


Reproductive behavior of *Erythrodiplax abjecta* (Rambur, 1842) from Andean Mountains

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Abstract. Research about the behavior of Neotropical species is crucial to understand how the rapid environmental changes in the Neotropics affect the reproduction of various organisms. The reproductive behavior of insects in tropical ecosystems, such as those belonging to the order Odonata, is as yet scarcely known. In this article, the reproductive behavior of *Erythrodiplax abjecta* is described from several localities in the Colombian Andean Mountains. Playing out between 10:00 and 14:30 h, male individuals of this species may exhibit either territorial or satellite behavior. Sexually mature males and females engage in tandem and copulation behaviors, which are brief and may occur either perched or in flight. Females of *E. abjecta* oviposit directly in the water at various times, alternating with periods of rest. During oviposition, males stand guard over females, perched or hovering, in a quest to protect them against other males. Conspecific males have been observed to engage in sieges of perching or ovipositing females, as well as mating pairs. Following a siege, either the female or the original pair flees, or the besieging male will succeed in outcompeting the original male, take the female in tandem, copulate with her, and then guard her while she oviposits. If the female flees, she may perch elsewhere, continue ovipositing, or may be taken by another male. The intense male guarding behavior during oviposition could represent an adaptation to temporarily high male densities at oviposition sites and a high level of competition during the short period in which active copulation takes place.

Research Article

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All relevant data are within the paper.

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Introduction

Studies on odonate reproductive behavior have revealed that dragonflies exhibit considerable variation in reproductive parameters (Clausnitzer, 2002; Conrad & Pritchard, 1992; Miller, 1983; Miller & Miller, 1985; Ware et al., 2012). As a result, studying odonates has become captivating and interesting work due to their enormous behavioral diversity, the conspicuity of the males, and the opportunity to collect data on these organisms in the field (Corbet, 1999). Although some studies have already been conducted on Neotropical libellulid reproductive behavior (e.g., Bañuelos-Irusta & Araujo, 2007, and references therein), our understanding of the behavior of most South American species remains limited (Miguel et al., 2017).

The Libellulidae is a family of the suborder Anisoptera in which two types of mate-guarding behavior during oviposition are observed: (a) non-contact guarding, where the male accompanies the ovipositing female, or (b) tandem guarding, where the male physically attaches himself to the ovipositing female (cf., Conrad & Pritchard, 1992; Ware et al., 2012). In species with a short tandem phase, the male leaves and the female continues to lay her eggs independently (Beckemeyer, 2004; Sternberg & Buchwald, 2000). While egg size is random in tandem guarding species, egg size is inversely proportional to the laying order in non-contact guarding species, (Schenk et al., 2004).

Erythrodiplax Brauer, 1868 is a highly diverse genus within the Libellulidae family that comprises at least 60 known species (Schorr & Paulson, 2023). Most of these species are considered generalists, except for the saline-dwelling *E. berenice* (Drury), and the bromeliad ovipositors *E. laselva* Haber, Wagner & De La Rosa and *E. bromeliicola* Westfall (Haber et al. 2015; Needham et al., 2000; Wilson, 2008). They show greater behavioral diversity due to their ability to generate various ecophysiological responses (Resende et al., 2021). However, territoriality and reproductive behavior have been studied only in a limited number of species within this genus. Research has so far shown that males perch on branches, blades of grass, macrophytes, or directly on the soil while their females lay their eggs along the shoreline of a pond, either directly on the water or on submerged vegetation (De Marco et al. 2005; Resende & De Marco, 2008).

The objective of the present study is to describe the reproductive behavior of *Erythrodiplax abjecta* (Rambur) at several localities within the Colombian Andean region. The duration of reproductive behaviors such as

tandem in flight and on perches, copulation in flight and on perches, oviposition, and intraspecific and interspecific sieges were recorded.

Methods

Study species

Erythrodiplax abjecta (Rambur, 1842) is a species widespread in Central America, Venezuela, Ecuador, and Colombia (Borror, 1942; Paulson, 2017). Males of *E. abjecta* have a dark brown head, with the eyes, thorax, and occasionally the first few abdominal segments being dark reddish brown (Fig. 1a). The middle of the abdomen is lavender and is covered with a grayish blue pruinescence. Females are yellow (Fig. 1b) (Palacino-Rodríguez et al., 2020) and likely change to green with age (Fig. 1c) (the possible color changes of the marked females were not documented in this study; however, both green and yellow females were sexually active and capable of reproduction and oviposition [e.g., Fig. 1d]).



Figure 1. (a) Male of *E. abjecta*. Photo: C. Bota-Sierra; (b) Brown female of *E. abjecta*. Photo: C. Bota-Sierra; (c) Green female of *E. abjecta*; (d) *E. abjecta* copulating. Photo: D. Gutierrez.

Study area

The reproductive behavior of *E. abjecta* was recorded in ten lentic habitats including three wetlands (Jaime Duque, Camino Viejo, and Salitre), two sectors at the Tominé Dam (Club Náutico El Muña and Zona Pública), and at five ponds in habitats otherwise utilized for farming crops and livestock, all in the Colombian Andes (Table 1, Figs 2a–j). Habitats are located at an elevation of 2,600 m where they receive an average annual precipitation of between 600 and 2,000 mm (IDEAM, 2022).

The dominant vegetation in these localities includes *Eleocharis elegans* (Kunth), *Eichornia crassipes* (Mart.) Solms, *Pennisetum clandestinum* Hochst. ex Chiov., *Schoenoplectus californicus* (C.A. Mey.) Soják, *Cyperus papyrus* Linnaeus, *Juncus ramboi* Barros, *Polygonum punctatum* Elliott, *Bidens laevis* (Linnaeus), *Carex* sp., *Juncus effusus* Linnaeus, *Hydrocotyle ranunculoides* Linnaeus, *Acacia* spp., and *Eucalyptus* sp. In most of these habitats, the Andean Forest ecosystems have been converted into agricultural land (Mora, 2015). Data were collected during the dry period between October and

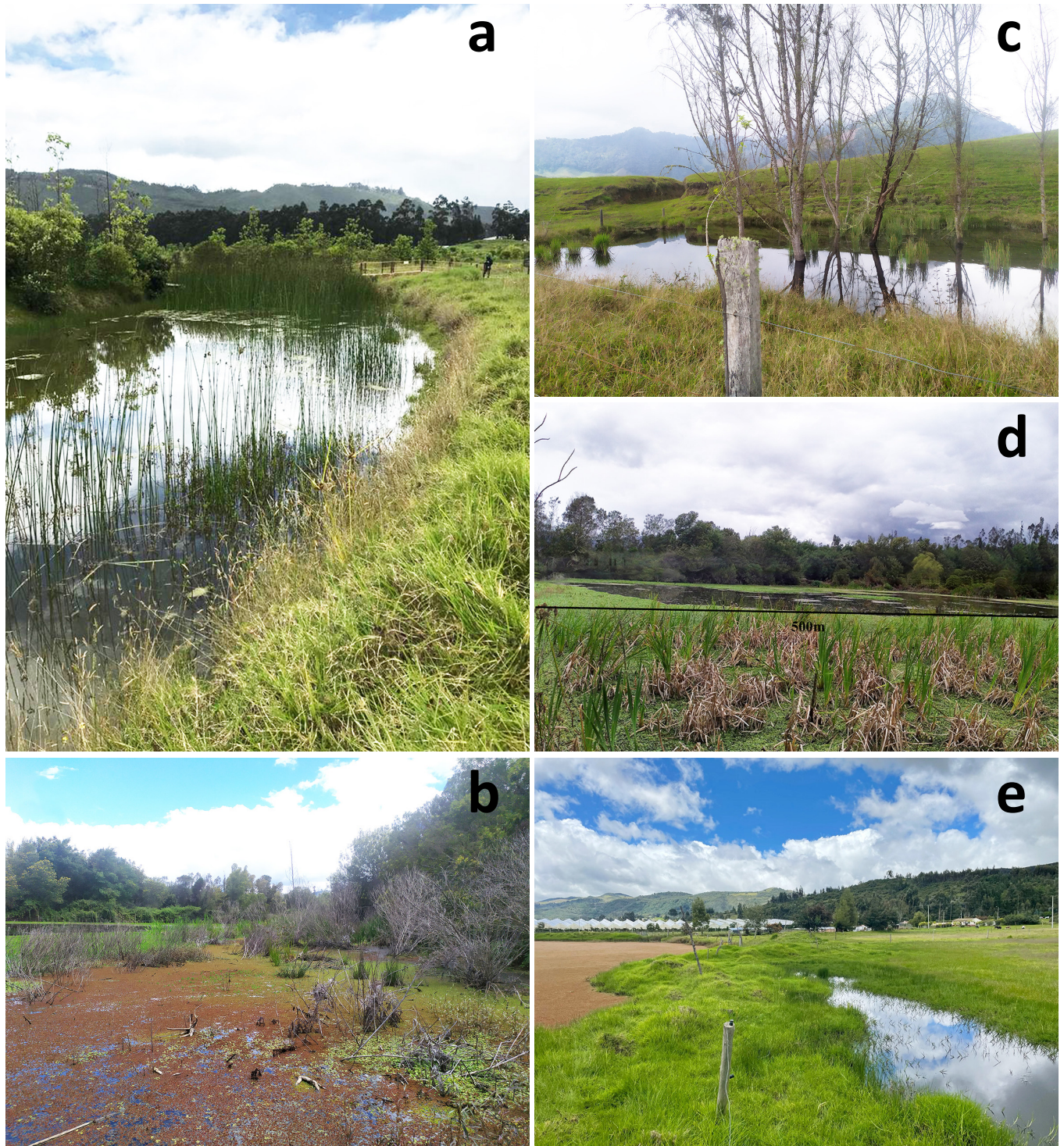


Figure 2. Colombian Andean localities where the behavior of *E. abjecta* was studied. (a) Jaime Duque Reserve. Photo: K. Ríos-Olaya; (b) Club Náutico El Muña Protected Area; (c) Camino Viejo; (d) Agregados reserve; (e) Checua. Photo: K. Ríos-Olaya.

December from 2016 to 2019, and in 2022. The temperatures ranged from 18 to 25°C (IDEAM, 2022). During the rainy season, no information was recorded, because high precipitation could reduce the effectiveness of sampling procedures (May, 1976). Previous studies have consistently revealed a higher diversity of adult Odonata during the dry season (Fulan & Henry, 2007; Oliveira-Junior et al., 2015, 2019).

Data collection

Individuals of *E. abjecta* were captured and marked, recording their sex and colorations. The marking process

took less than a minute for each individual (Alvarez-Covelli et al., 2015; Palacino-Rodríguez & Contreras-Sánchez, 2014). The observations followed the protocol of the focal animal temporal sampling technique (Altman, 1974; De Marco et al., 2002; Resende & De Marco, 2010). Each observation session took place between 09:00 and 15:00 h Colombian time (COT, UTC-5). The time, duration, and sequence of reproductive behaviors were observed and recorded. The observations were categorized as follows: (i) tandem—in flight or perching; (ii) mating—in flight or perching; (iii) oviposition; and (iv) intra- or interspecific sieges—when a male approaches a female or a pair to bar their

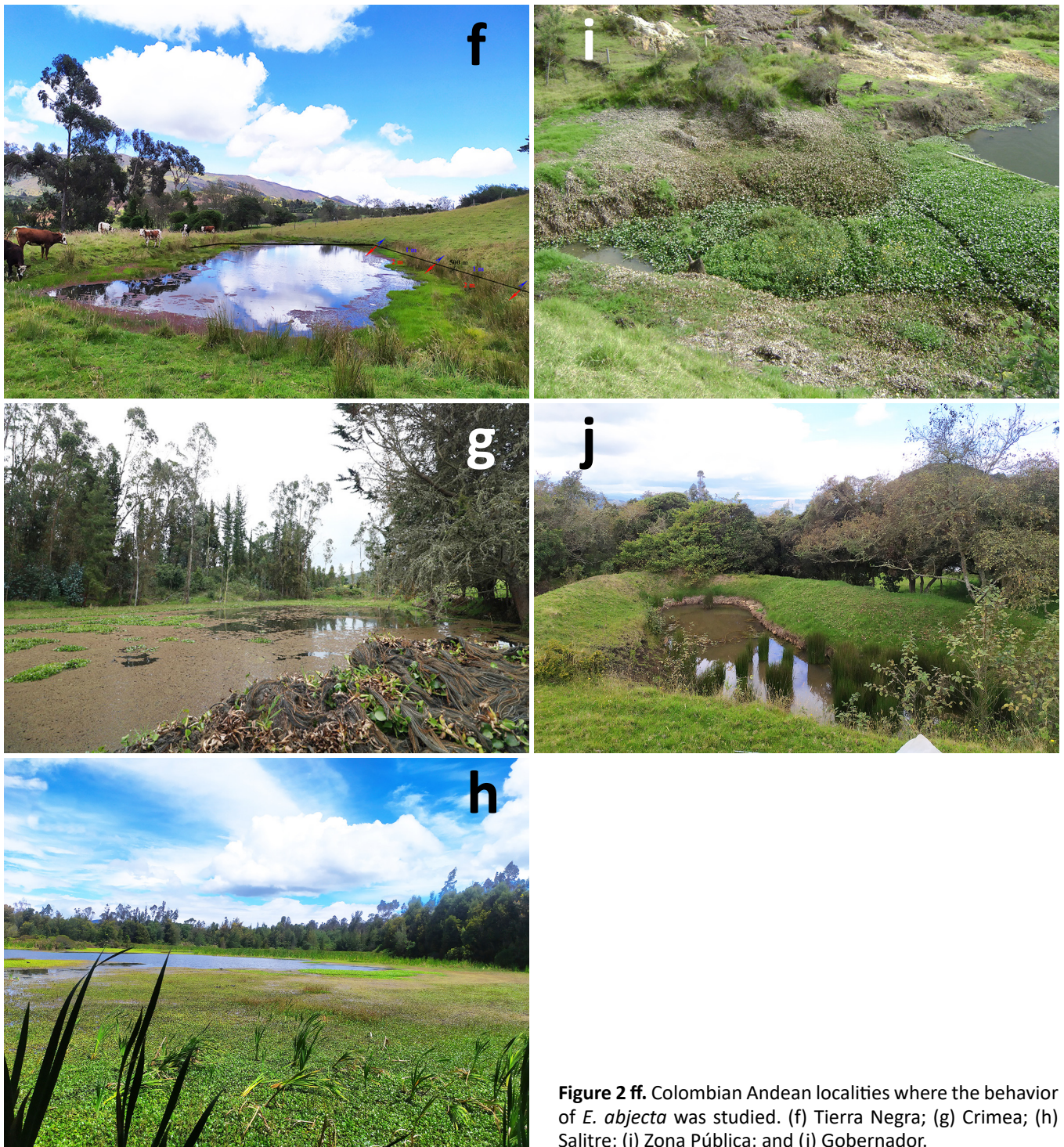


Figure 2 ff. Colombian Andean localities where the behavior of *E. abjecta* was studied. (f) Tierra Negra; (g) Crimea; (h) Salitre; (i) Zona Pública; and (j) Gobernador.

Table 1. Sex ratios per locality in the Colombian Andes. M: males; F: females. *This locality is located in the Tolima Department, whereas the other locations are in the Cundinamarca Department.

	Municipality	Coordinates	Elevation (m a.s.l.)	M	F	ratio
Jaime Duque	Tocancipá	4.949419 N, 73.962808 W	2560	3,128	1117	2.8
Muña	Sesquilé	5.006686 N, 73.808296 W	2588	2,282	737	3.1
Camino Viejo	Líbano*	4.916667 N, 75.05 W	1700	1,253	416	3.0
Agregados	Guasca	4.890278 N, 73.876944 W	2597	1,133	419	2.7
Checua	Nemocón	5.111327 N, 73.864438 W	2578	1,038	207	5.0
Tierra Negra	Sesquilé	4.1998478 N, 73.783606 W	2801	901	190	4.7
Crimea	Guasca	4.835111 N, 73.916389 W	2750	782	156	5.0
Salitre	Guasca	4.828667 N, 73.914034 W	2705	510	101	5.0
Zona Pública	Guatavita	4.936598 N, 73.840754 W	2581	490	100	4.9
Gobernador	Sesquilé	5.055578 N, 73.783760 W	2638	477	95	5.0
Total	–	–	–	11,994	3,538	3.4

Table 2. Duration (in seconds) of reproductive behaviors for *E. abjecta* in the Colombian Andes.

Behavior	No. of records	Range (s)	Average (s)	Standard deviation
Flying in tandem	3,323	1–4	2.48	± 1.12
Perched in tandem	215	1–3	1.79	± 0.71
Copulating in flight	1,219	8–25	14.50	± 3.16
Copulating while perched	2,319	5–25	14.37	± 3.51
Oviposition	3,538	33–453	245.63	± 102.30
Intraspecific siege	10,998	1–7	3.98	± 1.99
Interspecific siege	996	1–4	2.52	± 1.13

passage and attempts to take the female in tandem) (Baird & May, 1997). The observations were conducted with the naked eye or using 10×50 JHOPT™ binoculars (Brighton, CO, USA). At each location, data were collected along a 500 x 3 m transect, extending 1 m onto the shore and 2 m over the water (Fig. 2f). Transects were measured out on a single shore (e.g., Fig. 2d) or composed of several sections of the shore summing up to 500 m (e.g., Fig. 2f). To minimize disturbance effects, behaviors were recorded in four-day periods: the first day was spent only to mark individuals, while the subsequent three days were spent recording their behaviors. Thus, behaviors were recorded for the marked individuals only.

Territory was defined as the area an individual defends against conspecifics in order to claim for itself one or more resources that enhance that individual's fitness (Kaufmann, 1983). A male was identified as a territory owner if he was observed consistently at the same location (within 2 m) for at least two consecutive days. Behaviors were documented over a period of 1,200 hours on 200 days (i.e., 120 hours and 20 days per locality). To establish whether the number of interferences by other males depends on male guarding time during oviposition, a simple linear regression test was performed with R software v. 4.3.1 (R Core Team, 2010).

Results

Immature males or females were observed in the water. A total of 11,994 sexually mature males (dark brown-black males) and 3,538 mature females were recorded. The sex ratio of females to males in the study was 1:3.4 (Table 1). Comparing data from the various localities, the sex ratio varied from 1:2.7 to 1:5 (Table 1). The number of observations, range and duration, average time, and standard deviation for each behavioral category are presented in Table 2. Correlations were not identified by linear regression analyses between the number of interferences by other males and male guarding time on yellow or green females ($\beta = 0.00005$; $p = 0.61$; $r = 0.013$; $p = 0.74$; $r = -0.008$, respectively).

Reproductive behavior typically is seen between 10:00 h, when individuals appear on perches on the shore or on emergent plants within the body of water, and 14:30 h, when reproductive events ebb. The sequence of the reproductive behaviors of *E. abjecta* (enumerated 1 to 16) is illustrated in Figure 3. A sexually mature male (Fig. 3, #1) (A) encounters a flying or perching female (Fig. 3, #2). The male takes the female in tandem during flight (#3) or on a perch (#4). The tandem phase is short and followed by intra-male sperm translocation and copulation, which can occur in flight or on a perch (#5). If copulation occurs in flight, the

pair will eventually land on a perch, where the female separates from the male. At this point, the female can perch (#6) or oviposit while flying very close to the water surface (≤ 5 cm) (#7), all the while being guarded by the male that may be perched or in flight (#6–7). Oviposition occurs in various spots of the habitat, including muddy bottoms, litter, near dry plants, clearings between dry branches; shallow water with emergent plants; areas covered with floating and emergent plants; near bushes; water littered with dry branches; flooded pastures, as well as shacks, and plants such as *Azolla filiculoides* and *Eichornia crassipes* (Figs 4a–h).

Guarded females may be besieged (#8–10) by other sexually mature males (B) of *E. abjecta* or by males of *Sympetrum gilvum* (Selys). In some cases (~10%), females that had just copulated but not yet begun to oviposit were taken by another male for copulation (e.g., Fig. 1d). During a siege by a conspecific male, three possible outcomes may occur: if males A and B confront each other, the female flees (#11), or the original pair flees (#12), or male B wins the confrontation, takes the female in tandem, copulates with her, and guards her while she oviposits (#13). If the female flees (#11), she may perch (#14), continue ovipositing alone (#15), or

be taken by a male C (#16). Territorial males guard their territories and engage in confrontations with males from neighboring territories, satellite males (Table 3), or *S. gilvum* males. Copulation events may occur within male territories or while flying over and searching for perches in other territories. Although seven female individuals of *E. abjecta* were observed mating several times with different males (at least five times), this variable was not assessed for all females in this study. The difference between the 10% of the females taken by other males for copulation mentioned above and the females observed here mating several times, is that the latter were ovipositing between copulations, while the former did not oviposit between copulation events. During sieges by interspecific males, clashes were short, and *S. gilvum* males continued to fly on to other territories.

Discussion

Males of *E. abjecta* present non-contact guarding behavior, where they follow and protect females, driving her away from other males (i.e., non-contact guard-

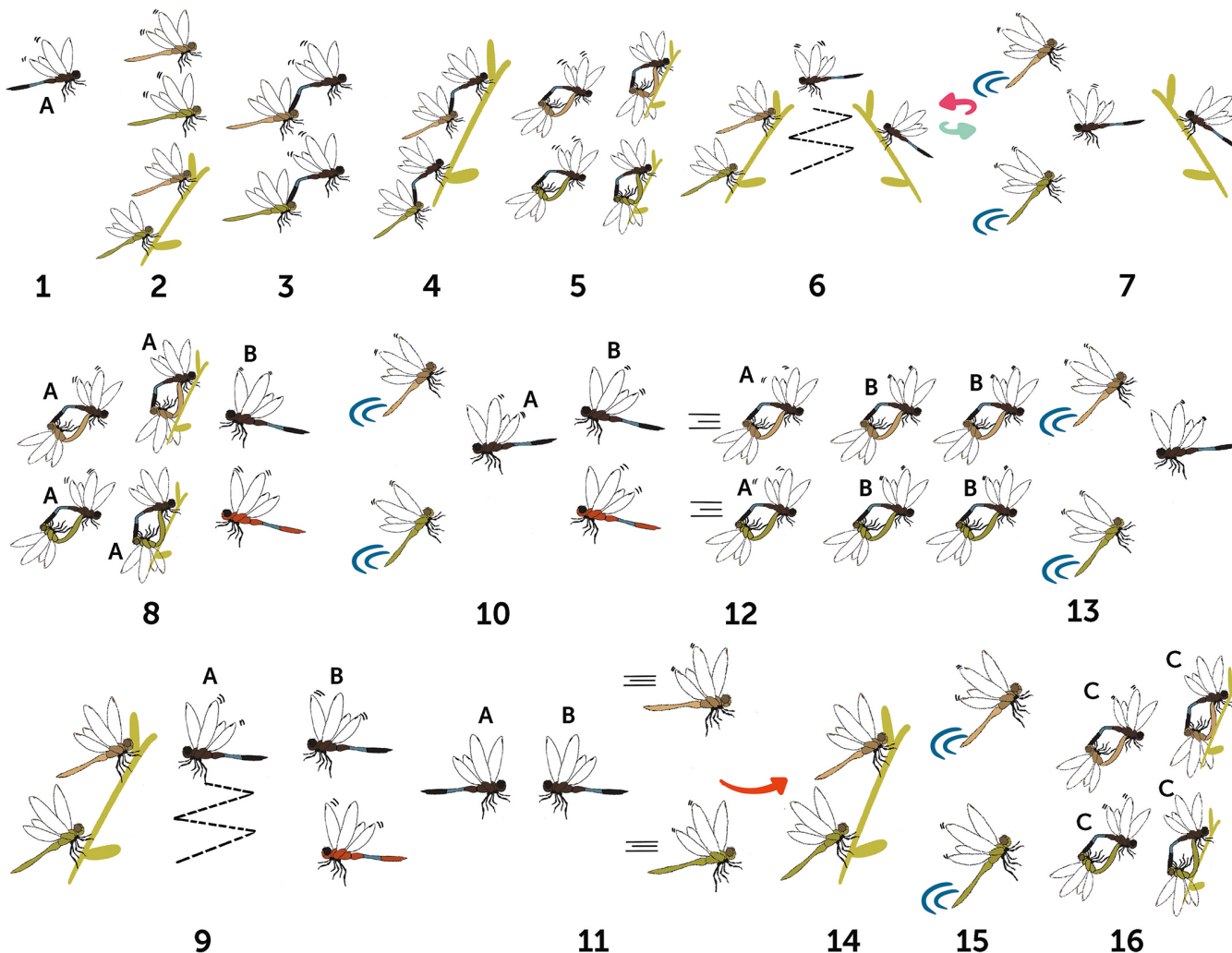


Figure 3. *Erythrodiplax abjecta* reproductive behavior; the numbers indicate the sequence described in the Results section. Drawings: P. Camacho.

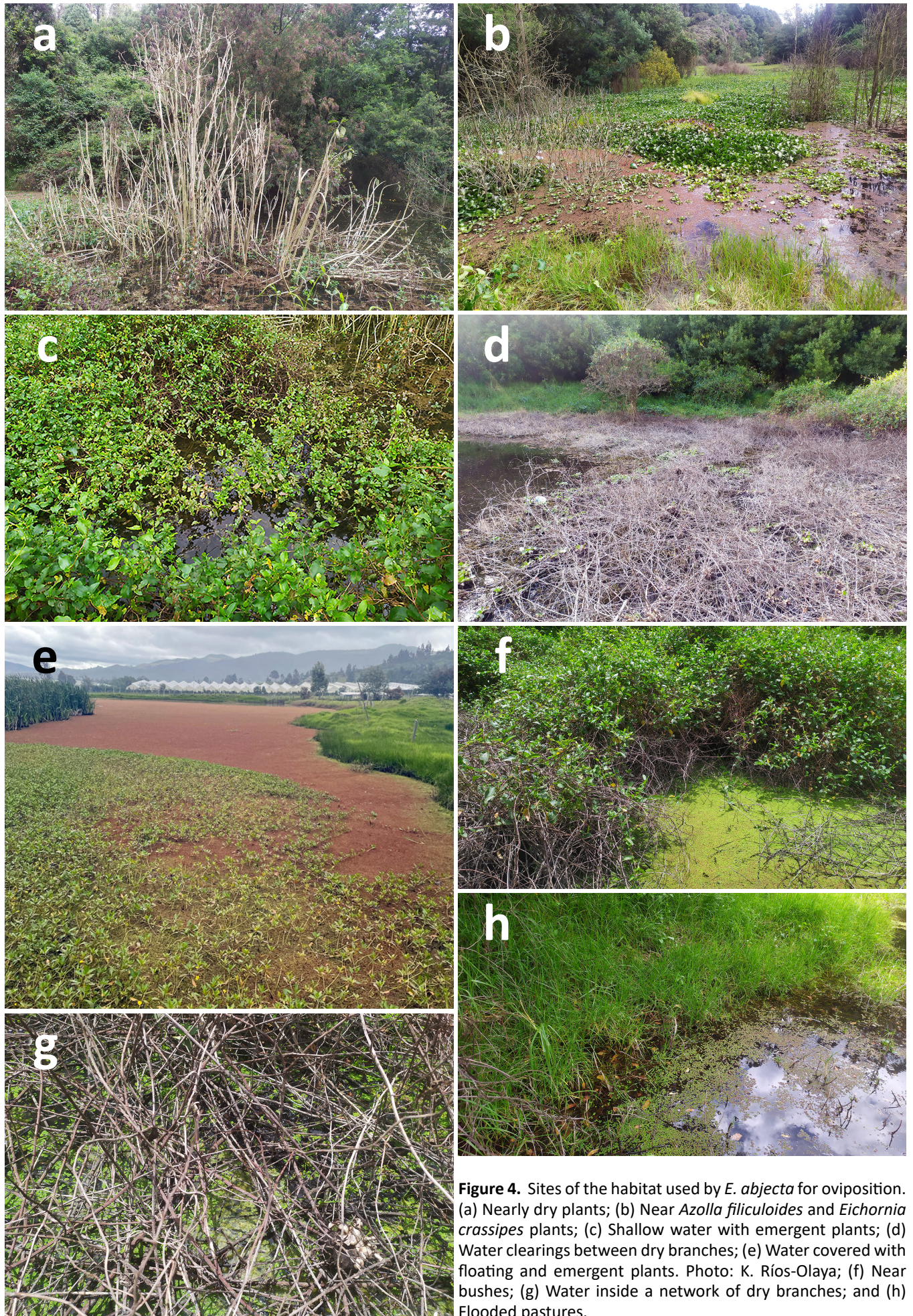


Figure 4. Sites of the habitat used by *E. abjecta* for oviposition. (a) Nearly dry plants; (b) Near *Azolla filiculoides* and *Eichhornia crassipes* plants; (c) Shallow water with emergent plants; (d) Water clearings between dry branches; (e) Water covered with floating and emergent plants. Photo: K. Ríos-Olaya; (f) Near bushes; (g) Water inside a network of dry branches; and (h) Flooded pastures.

Table 3. Number of mating events (#M) and number of simultaneous male-male interactions (MI) in *E. abjecta* males from several Colombian Andean localities; n: number of males; T: average time of male-male interactions.

# M	n	Jaime Duque		Club Náutico El Muña			Agregados		
		MI	T	n	MI	T	n	MI	T
0	87	2.57 ± 1.17	12.75 ± 7.07	76	2.68 ± 1.21	13.32 ± 7.34	49	2.65 ± 1.29	14.51 ± 7.98
1	60	7.55 ± 2.55	35.01 ± 12.37	71	8.00 ± 2.14	35.07 ± 11.05	88	7.72 ± 2.30	33.97 ± 10.86
2	78	7.74 ± 2.48	33.38 ± 11.45	68	7.45 ± 2.22	31.47 ± 11.12	78	7.47 ± 2.49	32.93 ± 11.69
3	63	14.44 ± 4.33	62.07 ± 18.88	57	14.49 ± 4.16	62.40 ± 19.12	73	14.35 ± 4.77	60.06 ± 21.00
4	67	15.16 ± 4.74	64.31 ± 22.93	77	14.63 ± 4.92	64.09 ± 22.17	74	13.41 ± 4.36	57.52 ± 18.26
5	63	19.99 ± 5.10	87.31 ± 28.91	69	25.33 ± 4.62	113.81 ± 31.47	61	26.50 ± 3.92	114.52 ± 25.43
6	74	27.63 ± 6.40	120.78 ± 36.43	69	26.49 ± 6.27	115.84 ± 34.63	71	25.33 ± 6.41	107.45 ± 34.30
Checua									
0	74	2.66 ± 1.36	13.18 ± 7.89	85	2.65 ± 1.25	14.52 ± 7.79	63	2.30 ± 1.31	12.14 ± 8.06
1	76	7.52 ± 2.08	31.68 ± 10.40	60	7.63 ± 1.93	32.21 ± 9.90	69	7.21 ± 2.21	33.46 ± 10.59
2	64	7.57 ± 2.52	33.48 ± 12.61	70	7.64 ± 2.27	32.95 ± 11.59	65	7.47 ± 2.20	32.58 ± 11.36
3	81	14.38 ± 4.49	61.66 ± 21.34	81	14.16 ± 4.65	61.28 ± 21.05	70	15.50 ± 4.81	65.82 ± 23.31
4	85	14.68 ± 4.49	61.88 ± 22.49	72	14.48 ± 4.89	63.87 ± 21.88	67	15.43 ± 4.33	67.14 ± 21.33
5	78	25.48 ± 5.09	112.02 ± 30.48	60	23.95 ± 4.46	100.91 ± 25.73	68	24.94 ± 5.26	109.02 ± 29.31
6	77	25.98 ± 6.34	116.18 ± 38.49	69	26.24 ± 6.73	111.10 ± 32.89	–	–	–
Tierra Negra									
Crimea									
# M		Salitre		Zona Pública			Gobernador		
0	70	2.51 ± 1.17	13.25 ± 7.75	68	2.51 ± 1.44	13.44 ± 8.09	30	2.15 ± 1.35	13.48 ± 7.73
1	69	7.72 ± 2.18	32.40 ± 10.72	60	7.31 ± 2.29	31.18 ± 9.41	47	7.56 ± 2.25	33.74 ± 10.74
2	74	7.02 ± 2.43	30.17 ± 11.56	75	7.46 ± 2.30	32.92 ± 12.50	60	7.40 ± 2.21	31.78 ± 10.94
3	60	14.83 ± 4.50	63.88 ± 23.31	76	14.35 ± 4.94	59.59 ± 23.13	51	15.37 ± 4.64	67.29 ± 23.02
4	73	13.31 ± 4.79	56.83 ± 21.72	64	14.14 ± 4.84	60.82 ± 21.21	44	14.05 ± 5.00	60.10 ± 21.88
5	–	–	–	–	–	–	50	26.62 ± 4.77	119.40 ± 26.24

ing). This intense guarding pattern is presumably an adaptation to temporarily high densities of males at oviposition sites (Martens et al., 2012). The habitats of *E. abjecta* host males in high numbers, which results in intense male-male competition (Table 3). As is to be expected, increased male densities lead to situations that can affect individual reproductive success, such as shifting energy for reproduction to activities such as siege, defense against disturbance by other males (Conner, 1989), searching for areas with lower rival density (Goldsmith & Alcock, 1993; Koch, 2006), or searching for areas with better resources (McLain, 1982). Therefore, a direct relationship between population density, male-male competition, and frequency of matting could also be expected (Fincke et al., 1997). Nagy et al. (2011) proposed that territory size influences male behavior and as a result the frequency of male-male interaction. According to these authors, male-male competition can decrease when males occupy larger territories (15–20 m long), change their mating strategy from territoriality to non-territoriality, intensify mate guarding, and try to enforce tandeming (Cordero-Rivera, 1999).

However, increased intraspecific fighting has been described for several species where males defend smaller territories (Alcock, 1989; Pezalla, 1979). *Erythrodiplax abjecta* defends territories smaller than 2 m long and constantly interacts with intraspecific or

interspecific males. From this, it may be hypothesized that sexually mature *E. abjecta* males expend a lot of energy on intensive male-male interactions, guarding mates, and enforcing tandeming. To conserve energy, they employ a non-contact guarding strategy. Similar to other species (Tsubaki & Ono, 1985), males protect ovipositing females by hovering above them and chasing off intruding males. At the same time, males prevent females from leaving the oviposition site (Tsubaki & Ono, 1985). However, in the case of *E. abjecta*, this strategy failed when males were engaged in fights with intruders and left their females unprotected, so that these were taken by neighboring territorial males to copulate with. Although these females often returned to the reproduction site and mated with other males, *E. abjecta* females may also perch, continue ovipositing, or leave the site. Despite the fact that the presence of males may provide information to females on location sites and the likelihood of protection during oviposition, females may choose to oviposit alone after a siege in available spots that may be easy to find (Waage, 1987).

The intensity of mate guarding depends on the likelihood of females re-mating with another male before oviposition is completed and the probability of the males to find further mates while the original mate is still busy ovipositing (Alcock, 1982). In the case of *E. abjecta*, the success of mate guarding was regulated by

the intensity of sieges from other males, as a result of which females were or were not able to leave the oviposition site. No territorial males of this species were observed to obtain additional mates while guarding the original female. High variation in the degree of interference by other males during periods of guarding could be due to the variation in male density at microhabitat level. It is probable that microhabitats with more complex structures (e.g., Figs 4d, g) that shelter a pair and make it less visible to other males during oviposition, together with male guarding, reduce the amount of energy required for engaging in behaviors to fend off competitor interference compared to less complex microhabitats (e.g., Figs 4c, h). Further studies are necessary to learn whether there is a possible causal association between these variables.

A short duration of copulation (< 20 s) has been proposed as an economic consequence for species with active males (Emlen & Oring, 1977), sperm reposition (Waage, 1984), and less male-biased operational sex ratios (i.e., the ratio of sexually active males to receptive females; Emlen & Oring, 1977). However, this is a possibility if the male has both a higher potential mating rate and a reduced risk of competition (Simmons & Siva-Jothy, 1998). My observations suggest a contradictory relationship between these factors for *E. abjecta*, which has a high mating rate in spite of intense male-male competition (Table 3). In species with intense antagonistic competition for mates, males may differentially invest energy due to constraints associated with muscle form or fat reserves (i.e., resource-holding potential; Marden, 1989). Consequently, females of these species may assess male quality or attractiveness based on information about their resource-holding potential and their potential to obtain mates (Briffa & Sneddon, 2007). Nevertheless, further studies are needed to clarify if these mechanisms regulate the reproductive dynamics in *E. abjecta*.

The information provided by this study will serve as a foundation for future research on differences in reproductive success between territorial and non-territorial males, the benefits provided by resource-holding potential for both males and females, territory size and location, intensity of male-male competition, mating rate, mating system, and potential differences in the duration of behavioral expressions between natural and altered areas.

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