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Relationship between environmental conditions and host-seeking activity of *Ochlerotatus albifasciatus* (Diptera: Culicidae) in an agroecosystem and in an urban area in Chubut, Central Patagonia, Argentina

M. G. Freire[a], N. J. Schweigmann[a,b], W. S. Svagelj[b,c], M. V Loetti[a], O. Jensen[d] and N. E. Burroni[a,b]

[a]Grupo de Estudio de Mosquitos, Departamento de Ecología, Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; [b]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; [c]Instituto de Investigaciones Marinas y Costeras (CONICET-UNMdP), Universidad Nacional de Mar del Plata, Mar del Plata, Buenos Aires, Argentina; [d]Departamento de Zooartroponosis, Ministerio de Salud, Provincia de Chubut, Argentina

ABSTRACT

Ochlerotatus albifasciatus is associated with aquatic environments that are frequently flooded. Awareness of blood hematophagic activity of female mosquitoes is particularly important in species which are vectors of human disease and domestic animals. The study of host-seeking activity allows us to infer the risk of transmission of these parasites. The objective of this work was to study in an agro-ecosystem and urban area of central Argentine Patagonia the relationship between the circadian rhythm of activity of host-seeking of *Oc. albifasciatus*, and environmental variables. During January 2003, 99 human bait catches were carried out, of which 77.8% registered at least one individual of *Oc. albifasciatus*. Generalised linear models were used to evaluate the relationship between *Oc. albifasciatus* biting activity rate and capture time, environmental humidity, air temperature, sunshine degree, wind speed, habitat type and proximity of larval habitat. The model that best explained the variation in biting activity rate included the capture time, environmental humidity, air temperature, sunshine degree and wind speed as predictor variables. Host-seeking activity was higher in the evening than in the morning or afternoon, and it was positively related to mean air temperature and environmental relative humidity (RH), but negatively to sunshine degree and wind speed. The combination of these characteristics (wind speed less than 20 km/h, environmental temperature greater than 26°C, sunshine less than 40% and (RH) greater than 50%) would provide favourable conditions to allow seeking activity and to feed on the host. The dispersion of this mosquito could be among environmental patches that present these characteristics.

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CONTACT N. E. Burroni nburroni@ege.fcen.uab.ar Grupo de Estudio de Mosquitos, Departamento de Ecología, Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, Buenos Aires (C1428EHA), Argentina.

Introduction

Awareness of blood hematophagic activity of female mosquitoes is particularly important for species that act as vectors of human disease and domestic animals. The circadian rhythm of mosquito populations is required as baseline knowledge to understand vector-borne pathogen transmission dynamics (Reiter 2001; Lord 2004).

Human rate catches permit the estimation of biting and infection rates, the assessment of control operations and the monitoring of temporal changes in relative population size (Service 1976). The human biting rate, or the number of bites/person/day, is estimated by human landing catches as the most direct method. This rate is the product of adult mosquito density in relation to the human population and the proportion of mosquitoes feeding on humans. It is an important component of the entomological inoculation rate (Silver 2008).

Host-seeking activity by active flight is mainly affected by temperature, wind, rainfall, humidity, sunshine degree and photoperiodicity (Bidlingmayer 1985; Reiter 2001). Knowledge regarding relations between environmental factors and mosquito assemblages is highly relevant for the study of current processes, future changes and effective control measures (Beketov et al. 2010). Mosquitoes bite their host at any time of day depending on the species, but wind speeds greater than about 3 km/h often drastically reduce host-seeking flights (Service 1993). Some species breed in woods, as forests are considerably protected from wind by the shelter of dense vegetation, and those that breed on ground water collections disperse very little (Service 1971).

These conditions have been widely studied in several areas of South America for many mosquito species, by several authors (Guimarães et al. 2000, 2001; Loetti et al. 2007; Turell et al. 2008; Stein et al. 2013), although they have not been yet studied for Patagonia, the southernmost tip of the continent.

There are seven species mentioned: *Culex* (*Culex*) *acharistus*, *Culex* (*Culex*) *apicinus*, *Culex* (*Culex*) *articularis*, *Culex* (*Culex*) *dolosus*, *Culex* (*Culex*) *eduardoi*, *Culex* (*Culex*) *pipiens* and *Ochlerotatus (Ochlerotatus* Subgenus uncertain) *albifasciatus* (Rossi and Vezzani 2011).

Oc. albifasciatus is a floodwater mosquito whose females lay their eggs on moist soils of environments that are subject to flooding and drought cycles (Forattini 2002). This species is widely distributed in South America, from Bolivia and southeastern and southern Brazil to Tierra del Fuego (Burroni et al. 2013).

Oc. albifasciatus has been identified as a possible vector of the Western equine encephalitis virus (Aviles et al. 1992), Bunyamwera virus (Bianchini et al. 1968), Eastern equine encephalitis virus and Cache Valley virus (Sabattini et al. 1985, 1998), for which there were found infected humans in the province of Río Negro (Sabattini et al. 1998), northern edge of Patagonia (40°48′S, 63°00′W). This mosquito is also transmitting the nematode *Dirofilaria immitis* in 10 Argentinean provinces, but it has not been observed transmitting this parasite in Patagonia yet (Vezzani et al. 2006).

In addition, certain climatic and environmental conditions, such as rain and warm temperature, are favourable for development of immature stages. Bachmann and Bejarano (1960) and Ludueña Almeida and Gorla (1995) mentioned that the persistent biting of this mosquito causes considerable discomfort to humans as well as to cattle (Ludueña Almeida and Gorla 1995) in several areas of Argentina. The peak population abundances of this mosquito in rural areas of central Argentina interfere with normal feeding of the cattle, causing losses in milk and meat production (Ludueña Almeida and Gorla 1995). Furthermore, their insistent bites make field work and the harvesting of berries, as well as some recreational activities related to tourism, difficult (unpublished data).

The objective of this work was to study in an agro-ecosystem and urban area of central Argentine Patagonia the relationship between the circadian rhythm of activity of host-seeking of *Oc. albifasciatus*, and environmental variables.

Materials and methods

Study area

Sarmiento Valley is a floodplain supplied by the River Senguer. It is located in the central Patagonian plateau. This green valley (71.4 km^2, 260 m above sea level) is surrounded by an extremely arid steppe. The xerophytic steppe vegetation contrasts with shrubby species and the bushes of the valley (Cabrera 1971). Moreover, agricultural and livestock activities are very important in the area. This valley is framed by Muster and Colhué Huapi lakes.

Sarmiento city (45°35′S, 69°05′W) has 11,396 inhabitants (INDEC 2010) and a population density of 0.69 people per km^2. At the time of the study, 7% of the total area was occupied by 131 farms and the remaining area by 256 lots of fields for grazing. Watering is done by periodic flooding of the fields through channels supplied by River Senguer.

The temperate climate of this region is dry and cold (Paruelo et al. 1998). The climate is markedly continental because the area is surrounded, except to the south, by peaks above 700 m. The absolute temperature recordings vary between a maximum temperature of 39.3°C and a minimum temperature of −33°C. However, average temperature only ranges between −0.2 and 23.9°C. The monthly mean temperatures range between 2°C (in July – winter) and 24°C (in January – summer) (Servicio Meteorológico Nacional 2013). The average rainfall was 147.2 mm between the years 1931 and 1960 (Servicio Meteorológico Nacional 2013). The coldest season has higher rainfall records (Elissalde et al. 1998). During the summer, 65% of the prevailing winds are from the west. In contrast, winter is the season of the lowest wind records (Coronato and Del Valle 1988).

Sampling collections

During the study period, 11 to 23 January 2003, 99 adult mosquitoes catches were made using a human as bait (Service 1976). The capture events were all in different areas, so that the catches were independent of each other. The samplings were carried out with a capture effort of 20 minutes each between 6:00 a.m. and 9:00 p.m., sunlight hours for the month of January in this latitude. Capture time was recorded in order to study the circadian rhythm of the species. Capture time was categorised into three levels: morning (6:00 a.m. to 1:00 p.m.), afternoon (1:01 p.m. to 5:00 p.m.) and evening (after 5:00 p.m.).

Volunteers who were involved in the catches wore hooded screened jackets to prevent mosquitoes and other biting flies from feeding. They only exposed the lower half of one arm and used manual aspirators to collect mosquitoes as they landed in an attempt to feed (Jones et al. 2004; Silver 2008).

Environmental variables

The habitats where the study was carried out were classified into four categories: (1) urbanised areas (home areas or outside houses); (2) grazing areas (artificially flooded areas to allow grass growth for animal feeding); (3) irrigation and drainage canals (areas related to artificial watering of grazing areas); and (4) vegetated areas (shrub and herbaceous species, different from those in grazing areas).

In each location, the following environmental variables were recorded where the collections were made: (1) air temperature; (2) air environmental relative humidity (RH) (both measured with a Digital Thermohygrometer Triple Display Thechnidea); (3) wind speed according to the Beaufort scale. This method is suitable for measuring wind speed *in situ* (Servicio Meteorológico Nacional 2013). The speed is estimated by observing the effect of the wind on the trees. The categories considered were: 'calm', with Beaufort number = 0 (0–1 km/h, average: 0.5 km/h; 0–0.9 knots); 'breeze', with Beaufort number = 1–4 (2–28 km/h, average: 15 km/h, 1–16 knots); 'wind', with Beaufort number = 5–6 (29–49 km/h, average: 39 km/h, 17 to 27 knots); 'strong wind', with Beaufort number = 7–8 (50–74 km/h, average: 62 km/h, 28–40 knots). Furthermore, in each event capture wind conditions were recorded twice and then averaged; (4) Sunshine degree: percentage of sunlight on the sites of capture. The sunlight degree varied according to the height of the sun over the surrounding vegetation (type, number and size). The variation registered was between 0% (all shadow) and 100% (full sun) in an area of 10 m^2, and these percentages were still estimated at sunset times; (5) proximity to a larval habitat: we considered the adult catches close to a larval habitat of conspecifics mosquitoes when at least one of these was registered in a 20-m radius of where the catch was made. All potential larval habitats in this area were sampled, and collected immatures were taxonomically identified to confirm this record.

Adult specimens caught by bait were identified under a stereoscopic microscope using keys for Argentine mosquitoes (Darsie 1985).

Statistical analysis

The effect of predictor variables on *Oc. albifasciatus* biting activity rate (i.e. number of individuals captured on the bait during 20 minutes of exposition) was evaluated using generalised linear models (GLM; Crawley 2007) with negative binomial error distribution and log link function. The variables habitat type (four levels: 'urbanised areas', 'grazing areas', 'irrigation and drainage canals' and 'vegetated areas'), capture time (three levels: 'morning', 'afternoon' and 'evening') and proximity to a larval habitat (two levels: presence or absence) were included as categorical variables. Air temperature, air environmental RH, wind speed and sunshine degree were included as quantitative variables.

Model selection was based on information-theoretic procedures (Burnham and Anderson 2002). We considered models with all possible combinations of predictor variables, resulting in 128 candidate models. Akaike's information criterion corrected for small sample size (AICc) was used. Model comparisons were made with ΔAICc, which is the difference between the lowest AICc value (i.e. the best of the suitable models) and AICc from all other models. The AICc weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. Because there was substantial uncertainty in model selection, parameter estimates from predictor variables were calculated using multiple model inference (Burnham and Anderson 2002). To evaluate the support for parameter estimates, 95% confidence intervals were calculated using unconditional variances (Burnham and Anderson 2002). Statistical analyses were carried out using R software, version 3.0.2 (R Development Core Team 2013). For model selection, we used the MuMIn package (Bartoń 2013). Results are presented as mean ± standard error (SE), and for null hypothesis testing, statistical tests were considered significant at α = 0.05.

Results

The study period corresponded to January 2003. During this period, the air temperature varied in the range 12.6 to 24.8°C (mean temperature 18.5°C), and accumulated precipitation was 0.87 mm (NOAA 2013). During the sampling, made from 11 to 23 January 2003, air temperature varied between 9.8 and 32.9°C (mean = 23.67; standard deviation (SD) = 4.79), mean air environmental RH was between 18 and 61% (mean = 35.49; SD = 9.54), sunshine degree was between 0% and 100% (mean = 34.14; SD = 33.53), and wind speed was from 98 to 0.5 km/h (mean = 33.61; SD = 18.27) at the capture sites studied.

Seventy-eight percent (77/99) of capture events registered at least one individual of *Oc. albifasciatus*. Mean biting activity rate was 26 mosquitoes per bait (SD = 47, median = 8, N = 99), ranging from 0 to 208 mosquitoes per bait (Figure 1). In addition, one time only one individual was captured, and 22% of the captures were of between one and five individuals.

A higher number of mosquitoes were collected in grazing areas (Figure 2A). The lowest mean air temperature at which mosquito activity was registered was 15.0°C (with an interval of minimum air temperatures during capture of 14.1–15.9°C). The highest mean air temperature at which a mosquito was captured was 32.2°C (interval of maximum air temperatures

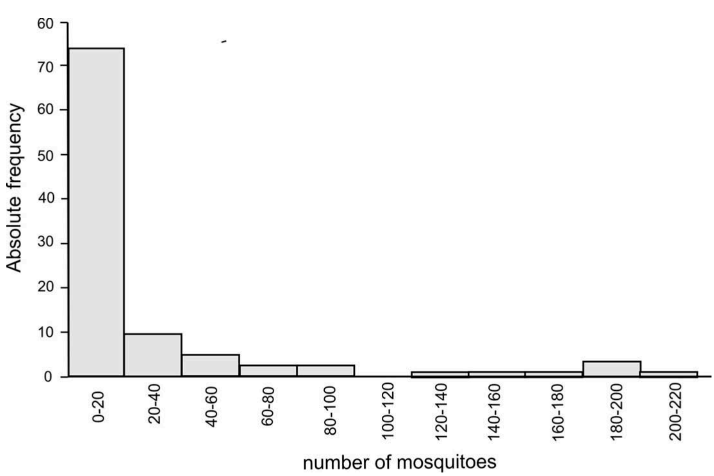

Figure 1. Absolute frequencies of *Ochlerotatus albifasciatus* for the catches in Sarmiento Valley.

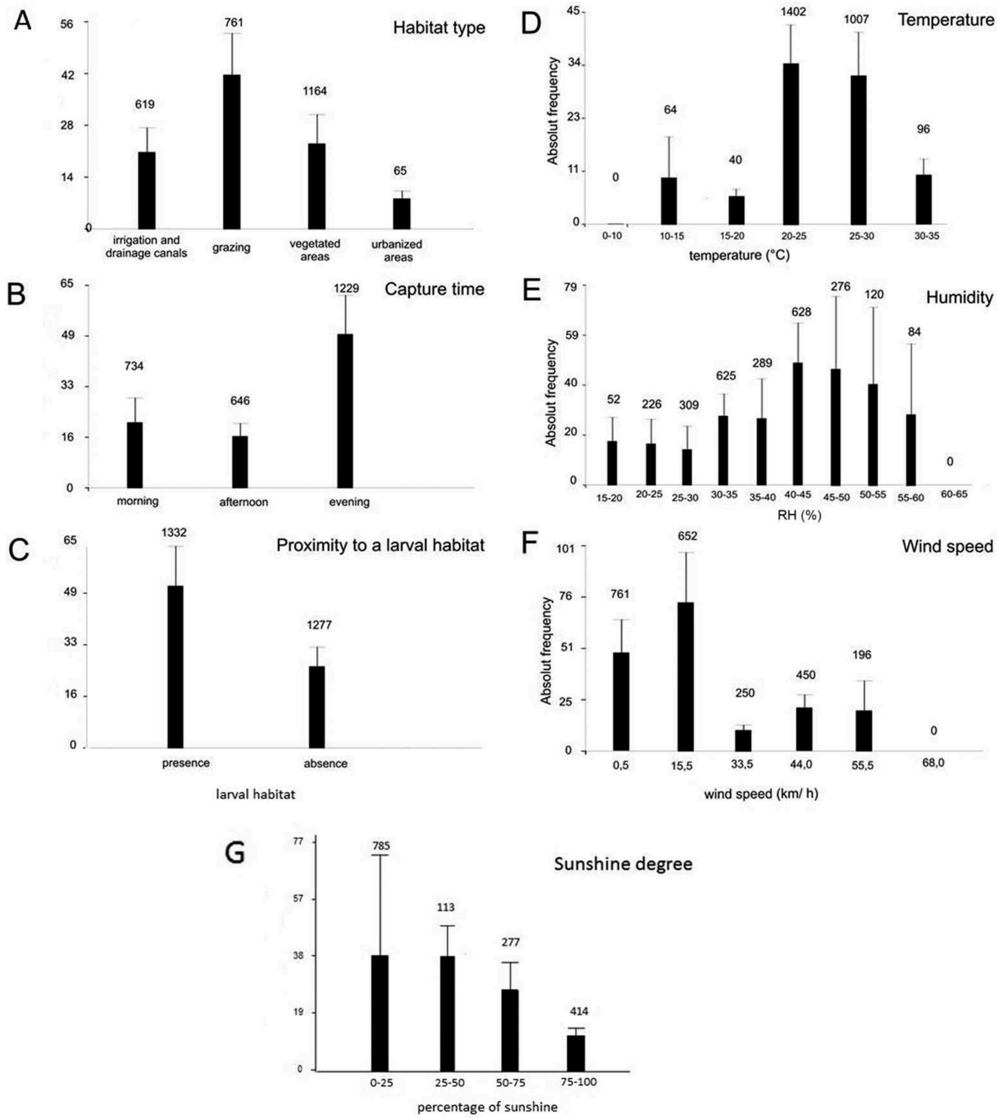

Figure 2. Absolute frequencies of *Ochlerotatus albifasciatus* for the catches in Sarmiento Valley mean and standard error for the catches of *Oc. albifasciatus* according to different variables: (A) habitat type ; (B) capture time; (C) proximity to a larval habitat; (D) air temperature; (E) air environmental RH; (F) wind speed; and (G) sunshine degree. Variables D, E, F and G were categorised here to make the corresponding graphics. The number above each bar is the absolute frequency of mosquitoes in this category.

during capture of 28.9–35.4°C,). The greatest number of mosquitoes were captured between 20 and 30°C (Figure 2D). The environmental relative humidity recorded during the capture periods varied between 18 and 56.5% (mean = 19%), with the highest values of catches between 40 and 55% (Figure 2E). Larval habitats were found within a 20-m radius around where the adults were captured 34.3% of the time (Figure 2C). The wind speed according to the Beaufort scale ranged between 0.5 and 68 km/h, and more individuals were captured at

Table 1. Mean and SD for temperature, RH, wind speed and degree of insolation recorded at the capture time levels.

Capture time	Capture events (n)	Air temperature (°C) mean (SD)	Min–max	Air environmental RH (%)	Min–max	Wind speed (km/h)	Min–max	Sunshine degree (%)	Min–max
Morning	(a) = 35	22.17 (5.66)		39.50 (9.42)		35.06 (18.94)		66.43 (30.88)	
	(b) = 25	20.3 (3.51)	17.00–29.85	38.07 (7.31)	28.00–45.00	30.72 (16.60)	0.50–55	31.0 (30.67)	0–100
Afternoon	(a) = 39	27.67 (3.21)		30.16 (9.88)		32.24 (17.94)		66.03 (37.38)	
	(b) = 20	26.91 (3.45)	21.6–32.50	73.75 (33.90)	18.00–50.00	30.45 (18.42)	0.50–55	30.55 (8.79)	0–100
Evening	(a) = 25	20,33 (5.03)		36.58 (9.76)		32.18 (18.44)		58.0 (31.22)	
	(b) = 11	20.96 (7.20)	14.65–20.05	59.1 (28.0)	23.00–42.50	37.73 (19.48)	0.50–55	31.60 (7.20)	25–100

low wind speeds, of 0.5 to 15.5 km/h (Figure 2F). The sunshine degree varied between 0% (shadow) and 100% (full sun) (mean = 62.9%). The highest catch values were at below 50% of sunshine (Figure 2G).

The mean registers with their standard deviations of air temperature, air RH, wind speed and sunshine degree at capture sites, and the mean and range of these variables in places where *Oc. albifasciatus* was effectively captured, are given in Table 1.

The model that best explained the variation in biting activity rate included capture time, air temperature, air environmental RH, wind speed and sunshine degree as predictor variables (Table 2). Because there was substantial uncertainty in model selection with two competing models (Table 2), parameter estimates from predictor variables were derived using multiple model inference (Table 3). Multiple model inference showed that the host-seeking activity varied with the capture time. There were no differences between the capture time categories 'morning' and 'afternoon', but the category 'evening' showed higher catches of mosquitoes than the other categories did (Table 3; Figure 3). Host-seeking activity was enhanced with the increase of air temperature and air environmental RH, whereas it decreased with increasing wind speed and sunshine degree (Table 3; Figure 3). The habitat type and the proximity of larval habitat were not related to *Oc. albifasciatus* host-seeking activity (Table 3). Although no significant relationship with any habitat type was detected, the host-seeking activity was higher in grazing areas and lowest in urbanised areas.

Table 2. Summary of model-selection results that explain *Ochlerotatus albifasciatus* biting rate variation. Predictor variables were HAB: habitat type; TIM: capture time; TEM: air temperature; HUM: air environmental RH; WIN: wind speed; SUN: sunshine degree; and PLH: proximity to a larval habitat (see Methods for details). k is the number of estimated parameters. Models are listed in decreasing order of importance. Models without support (wi < 0.05) were excluded from the table.

Candidate models	*k*	AIC_c	ΔAIC_c	w_i
TIM TEM HUM WIN SUN	8	743.46	0.00	0.43
TIM TEM HUM WIN SUN PLH	9	743.63	0.17	0.39
HAB TIM TEM HUM WIN SUN PLH	12	746.93	3.47	0.08
HAB TIM TEM HUM WIN SUN	11	747.55	4.09	0.06
Null model	2	789.53	46.07	0.00

Table 3. Parameter likelihoods, estimates (± standard error, SE) and 95% confidence interval limits (CL) for explanatory variables describing variation in *Ochlerotatus albifasciatus* biting rate. Parameters with CL excluding zero are in bold.

Explanatory Variable	Parameter likelihood	Parameter estimate ± SE	CL Lower	CL Upper
Intercept		**−5.47 ± 1.48**	**−8.43**	**−2.51**
Habitat type (grazing areas)[a]	0.14	0.31 ± 0.58	−0.83	1.46
Habitat type (irrigation and drainage canals)[a]	0.14	0.46 ± 0.54	−0.60	1.53
Habitat type (vegetated areas)[a]	0.14	0.88 ± 0.53	−0.17	1.92
Capture time (afternoon)[b]	1.00	0.26 ± 0.33	−0.40	0.91
Capture time (evening)[b]	**1.00**	**1.58 ± 0.35**	**0.89**	**2.27**
Air temperature	**1.00**	**0.26 ± 0.04**	**0.18**	**0.34**
Air environmental RH	**1.00**	**0.098 ± 0.018**	**0.062**	**0.134**
Wind speed	**0.96**	**−0.022 ± 0.007**	**−0.036**	**−0.007**
Sunshine degree	**1.00**	**−0.020 ± 0.004**	**−0.029**	**−0.012**
Proximity of larval habitat[c]	0.48	0.43 ± 0.29	−0.14	1.00

[a]Relative variable to value of habitat type (urbanised areas).
[b]Relative variable to value of capture time (morning).
[c]Relative variable to value of proximity of larval habitat (absence).

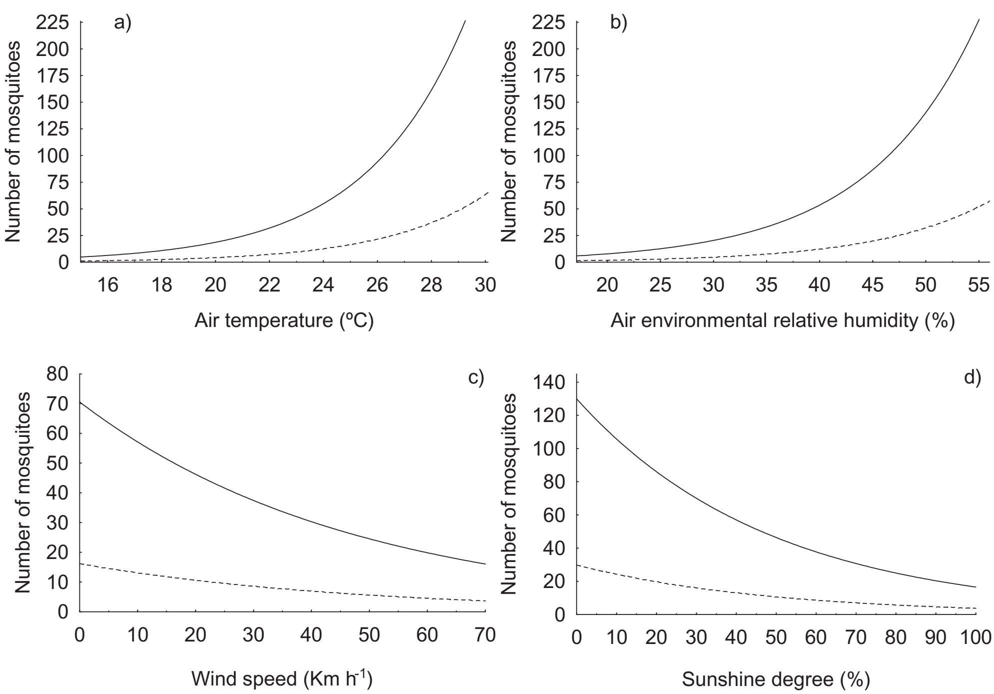

Figure 3. Relationship between biting activity rate of *Ochlerotatus albifasciatus* (number of mosquitoes captured on the bait during 20 minutes of exposition) and (A) air temperature, (B) air environmental RH, (C) wind speed and (D) sunshine degree. Continuous lines correspond to trials conducted in the evening, and dashed lines correspond to trials conducted in the morning and afternoon (pooled). Adjusted functions were obtained from a generalised linear model with negative binomial error distribution and log link function (see Methods for details).

Only one other species was registered. Two adults of *Culex eduardoi* were caught by active capture near a temporary pond.

Discussion

The univariate bar graphs indicate that air temperature greater than 24°C, and less than 30°C, and percentages of air humidity from 40 to 55%, would be appropriate for the blood-feeding activity of the mosquito. In terms of sunshine, conditions with less than 50%, and, for wind, speeds of less than 15 km/h, would be the most propitious. But considering all the variables involved, coincidentally, the GLM model obtained for blood-feeding activity of adults is related to certain meteorological and microenvironmental characteristics. The combination of these characteristics (wind speed less than 20 km/h, environmental temperature greater than 26°C, sunshine less than 40% and RH greater than 50%, according to the GLM plots obtained) would provide favourable conditions to allow seeking activity and feeding on the host.

The negative relationship between biting rate and degree of sunshine would be related to favourable conditions for activities outside the shelter as host-seeking for hematophagic feeding. Exposure of females to very high temperatures or high insolation and low environmental RH affects the survival of these exothermic animals, who cannot regulate their metabolism efficiently in these environmental conditions (Clements 1992).

Based on our results, it could be inferred that the low sun exposure of certain areas, when the wind speed is low, allows the environmental air temperature and RH to be high enough to enable the females to perform their host-seeking activities. On the other hand, the flight activity of haematophagous insects can be greatly reduced by wind. Consistent with this, we find a negative association between higher rates of biting and wind speed. Although wind usually inhibits flight, it appears that newly emerged adults of some mosquito species are specially adapted to take off and fly in windy weather, thus promoting dispersal and the colonisation of new areas (Service 1980). Even though some captures were made at high wind speeds, the results suggest that females could exploit periods between bursts to fly to their host. This species would be well adapted to fly in this condition. Hack et al. (1978) in the province of Corrientes (northeastern Argentina) registered hematophagic activity with wind bursts up to 35 km/h. In this study, females' hematophagic activity was recorded with wind bursts up to 55.5 km/h. *Oc. albifasciatus* females have been observed flying and biting humans on the island of Tierra del Fuego (Argentina) and Torres del Paine National Park (Chile) with high wind speeds (N. Burroni, N. Schweigmann and C. Marinone, unpublished data).

Oc. albifasciatus shows a host preference for domestics animals, like rabbits (Stein et al. 2013; Almirón and Brewer (1995) and chickens, but it is also anthropophilic. In a rural ecosystem with low human density, farm animals constitute an alternative food. In Sarmiento Valley, the low density of blood sources (both humans and other animals) could be one reason why there was no difference in biting rates between different environments, because *Oc. albifasciatus* females actively seek for their hosts, flying long distances. It was observed that adults of this species seem to disperse far away from larval habitats (Gleiser et al. 2002; Bejarán et al. 2008). This would also explain the lack of association between the biting rate and the proximity to breeding sites.

Although in this work we did not study host preference, it is likely that this mosquito is fed into this valley from farms and grazing animals, and wildlife (especially birds) and humans. Further studies could confirm this. Also, the atmospheric humidity was relatively higher in this valley compared to the surrounding steppe (RH values between 20 and 23%, studied in parallel in the surrounding steppe; data not shown), and the irrigation dynamic of grazing areas (flooding large areas of land periodically) should allow the proliferation of immature mosquitoes as well as the supply of blood to the females. The presence in urban areas of this study (although not markedly), in addition to the nonselective eating patterns for females of this species (including humans; Almirón and Brewer 1995), and their insistent bites in farms and recreational areas, would increase the importance of the species as a vector of pathogens and as an interfering factor in livestock activities.

Ludueña Almeida and Gorla (1995), in studies from Central Argentina, found hematophagic activity when the minimum daily temperature was higher than 6°C, and Hack et al. (1978) found the same in northeastern Argentina, when the temperature varied between 4 and 35°C. In our research, the minimum temperature at which hematophagic activity was found was 12.3°C, but there was no activity at 9.8 or 32.9°C in windy conditions higher than 30 km/h. In addittion, in this work, evening hours seemed to be the most favourable for *Oc. albifasciatus* female host-seeking, consistent with Ludueña Almeida and Gorla (1995) who also detected that the catches decrease at higher illumination, observing an evening peak of activity.

Therefore, evening matches daily periods of lower light intensity and mean air temperature high enough to allow flight activity of females. This mosquito disperses between environmental patches having the favourable characteristics that we mentioned above. In those sites, they can have hematophagous activity and fulfill their reproductive cycle, activities usually recorded relatively close to their breeding sites (Gleiser et al. 2000). However, the small abundance that we have recorded in the steppe could be an indication that this species would disperse to unfavourable areas, something that could be studied in future.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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