in
311 the autumn were examined. The exuviae-density index by line transects of *S. infuscatum* for each
312 line transect in each year was divided by two to obtain the mean of the two surveys and averaged
313 to obtain the mean exuviae density of *S. infuscatum* (the explanatory variable). The effect of the
314 mean density of *S. infuscatum* exuviae on the camera-detection frequency of *S. infuscatum* in the
315 same year was examined using a GLMM with a negative binomial error distribution (n = 51).
316 The log-transformed occasion index was included as the offset term, and the year and location ID
317 of a trap nested within the study plot were used as random effects. The effect of the camera-
318 detection frequency of *S. infuscatum* on the exuviae-density index of the transects of *S.*
319 *infuscatum* in the following year was also examined. The camera-detection frequency divided by
320 occasion index was averaged in each plot for each year as the mean detection frequency per
321 occasion. A GLMM with a negative binomial error distribution was then constructed using the
322 exuviae-density index by line transects of *S. infuscatum* for each transect in each year as a
323 response variable (the sum of values from two surveys was used rather than the mean because
324 integer values were required for the GLMM with negative binomial) and the mean detection
325 frequency per occasion of the previous year as an explanatory variable (n = 116). In the model,
326 year and transect nested within the rice paddy fields and study plots were included as random
327 effects. Similarly, the relationships between the exuviae-density index of other darter dragonflies
328 and detection frequencies of these species were examined. The GLMM was implemented using
329 the glmmTMB function in the glmmTMB package version 1.1.2 for R version 4.0.3 (Brooks et
330 al., 2017; R Core Team, 2020). See Code S1 for details of the GLMM.
331

Results

333 Our camera traps detected 23,084 pictures of darter dragonflies during autumn over three years
334 (Table S2). The most detected dragonflies were "other darter dragonflies" (i.e., species other
335 than *S. infuscatum*). The occasion index for camera traps (mean ± standard deviation) was 42.76
336 ± 11.14 days. From the line-transect surveys of adults in the autumn, the summer darter *S.*
337 *darwinianum*, banded darter *S. pedemontanum*, *S. kunckeli*, and *S. eroticum* were recorded in
338 addition to the major species *S. infuscatum* and *S. frequens* (Table S3). *S. frequens* was the most
339 abundant species in most plots, whereas *S. infuscatum* was the most abundant species in the
340 Harimichi plot. In line-transect surveys in early summer, exuviae of *S. infuscatum* were
341 documented in only Harimichi and Imada plots (Table S4). Most of the sampled exuviae were *S.*
342 *frequens*; however, *S. infuscatum*, *S. darwinianum* and *S. kunckeli* were also obtained. All
343 *Sympetrum* species observed in this study were univoltine (Inoue and Tani, 2010). Therefore, the

344 exuviae in the following year corresponded to the next generation of the adults detected in the
345 autumn.
346 A GLMM revealed significant positive relationships between the camera-detection frequency
347 and adult-density index by line transects (p = 0.000209 and 0.00296, respectively) for both *S.*
348 *infuscatum* and other darter dragonflies (Table 1; Fig. 2; Table S5). The estimated random effects
349 ($\pm$ conditional standard deviation) for each level of the trap version by the *ranef* function (Code
350 S1) were very small (*S. infuscatum*: version 1 $-2.00 \times 10^{-8} \pm 2.08 \times 10^{-4}$, version 2 $1.77 \times 10^{-8} \pm$
351 2.01×10^{-4}, version 3 $-1.41 \times 10^{-9} \pm 1.75 \times 10^{-4}$; other darter dragonflies: $3.91 \times 10^{-12} \pm 3.67 \times 10^{-6}$, -
352 $4.64 \times 10^{-12} \pm 4.29 \times 10^{-6}$, $2.86 \times 10^{-13} \pm 1.28 \times 10^{-6}$, respectively) relative to the fixed effects in Table
353 1. The relationships between exuviae and camera-detection frequencies in the same year were
354 not significant for *S. infuscatum* or for other darter dragonflies (Table 2; Fig. 3). A significant
355 positive relationship between the camera-detection frequency and the exuviae-density index in
356 the following year was obtained for only *S. infuscatum* (Table 3; Fig. 4). The analyses using the
357 adult-density index and the exuviae-density index of *S. frequens* instead of those of other darters
358 showed similar results (Table S8).
359
360

Discussion

361

362 Our results demonstrated that the detection frequency of darter dragonfly adults in autumn using
363 camera traps was positively correlated with the density index of adults obtained by transect
364 surveys for both *S. Infuscatum* and other darters. Thus, camera trap data represent a quantitative
365 indicator of the relative population density of mature adults of these dragonflies. A short-term
366 (two days) analysis of camera traps (Yoshioka et al., 2020) suggested that the correlation
367 between the camera-detection frequency and observational survey results is weak. Thus, the
368 camera-detection frequency might not reflect the true density of dragonflies, owing to the
369 dominant perching behavior of a small number of individuals (i.e., the detection frequency might
370 be saturated against density). However, over a longer study period (exceeding one month), our
371 findings suggest that the detection frequency obtained using adequate traps (three traps per plot
372 in our study) can accurately reflect the log-transformed density index of adult dragonflies
373 measured by line-transect surveys. The results for other darters here were considered to mainly
374 reflect the density of *S. frequens*, given their large abundance in the line-transect surveys, field
375 observations of perching behavior on the traps, and the results of analyses using data of *S.
376 frequens* in the line-transect surveys instead of other darters. Therefore, the results suggest
377 applicability of our camera trap to the mature adults of *S. infuscatum* and *S. frequens* during the
378 autumn in our study system. These two species are known to be typical and symbolic
379 biodiversity indicator species of rice paddy fields in Japan (AFFRC, NIAES, and NIAS, 2012b;
380 Jinguji et al., 2019). The camera trap version, which changed only the processor section and did
381 not change the detector part of the trap, was suggested to have hardly any effect on the results, as
382 shown by the small random effects relative to the fixed effects.

383 Although the detection frequency of camera traps reflected the population density of mature
384 adults, it was not predicted by the density of exuviae of new darter adult dragonflies. These
385 results suggest that the density of exuviae is not clearly related to the density of adult *S.
386 infuscatum* or other species in autumn of the same year. Adult darter dragonflies may be
387 substantially affected by environments other than farmlands (e.g., woodlands) that are inhabited
388 by individuals at the immature stage until they migrate to farmlands. However, our study was
389 limited to farmlands and did not evaluate different habitats.
390 Furthermore, the detection frequency of *S. infuscatum* was positively related to the exuviae
391 density in the following year; however, a similar relationship was not observed for other darter
392 dragonflies. These species-dependent relationships may be explained by differences in dispersal
393 ecology between *S. infuscatum* and *S. frequens* (the latter was the dominant species among other
394 darter dragonflies in our study). Specifically, *S. frequens,* which migrates to farmlands in autumn
395 from distant cooler areas several dozens of kilometers away (Corbet, 1999), makes it possible to
396 maintain a high density of mature adults in "sink" farmlands with a less suitable aquatic
397 environment for larvae. However, *S. infuscatum*, which returns to nearby paddy fields from
398 surrounding forests (Watanabe et al., 2004; Watanabe et al., 2005), may not be able to maintain
399 high population densities in farmlands with unsuitable aquatic habitats. Alternatively,
400 considering that males of *S. frequens* are known to be more abundant than females during late

401 autumn in paddy fields (Taguchi and Watanabe, 1986), if the number of females of *S. frequens*
402 was unexpectedly small in a plot with apparently high abundance of adults, it might result in
403 limited exuviae abundance of the next generation in the plot. Because we did not obtain adequate
404 data on sex in this study, we could not exclude this hypothesis. However, *S. infuscatum* similarly
405 shows higher male abundance in the paddy fields (Watanabe et al., 2004). In addition, a previous
406 study of *S. frequens* (Taguchi and Watanabe, 1986) showed that it is not rare that female
407 abundance in autumn does not explain the abundance of new emergent adults at the same
408 locations in the next year. Another likely and not mutually exclusive explanation is that low
409 detectability in the exuviae survey (Pearce-Higgins and Chandler, 2020) makes detecting the
410 relationships for other darter species difficult. Mitamura (2013) reported that the exuviae density
411 of darter dragonflies (mainly *S. frequens*) substantially varied within a few weeks. In our study, a
412 small number of line transects showed extremely high densities, and many transects showed zero
413 values. At the very least, however, the lower frequency of exuviae of *S. infuscatum* (found at
414 only two plots during three years) compared with *S. frequens* appears to be due to low abundance
415 in our study system and not due to lower detectability in the line-transect surveys than that of *S.*
416 *frequens*, given that the size of their exuviae is similar (Inoue and Tani, 2010) and the timing of
417 emergence of exuviae of these species is known to overlap (Jinguji et al., 2019). Although the
418 perching behavior of darter dragonflies in farmlands in early summer is considerably less
419 conspicuous, camera trapping during this season may resolve this issue. Notably, our preliminary
420 camera traps set in a few farmlands in early summer detected some darter dragonflies, although
421 the frequency was lower than in autumn. In addition, discerning the exuviae of *S. infuscatum*
422 from those of the summer darter *S. darwinianum* is relatively difficult owing to their
423 morphological similarity (Ozono et al., 2019). Accordingly, camera trapping for adults is a
424 complementary tool because adult *S. infuscatum* can be easily identified.
425 Although the results demonstrated that our camera trapping focusing perching behavior would be
426 effective for surveying the relative population density of a few indicator species (*S. infuscatum*,
427 and partly, *S. frequens*) in some paddy-dominated landscapes in Japan, there are many steps
428 required for camera trapping to be alternative to, or supporting tool for, monitoring programs
429 targeting whole communities of dragonflies. First, applicability of the traps to darters other than
430 *S. infuscatum* and *S. frequens* remains to be demonstrated, though these two species are typical
431 darters that reproduce in the paddy fields in Japan. Thus, application of the camera traps to areas
432 with a higher density of other darter species requires a caveat. Males of some species may show
433 more conspicuous territorial behavior and bias the camera-detection frequency. Also,
434 improvement of hardware may be required. For example, it is necessary to set the camera closer
435 to the top of detector to capture keys for identifying species and/or sex, which are usually found
436 on the side of the thorax and the base or tip of the abdomen (Sugimura et al. 1999). In addition,
437 there is a room to improve the effort required for application of our method. In this study, field
438 work (setting, checking, and collecting traps) for camera trapping roughly required two person-
439 hours for each plot (three camera traps) per season (autumn). However, the time required for
440 visual inspection of all captured images was roughly estimated as 10 person-hours for each plot

441 (three camera traps) per season. This appeared not to be time-efficient considering that line-
442 transect surveys of adult darters took about one hour for each plot per season. Further, a long-
443 term monitoring survey of the Odonata community by Dolný et al. (2021), for example, took
444 eight (two hours × four visits) person-hours for each site per season (May to September). To
445 conduct monitoring sustainably with limited effort, techniques for thinning pictures or automatic
446 image classification will be required. Furthermore, percher species does not always prefer to stay
447 on the top of a perch. Damselflies often stay on the side of a perch. In ecosystems with a more
448 complex vegetation structure, the perch-like detector may be overlooked by dragonflies. To
449 automatically capture them, development of other detectors or post-process of time-lapse
450 pictures by automatic image classification technique may be alternatives. Not only the type of
451 ecosystem, but also social aspects may also be important for the applicability of camera trapping.
452 In this study, no camera trap was lost, but risk of vandalism may be not low in other countries or
453 regions. Under such circumstances, the understanding and cooperation of local community
454 members may be more important for camera trapping studies (Sharma et al., 2020).
455 Nevertheless, our camera trapping showed some merits compared with traditional field survey
456 methods. Continuous monitoring would lead to high detectability. Our camera traps detected *S.*
457 *infuscatum* at all the six plots, but line-transect surveys for adults and exuviae detected the
458 species at five and two plots, respectively. In addition, camera trapping was also less affected by
459 weather and the schedule of the trained investigator. Furthermore, evidence of monitoring could
460 be stored in a digital format. Applicability to difficult-to-enter zones (such as remote islands or
461 evacuation zones) will be a merit of our method (Yoshioka et al. 2020), though this may be
462 beyond the scope of our present study in the agricultural landscapes.

463 Conclusions

464 Our results suggest that camera traps are effective not only for measuring the density index of
465 adult darter dragonflies in terrestrial habitats but also, to some extent, for indicating exuviae
466 density, which reflects aquatic habitat status. These results suggest the potential of applying
467 camera traps to other multihabitat users inhabiting agricultural landscapes, such as waterfowls,
468 amphibians, and other aquatic insects. Compared with terrestrial environments, camera trapping
469 has been applied in aquatic environments to a lesser extent (Bilodeau et al., 2022, but see
470 McCleery et al., 2014).
471 The applicability of terrestrial camera trapping to analyze population dynamics, including life
472 stages in aquatic habitats, may depend on species and life history traits. Our study suggested that
473 dispersal traits or spatial scale may be key factors explaining difference between *S. infuscatum*
474 and other darters (mainly *S. frequens*). However, true population density and dynamics were not
475 analyzed in this study and may require a mark-recapture technique. Although the recapture rate
476 of the darters in Japan is generally low (Taguchi and Watanabe 1986; Watanabe et al. 2004;
477 Fukui 2012), our camera trap can serve as a good continuous observer because marks on the
478 wings of perching dragonflies are expected to be relatively easily captured in a picture.

479 At present, our study has demonstrated the applicability of camera trapping to only a small
480 number of biodiversity indicator species in limited landscapes. There is still room for
481 improvement in automatic monitoring of Odonata diversity. Nevertheless, by revealing the
482 benefits and limitations of camera trapping, our study provides a basis for developing a
483 combination of efficient and sustainable biodiversity monitoring tools. For example, eDNA is a
484 promising tool for efficiently identifying aquatic fauna; however, this approach is less effective
485 for the quantification of population dynamics and community composition, owing to detection
486 uncertainty (Fukaya et al., 2022). Combining screening of indicator species using eDNA
487 metabarcoding and continuous and quantitative monitoring by camera traps customized to the
488 species may be effective. In addition, underwater camera trapping, a developing technique for
489 monitoring ocean biodiversity (Bilodeau et al., 2022), may be combined with the biodiversity
490 monitoring of agricultural landscapes, including rice paddies. Surveys based on expert
491 observations are expected to play an essential role in validating new tools. Complex
492 combinations of monitoring tools will generate rich biodiversity data and robust statistical
493 inferences (Iijima et al., 2013), providing a basis for evidence-based conservation policy-making.
494

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500

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645

Figure 1

Study area.

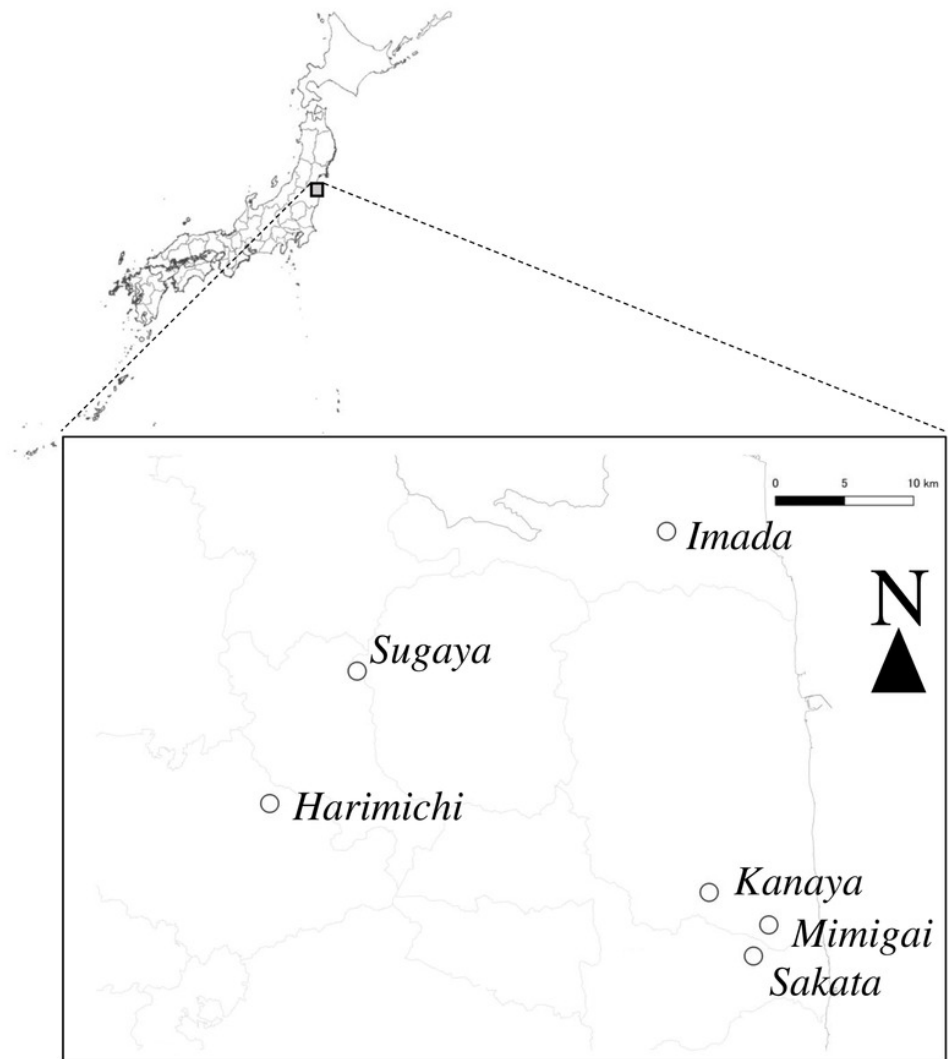
Open circles show the study plots. The background maps were obtained from the Geospatial Information Authority of Japan (2013) following the Geospatial Information Authority of Japan Website Terms of Use (https://www.gsi.go.jp/ENGLISH/page_e30286.html, accessed 2022-11-11), which is compatible with the Creative Commons Attribution License 4.0 (https://creativecommons.org/licenses/by/4.0/legalcode, accessed 2022-11-11).

Source of the background maps:
Geospatial Information Authority of Japan

Figure 2

Relationships between the mean adult-density by line-transects of darter dragonflies and mean camera-detection frequency per occasion of them for each year each plot.

Solid and open symbols correspond to *S. infuscatum* and other darter dragonflies, respectively. Squares, circles, and triangles correspond to 2018, 2019, and 2020, respectively. When a statistically significant effect of the explanatory variable was obtained, the prediction curve (solid line) and 95% confidential intervals (dashed lines) by GLMM (all random effects were set to zero, and new random effect levels were not considered for simplicity) were also plotted. Thick and thin lines correspond to predicted values for *S. infuscatum* and other darter dragonflies, respectively.

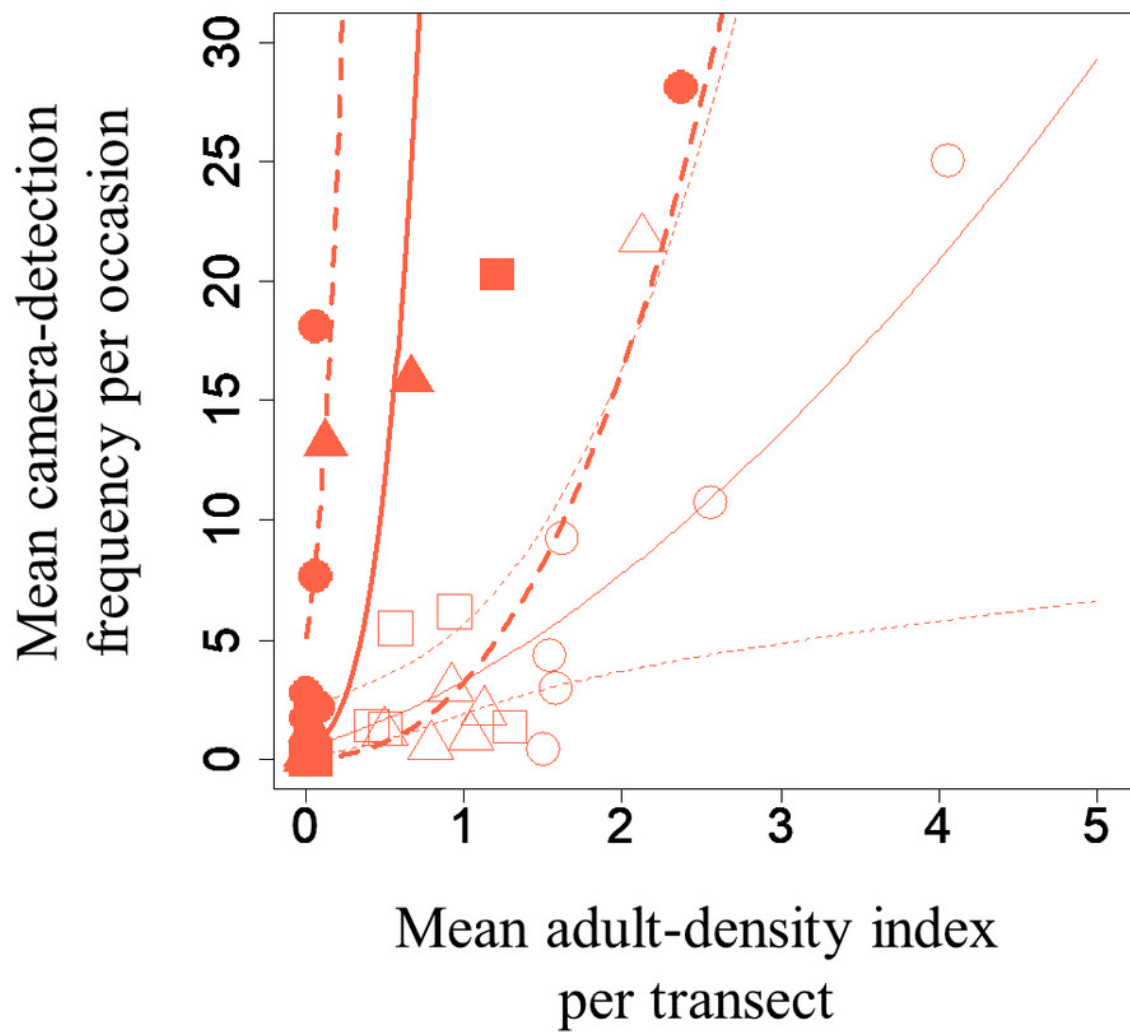



Figure 3

Relationships between the mean exuviae-density index per transect obtained from the line-transect survey in early summer and mean camera-detection frequency per occasion in the same year.

(a) *S. infuscatum* and (b) other darter dragonflies. Squares, circles, and triangles correspond to 2018, 2019, and 2020, respectively.

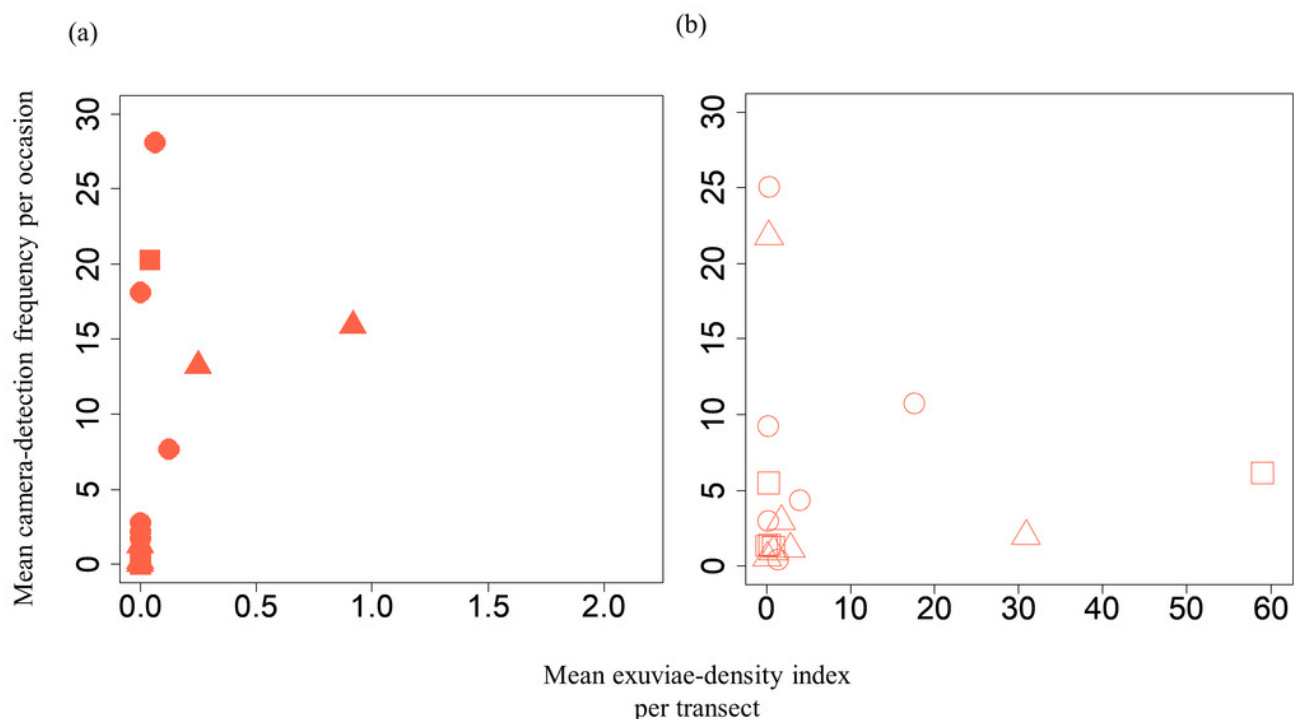
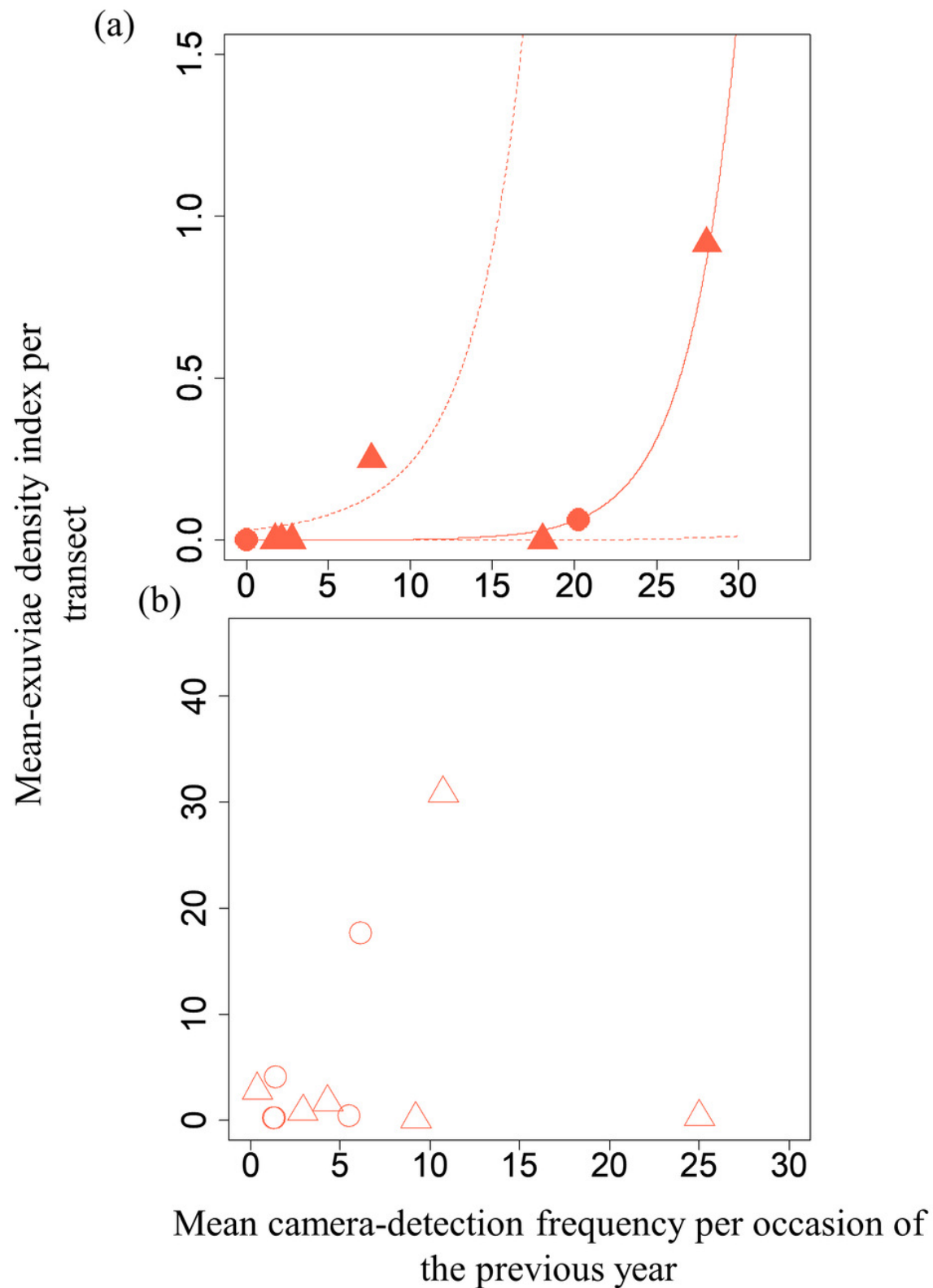



Figure 4

Relationships between the mean exuviae-density index per transect obtained by line-transect survey in early summer and mean camera-detection frequency per occasion in the autumn of the previous year.

(a) *S. infuscatum* and (b) other darter dragonflies. Circles and triangles correspond to 2019 and 2020, respectively. Because the result of GLMM for *S. infusactum* exhibited a statistically significant effect of the explanatory variable, the prediction curve (solid line) and 95% confidential intervals (dashed lines) were plotted (all random effects were set to zero, and new random effect levels were not considered for simplicity).

Results of GLMM which estimated the effects of log-transformed mean adult-density index by line-transect survey on camera-detection frequency for (a) *S. infuscatum* and (b) other darter dragonflies.

1 Table 1. Results of GLMM which estimated the effects of log-transformed mean adult-density
2 index by line-transect survey on camera-detection frequency for (a) *S. infuscatum* and (b) other
3 darter dragonflies.

Explanatory variables (Fixed effects)	Estimated value	Standard Error	Z value	P value (Z)
(a)				
Intercept	2.45	1.43	1.72	0.0862
Mean adult-density index of *S. infuscatum* (log-transformed + 0.5)	5.13	1.38	3.71	0.000209
(b)				
Intercept	0.508	0.379	1.34	0.180
Mean adult-density index of the other darter *dragonflies* (log-transformed + 0.5)	1.68	0.566	2.97	0.00296

Results of GLMM which estimated effects of mean exuviae density index by line-transects in early summer on camera-detection frequency for adults in autumn of the same year.

(a) *S. infuscatum* and (b) other darter dragonflies

1 Table 2. Results of GLMM which estimated effects of mean exuviae density index by line-
2 transects in early summer on camera-detection frequency for adults of (a) *S. infuscatum* and (b)
3 other darter dragonflies in autumn of the same year.

Explanatory variables (Fixed effects)	Estimated value	Standard Error	Z value	P value (Z)
(a)				
Intercept	0.447	1.46	0.307	0.759
Mean exuviae-density index of *S. infuscatum*	-0.456	2.63	-0.173	0.862
(b)				
Intercept	1.36	0.488	2.789	0.00529
Mean exuviae-density index of the other darter dragonflies	0.00820	0.0234	0.350	0.726
☐	☐	☐	☐	☐

Results of GLMM which estimated the effects of mean camera-detection frequency of adult individuals in autumn of the previous year on mean exuviae-density index in early summer.

(a) *S. infuscatum* and (b) other darter dragonflies.

1   Table 3. Results of GLMM which estimated the effects of mean camera-detection frequency of
2   adult individuals in autumn of the previous year on mean exuviae-density index in early summer
3   for (a) *S. infuscatum* and (b) other darter dragonflies.

Explanatory variables (Fixed effects)	Estimated value	Standard Error	Z value	P value (Z)
(a)				
Intercept	-8.79	3.04	-2.89	0.00384
Mean camera-detection frequency per occasion of *S. infuscatum* in the previous year	0.333	0.110	3.02	0.00254
(b)				
Intercept	0.926	0.673	1.38	0.169
Mean camera-detection frequency per occasion of the other darter dragonflies in the previous year	-0.0228	0.0264	-0.86	0.388
☐				
	☐	☐	☐	☐