

1 Title: Ecological and life-history traits and their relationship with West Nile virus and Saint Louis  
2 Encephalitis virus exposure risk.

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17 Body mass, Migratory status

18 Abstract:

19 Host life-history traits can influence host-vector encounter rates, and so differentially determine the  
20 exposure risk of bird species. This modulation of host-virus encounters' dynamics is especially  
21 important when facing "generalist" arboviruses like West Nile virus (WNV) and Saint Louis  
22 Encephalitis virus (SLEV). Using prevalence data collected by our laboratory since 2004, we tested  
23 several hypothesis that included birds' ecological and life-history traits to determine which traits were  
24 better predictors of birds' exposure risk to these arboviruses. By means of information-theoretic  
25 procedures and generalized mixed linear models, we observed that body mass was an important trait  
26 when predicting birds' exposure risk to WNV and SLEV and migratory status significantly influenced  
27 birds' exposure risk only to WNV. Our study highlights important traits to consider when studying the  
28 transmission system of these arboviruses, being useful to focus resources when characterizing viral  
29 transmission networks and discuss the repercussions of these traits over birds' immune function  
30 throughout the pace of life syndrome and trade-offs theory.

31 Introduction

32 West Nile Virus (WNV) and Saint Louis Encephalitis Virus (SLEV) are two emerging arboviruses  
33 belonging to the family Flaviviridae. Both are causative agent of encephalomyelitis and are  
34 considered of global health concern (Guth et al. 2020), affecting not only humans but also wildlife  
35 (LaDeau et al. 2007; Ong et al. 2021). Both, WNV and SLEV are maintained in a diverse 'multi-vector  
36 multi-host' transmission network, with intrinsic spatial and seasonal fluctuation (Diaz et al. 2013b).  
37 West Nile and SLE viruses share an ecological resemblance in their maintenance network being  
38 predominantly maintained by members of the Culex genera and a wide range of avian hosts' species  
39 (mainly Passeriformes and Columbiformes) (Reisen 2003, 2013; Diaz et al. 2013a; Ciota 2017;  
40 Rochlin et al. 2019; Giayetto et al. 2021). However, there are differences in their hosts' species range  
41 and in the consequences that these viruses might have on the health status of their hosts. For  
42 example, WNV tends to have an increased mortality in a higher range of bird species (Lanciotti et al.  
43 1999; Lord & Day 2001; Maharaj et al. 2018).

44

45 To be maintained in nature, both WNV and SLEV need a competent vector to feed on a competent  
46 host. Consequently, mosquitoes feeding patterns take an important role in viral dynamics (Kilpatrick  
47 et al. 2006a), affecting host-vector encounter rates and favouring certain host species to be chosen  
48 by competent vectors. Despite certain evolutionary and environmental conditions that affect  
49 mosquitos feeding patterns- i.e., host availability, hosts defensive behaviours and blood nutritive  
50 value- there are interspecific differences in host life-history traits that can influence host-vector  
51 encounter rates, and so differentially determine the exposure risk of bird species and modulate the  
52 host-viral encounters dynamics (Lyimo & Ferguson 2009; Kernbach et al. 2021).

53

54 Some of the life history traits that can have repercussions in modelling exposure risk in host species  
55 are nest characteristics, body mass, clutch size, migratory behaviour, and diet type, among others.  
56 Particularly, it has been described nest height and type were able to predict the infection probability  
57 to heamosporidian parasites transmitted by Culex species in central and southern African birds (Lutz

58 et al. 2015; Ganser et al. 2020). Body mass and clutch size affect vector-hosts interactions since  
59 larger and bigger bodies as well as bigger clutches releases more olfactory cues to vectors, as  
60 observed by Figuerola et al. where a greater seroprevalence of WNV was observed in larger hosts  
61 (Figuerola et al. 2008; Takken & Verhulst 2013). Migratory behaviour and seasonality also influence  
62 vector-host encounters by affecting mosquito host availability (Rappole et al. 2000; Peterson et al.  
63 2004). Finally, differences in hosts' diet type have previously been associated with the infection risk  
64 to other arboviruses, potentially due to the relationship between the type of diet and the foraging time  
65 during which an individual may be exposed to a mosquito bite (González et al. 2014; Walsh 2019;  
66 Skinner et al. 2021).

67 In the previously described frame, we hypothesize ecological and life history traits can modulate  
68 vector-host encounters and consequently predict birds' exposure risk to vector-borne pathogens, we  
69 expect differences among traits when trying to predict exposure risk to WNV and SLEV in birds, with  
70 some of such traits being better predictors than others. In evaluating whether the selected ecological  
71 and life history traits are able to predict birds' exposure risk to WNV and SLEV, we were able to  
72 establish that certain hypothesis (and consequentially, certain traits) are better when predicting birds'  
73 exposure risk to WNV and SLEV.

74

## 75 Methods

### 76 Prevalence data

77 We used the serological state against WNV and SLEV (presence/absence of neutralizing antibodies)  
78 data from free-ranging birds, obtained between 2004 and 2019 in 5 different Argentinean provinces  
79 (Córdoba, Chaco, La Pampa, San Luis, and Tucumán) (Figure 1). For Córdoba province, we used  
80 data obtained in 2004, 2005, 2006, 2012, 2013 and 2014 from Cordoba city, and La Para (Diaz et al.  
81 2008, 2016). For Chaco and Tucumán provinces, data were obtained in 2005 and 2006 respectively  
82 (Diaz et al. 2008). The province of San Luis was sampled in 2011. Finally, data from La Pampa was  
83 obtained between 2017 and 2019 (Mansilla et al. 2022). Within each province, several sample sites  
84 were used (Figure 1). The presence of neutralizing antibodies in avian sera was used as indicative

85 of a previous exposure to WNV and/or SLEV and the posterior survival of the individual. Birds'  
86 sampling procedure was performed as described elsewhere (Diaz et al. 2016). Briefly, birds were  
87 captured using mist nets. After capture, birds were taxonomically determined and then bled by  
88 jugular veinpuncture. Blood samples were diluted in Minimum essential Medium and then centrifuged  
89 for serum obtention. Serum was stored at -20°C until analysis. Finally, samples were screened for  
90 the presence of WNV- and SLEV-reactive antibodies by plaque-reduction neutralization test (Tauro  
91 et al. 2012).

92

### 93 Ecological and life-history traits data

94 We combined a dataset of ecological and life-history traits that were potentially relevant to explain  
95 WNV and SLEV birds' exposure risk (Rappole et al. 2000; Peterson et al. 2004; Figuerola et al. 2008;  
96 Takken & Verhulst 2013; González et al. 2014; Lutz et al. 2015; Walsh 2019; Ganser et al. 2020;  
97 Skinner et al. 2021). We selected the following six traits: body mass, clutch size, nest height, nest  
98 type, diet type and migratory status. Both, body mass and clutch size were included as each species'  
99 media value. Nest height was classified in three categories, as ground, understory (nests  
100 predominantly found above ground and below 3m) or canopy/sub-canopy (nests predominantly found  
101 above 3m). Nest type was classified in three categories, as open cup, closed cup or cavity. Diet type  
102 was categorized into 7 groups according to the primary diet of each species: Folivore-Frugivore,  
103 Frugivore-Insectivore, Granivore, Granivore-Insectivore, Insectivore, Insectivore-Carnivore and  
104 Omnivore. Finally, migratory status was categorized as resident or migrant. For body mass and clutch  
105 size, data was extracted from Cooke et al., 2019 dataset (Data available from figshare repository:  
106 <https://doi.org/10.6084/m9.figshare.5616424.v1>) (Cooke et al. 2019). Information referring to nest  
107 characteristics, diet and migratory status was extracted mainly from The Cornell Lab of Ornithology  
108 website (<https://birdsoftheworld.org>). We supplemented missing species traits with additional data to  
109 have all the mentioned traits for each species included in this study (Mason 1986; Wiley 1988; Aráoz  
110 et al. 2016).

111

112 Statistical analysis

113 To test the effects of ecological and life-history traits on birds' exposure risk, data including WNV and  
114 SLEV birds' serological status was used as response variable (Kernbach et al. 2021). We used  
115 generalised linear mixed models (GLMM) with Binomial error distribution and logit link function. Nest  
116 type, nest height, migratory status, migration type and diet type were included as categorical fixed  
117 effects, while clutch size and body mass were standardized (mean=0; SD=1) and included as  
118 continuous fixed effects. As both viruses shown stational and geographical variations in their  
119 circulation (Diaz et al. 2013b), sampled year and sample sites nested within province were included  
120 as a random effect. Birds' family was also included as a random effect to account for the statistical  
121 lack of independence within host phylogenetic relationships.

122 Twenty candidate models for each virus were evaluated following information-theoretic procedures  
123 (Burnham & Anderson 2002). We considered models that tested each of our candidate hypothesis  
124 over ecological and life history traits that could account for birds' exposure risk to SLEV and WNV  
125 (Table 1). Within the candidate models, we included those with the individual effects of each of the  
126 selected traits as well as models containing the additive effects of certain mentioned traits.

127

128 Models were tested for Akaike's information criterion corrected for small sample size (AICc) (Burnham  
129 & Anderson 2002, 2004) for the analysis of variation in WNV and SLEV seroprevalence. Model  
130 comparisons were made with  $\Delta AICc$ , calculated as the difference in the AICc values between each  
131 model and the best-fitted model in the set. Akaike weight ( $\omega AICc$ ) was also calculated for each model  
132 to evaluate the weight of evidence in favour of each candidate model. Parameter estimates were  
133 calculated using model-averaged parameter estimates based on the  $\omega AICc$  from a subset of  
134 candidate models. The subset was established considering models with  $\Delta AICc < 7$  (Burnham &  
135 Anderson 2004). To supplement parameter-likelihood evidence of important effects, we calculated  
136 95% confidence interval limits (CI) of parameter estimates, considering that a parameter is  
137 significantly associated with the WNV or SLEV exposure risk when its CI did not include zero.  
138 Statistical analyses were performed in the 'lme4' package and 'MuMIn' (Bates et al. 2015; Barton

139 2020), in R v 4.0.3 (R Core Team, 2020). For data visualisation of birds seroprevalence we used non-  
140 metric multidimensional scaling (k=2) using Gower similarities distance between species ordered by  
141 their ecological and life history traits with the 'metaMDS' function from the vegan package (Oksanen  
142 et al. 2020) (Figure 2).

143

144 Results.

145 A total of 3487 tested birds were included in our analysis. WNV seroprevalence accounted for 4%  
146 distributed in 42 species. On the other hand, 8% of the tested birds were positive to SLEV distributed  
147 in 60 species. Only 1.5% of the avian sera tested performed a heterotypic immunological reaction  
148 indicating birds had been exposed to both viruses (Figure 2). As a first indicative of virus-host contact,  
149 birds belonging to Bucconidae, Caprimulgidae, Polioptilidae families where only exposed to WNV,  
150 whereas birds belonging to Charadriidae, Emberizidae, Falconidae, Mimidae, Passerellidae, Picidae,  
151 Recurvirostridae and Scolopacidae families where only exposed to SLEV.

152 Among the 20 models tested for both WNV and SLEV, 10 models were selected ( $\Delta AICc < 7$ ) for WNV  
153 and 7 for SLEV that could predict birds' exposure risk to these viruses (Table 3 and 4). The model-  
154 averaged for WNV included migratory status, body mass, clutch size, nest height, diet type and nest  
155 type as explanatory variables. The 95% CI for the parameter estimates for migratory status (0.85  
156 relative importance) and body mass (0.84 relative importance) did not include zero, indicating that  
157 these two explanatory variables significantly influenced birds' exposure risk to WNV (Figure 3). West  
158 Nile virus exposure risk increased 1.22 times for each increase in the standard deviation (28.6 g) of  
159 body mass ( $0.196 \pm 0.07$ , estimate and SD) and differed between migratory status, being resident  
160 birds 5 times more exposed than migrants ( $-2.89 \pm 1.5$ ;  $-4.47 \pm 0.88$ , estimates and SD for residents  
161 and migrant birds, respectively) (Figure 3). For SLEV, the model-averaged included migratory status,  
162 body mass, clutch size, nest height, and nest type as explanatory variables. The 95% CI for the  
163 parameter estimates for body mass (one relative importance) did not include zero, indicating that this  
164 explanatory variable significantly influenced birds' exposure risk to SLEV (Figure 3). SLEV exposure

165 risk was positively associated with body mass, increasing 1.18 times for each increase in the standard  
166 deviation (28.6 g) of body mass ( $0.176 \pm 0.06$ , estimate and SD).

## 167 Discussion

168 In this study, we analysed an extensive serological dataset on WNV and SLEV in relation to ecological  
169 and life-history traits of 132 bird's species from different provinces in Argentina. We tested if selected  
170 ecological and life history traits could predict bird's exposure risk to the afore mentioned viruses.  
171 Previous studies observed that nest characteristics and diet type influence the infection risk to  
172 mosquito-borne hemoparasites (González et al. 2014; Ganser et al. 2020), and that the number of  
173 offspring (i.e clutch size) and diet type positively correlate with other arboviral infections (Walsh 2019;  
174 Skinner et al. 2021). In addition, nest characteristics were previously associated with WNV infection  
175 risk in Senegal (Chevalier et al. 2009). Our study does not support the previously observed effects  
176 over WNV and SLEV exposure risk on the tested avian hosts species. Moreover, we observed that  
177 body mass and migratory status are important predictors for exposure risks to these arboviruses in  
178 our region. It should be noted that, differences in the selected traits between regions might be different  
179 due to changes in the maintenance networks of these mosquito-borne pathogens, particularly on  
180 those in which species of mosquitoes are involved in their transmission. We specifically observed that  
181 WNV exposure risk was higher in resident birds and increases as body mass increase. For SLEV,  
182 body mass was the only explanatory variable that predicted the exposure risk, being positively  
183 associated.

184 Previous studies have shown that body mass may play a significant role in vector-host contact rates,  
185 and hence, in host exposure risk to arbovirus (Takken & Verhulst 2013; Yan et al. 2017, 2018). The  
186 same pattern was observed for Ross River virus (a mosquito-borne arbovirus of the Togaviridae  
187 family) (Skinner et al. 2021), the vector-borne avian haematozoan parasites (Arriero & Møller 2008)  
188 and WNV in the southwest of Spain (Figuerola et al. 2008). Species with larger bodies, in which lead  
189 to higher body mass, might be more exposed to WNV and SLEV due the production of higher quantity  
190 of visual and olfactory cues, like carbon dioxide (Gillies & Wilkes 1972), and/or a diminished  
191 expression of anti-mosquitoes behaviours (Edman & Scott 1987; Mooring et al. 2004). Furthermore,



192 they tend to live longer periods than smaller birds, thus increasing the likelihood to be exposed along  
193 their life span. Studies performed in *Cx. pipiens* mosquitoes showed that body mass affect  
194 mosquitoes' feeding rates and host selection, even at an intraspecific level (Yan et al. 2017, 2018).  
195 This might indicate that both, intra and interspecific differences regarding ecological and life history  
196 traits are capable of modulating birds' exposure risk by influencing mosquitoes feeding patterns and  
197 behaviour.

198 Migratory behaviour was an important predictor of WNV exposure risk, being resident species more  
199 exposed than migrants. Twenty six of the 132 sampled species catalogued as migrant exhibited 5  
200 times lower exposure risk to WNV. Within these species, both Neotropical and Nearctic long-distance  
201 migrants were included (Hayes 1995). The former breeding in Argentina and migrating northward  
202 during non-breeding season, like the Vermilion flycatcher (*Pyrocephalus rubinus*), the Double-  
203 collared seedeater (*Sporophila caerulescens*), the White-banded Mockingbird (*Mimus triurus*) and  
204 species of the *Elaenia* genera. The latter, Nearctic long-distance migrants, breeds in North America  
205 and migrates southward during non-breeding season, like the White-rumped sandpiper (*Calidris*  
206 *fuscicollis*) and the Stilt sandpiper (*Calidris himantopus*). Despite these species show differences in  
207 their migratory behaviour, in addition to differences in other ecological and life history traits, none of  
208 them showed to be exposed to WNV nor SLEV (seroprevalence ranging from 0.007 to 0.04). These  
209 could indicate that neither the migratory routes nor the migratory behaviour of the evaluated species  
210 affects their exposure risk differentially. The observed values in exposure risk could be due to  
211 differences in viral circulation determined by local variations in the transmission networks between  
212 breeding and non-breeding areas (Kilpatrick et al. 2006b; Diaz et al. 2013b), as observed in Palearctic  
213 summer migrants in Spain and resident birds in Senegal (Figuerola et al. 2008; Chevalier et al. 2009).  
214 Lastly, it is important to highlight that exposure risk does not reflect the potential role of a specie in  
215 the transmission network, as it has been largely proposed that migratory birds are partially  
216 responsible in viral spreading (Rappole et al. 2000; Hoover & Barker 2016; Swetnam et al. 2018).

217

218 Life history traits are not only related with birds' exposure risk to vector-borne pathogens by  
219 modulating host-vector encounters, but they are also closely related to birds' immune function  
220 throughout the pace of life syndrome and trade-offs (Norris & Evans 2000; Zuk & Stoehr 2002;  
221 Tieleman 2018). Within this context, species with "slow-living" traits (longer life cycles, larger body  
222 size, slower reproductive rates, and higher adult survival) show differences in immune capacity and  
223 responses in contrast with "fast-living" species (characterized by opposite traits in the pace of life  
224 spectrum) (Martin et al. 2006; Hasselquist 2007; Johnson et al. 2012). Particularly, slow-living species  
225 will tend to favour specific immune defences over constitutive and proinflammatory responses (Lee  
226 2006; Martin et al. 2006, 2008). On the other hand, "fast-living" species will tend to emphasise more  
227 in the unspecific components of their immune responses (Lee 2006; Lee et al. 2008a). Moreover, life  
228 history traits like long-distance migrations are linked to trade-offs as well, limiting resources that could  
229 be used in immune function and, hence (Schmid-Hempel & Ebert 2003), modifying birds resource  
230 allocation (Buehler et al. 2010; Hasselquist & Nilsson 2012).

231

232 Traits like body mass and clutch size (that are included in the pace of life syndrome) has been  
233 previously used to explain differences in host competence index for WNV and Eastern Equine  
234 Encephalitis Virus, being negatively correlated with body mass and positively with clutch size (Huang  
235 et al. 2013). Now, knowing which life history traits were better able to predict WNV and SLEV  
236 exposure risks, we might ask if these selected traits can provide information about the possible  
237 outcome of viral infection. Both body mass and migration status have been shown to be related with  
238 the immune response. Firstly, body mass was used to explain differences in host competence index  
239 for WNV and Equine Encephalitis Virus (Huang et al. 2013). This pattern might be due to the  
240 relationship established between body mass, the pace of life continuum and immune function (Lee  
241 2006). Specifically, larger slow-living animals develop stronger induced cellular immune responses  
242 and rely more heavily on developing induced humoral immune responses, which are less expensive  
243 from an energetic perspective (Lee 2006; Palacios & Martin 2006; Lee et al. 2008b; Rauw 2012).  
244 These traits might give advantages to larger birds against their greater exposure risk when  
245 responding to arboviral infection while facing multiple environmental demands.

246 On the other hand, and regarding the differences between migrant and resident birds, migrants might  
247 compromise their ecological capital and resource allocation towards migration as a priority (Zuk &  
248 Stoehr 2002; Lee & Klasing 2004; Buehler et al. 2010). Consequently, they are not expected to have  
249 the full capacity to mount the required immune response against viral infection (Sitati et al. 2003;  
250 Rauw 2012). Nevertheless, a study performed by Owen et al. showed that there were not significant  
251 effects of displaying migratory activity over the infection outcome, but affected their migratory activity,  
252 changing the status of half the cohort to non-migratory (Owen et al. 2006). This might indicate that if  
253 the infection is prior to the migratory event, the resource allocation will favour solving the infection at  
254 the expense of migration. Still, it is uncertain what the outcome will be if the infections occur  
255 temporarily after the migratory event. In this context, it is possible for species with higher exposure  
256 risks (resident and larger) to have the resources to resist viral infection, thus being capable to afford  
257 the costs of the complex immune response required to resist viral infection (Zuk & Stoehr 2002;  
258 Samuel & Diamond 2006; Rauw 2012). Hence, these species might exhibit a lower contribution to  
259 the viral flow in the arboviral maintenance network, highlighting the fact that the trade-offs in viral  
260 amplification driven by immune system are also needed to be considered in transmission dynamics  
261 (Althouse & Hanley 2015).

262 Overall, our results suggests that body mass is the main driver or birds' exposure risk to WNV and  
263 SLEV. Moreover, larger resident birds might be prone to WNV exposure compared to smaller migrant  
264 birds. These results also provide information on our regional transmission system of these  
265 arboviruses, being useful to focus resources when describing local viral prevalence and  
266 characterizing viral transmission networks. Lastly and based on an immune-ecological approach, the  
267 most exposed bird's species might not be efficient host for the evaluated viruses, thus compensating  
268 the potential increased in transmission. This theoretical approach should be carefully considered  
269 although it needs to be further explored experimentally, considering the trade-offs that might occur  
270 within host viral replication.

271

272 Table 1. Structure of Generalized Linear Mixed Models analysing the association between birds'  
273 exposure risk to West Nile Virus (WNV) or Saint Louis Encephalitis Virus (SLEV) and ecological and  
274 life history traits. For all models, sampled year, sample sites nested within province and birds' family  
275 were used as random effects. For each model, the biological justification and predictions are  
276 explicated.

277

Models	Variables	Biological justification	Prediction
GLMM 0		The ecological and life history traits include in this study do not predict birds exposure risk to WNV or SLEV.	
GLMM 1	Nest Height	The vertical habitat distribution of mosquitoes' species influence their access to different host species and the possibility to transmit diseases. Particularly, mosquitoes of the genus <i>Culex</i> prefer to feed at ground level (Černý <i>et al.</i> 2011)	Birds' exposure risk decreases as nest height increases
GLMM 2	Nest type	Physical barriers generated by the nest structure can prevent contact between vectors and hosts, acting as a potential physical barrier (González <i>et al.</i> 2014)	Birds whose nests are closed or in cavities have a lower exposure risk.

GLMM 3	Diet type	Diet type influence over foraging time and the use of the environment. Both influence over the time and magnitude that birds are exposed to mosquito bites (González <i>et al.</i> 2014; Walsh 2019; Skinner <i>et al.</i> 2021)	Exposure risk decreases in birds' species with broader diets.
GLMM 4	Migratory status	Exhibiting a wide diversity of regions and geographic areas involved in the life cycle might affect differentially the exposure risk of migrant species, depending on the migration seasonality and the viral prevalence among migration sites (Figuerola <i>et al.</i> 2008; Chevalier <i>et al.</i> 2009)	Migratory birds are more exposed to WNV and SLEV.
GLMM 5	Clutch size	The number of chicks per nest can alter mosquitoes host seeking behaviour by changing the quantity of olfactory cues and heat production <sup>20,35</sup> .	Bird species with larger clutch size are more exposed to WNV and SLEV.
GLMM 6	Body mass	To seek for hosts, mosquitoes rely on olfactory and visual cues. In both cases, body size reflected in body mass can influence the number of clues that are released.	Bigger bird species are more exposed to WNV and SLEV

GLMM 7	Diet type + Migratory status	The exposure that birds may have in relation to their diet can vary depending on the area they are in during migration.	Migratory birds with broader diets are more exposed to WNV and SLEV
GLMM 8	Nest height + Nest type	Nest structure can facilitate or hinder the encounter between vectors and hosts only at certain heights of the nest.	Higher and open nest are more exposed to WNV and SLEV. This pattern increase with increasing body mass and clutch size.
GLMM 9	Body mass + Nest height + Nest type		
GLMM 10	Clutch size + Nest height + Nest type		
GLMM 11	Body mass + Clutch size + Nest height + Nest type		
GLMM 12	Body mass + Nest height		
GLMM 13	Clutch size + Nest height		
GLMM 14	Clutch size + Nest type		
GLMM 15	Body mass + Nest type		

GLMM 16	Body mass + Clutch size	Both bird size and clutch size can add olfactory and visual cues for mosquitoes	
GLMM 17	Body mass + Clutch size + Migratory status	Cues given by the clutch size and body mass can alter host seeking behavior depending on the region where the birds nest	
GLMM 18	Body mass + Migratory status	Birds body mass affects the number and period of the stopovers during migration, potentially affecting the exposure to pathogens in that area.	
GLMM 19	Clutch size + Migratory status	Based on where the breeding season occurs, clutch size may or may not be a factor affecting exposure risk	
GLMM 20	Body mass + Diet type	Variations in the items included in the diet (and hence in the use of the environment) may occur due to the size of the species	

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279

280

281 Table 2. Summary of model-selection results for models explaining variation in WNV exposure risk.

282 k is the number of estimated parameters. Models are listed in decreasing order of importance. Models

283 selected for model-averaged with  $\Delta AICc > 7$  are in bold.

284

Candidate Models	k	AICc	$\Delta AICc$	$\omega AICc$
<b>GLMM 18</b>	<b>6</b>	<b>1071.5</b>	<b>0.00</b>	<b>0.420</b>
<b>GLMM 17</b>	<b>7</b>	<b>1072.6</b>	<b>1.11</b>	<b>0.242</b>
<b>GLMM 4</b>	<b>5</b>	<b>1074.6</b>	<b>3.12</b>	<b>0.088</b>
<b>GLMM 19</b>	<b>6</b>	<b>1075.6</b>	<b>4.14</b>	<b>0.053</b>
<b>GLMM 12</b>	<b>7</b>	<b>1075.7</b>	<b>4.25</b>	<b>0.050</b>
<b>GLMM 6</b>	<b>5</b>	<b>1076.1</b>	<b>4.62</b>	<b>0.042</b>
<b>GLMM 16</b>	<b>6</b>	<b>1077.6</b>	<b>6.10</b>	<b>0.020</b>
<b>GLMM 7</b>	<b>11</b>	<b>1077.9</b>	<b>6.46</b>	<b>0.017</b>
<b>GLMM 11</b>	<b>10</b>	<b>1078.3</b>	<b>6.78</b>	<b>0.014</b>
<b>GLMM 9</b>	<b>9</b>	<b>1078.3</b>	<b>6.82</b>	<b>0.014</b>
GLMM 15	7	1078.5	7.06	0.012
GLMM 20	11	1079.7	8.21	0.007
GLMM 1	6	1080.5	9.05	0.005
GLMM 0	4	1080.6	9.13	0.004
GLMM 13	7	1081.7	10.23	0.003



GLMM 10	9	1082.0	10.47	0.002
GLMM 5	5	1082.0	10.52	0.002
GLMM 14	7	1082.5	10.98	0.002
GLMM 8	8	1082.5	11.04	0.002
GLMM 2	6	1082.6	11.11	0.002
GLMM 3	10	1085.2	13.75	0.000

285

286

287 Table 3. Summary of model-selection results for models explaining variation in SLEV exposure risk.

288 K is the number of estimated parameters. Models are listed in decreasing order of importance. Models

289 selected for model-averaged with  $\Delta AICc > 7$  are in bold.

290

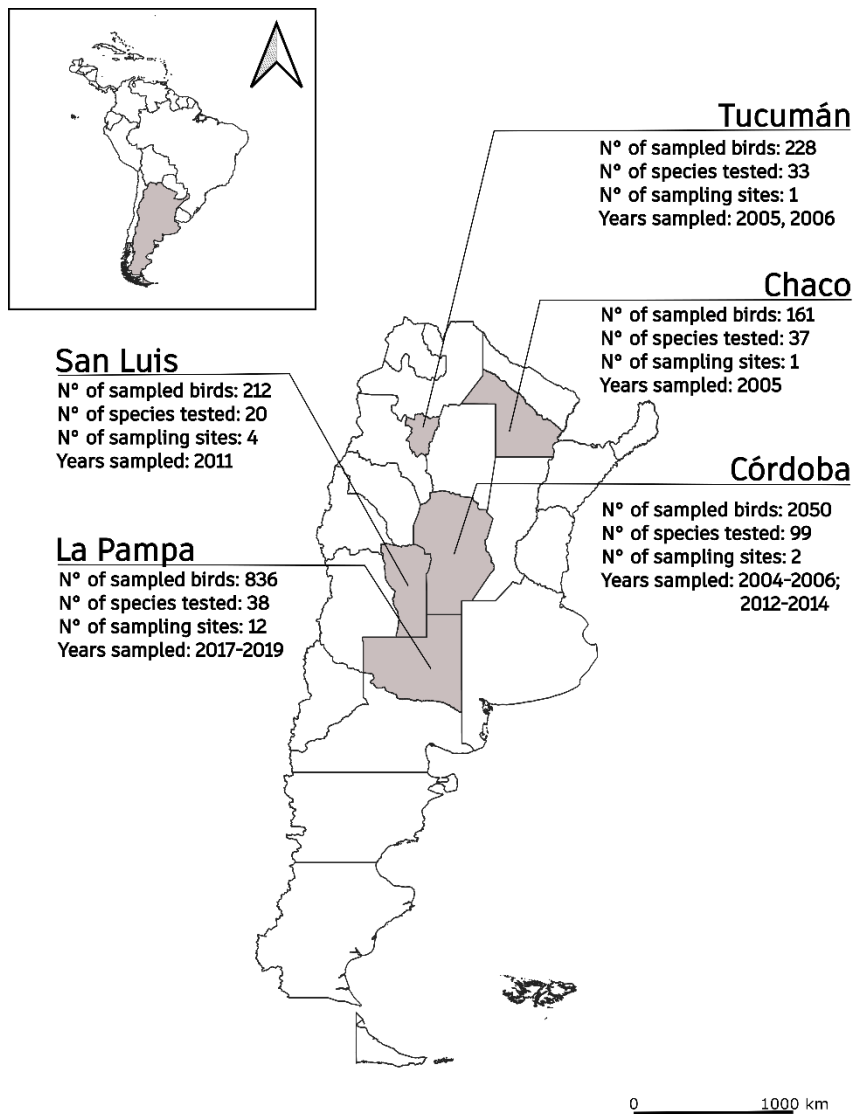
Candidate Models	K	AICc	$\Delta AICc$	$w_i$
<b>GLMM 6</b>	<b>5</b>	<b>1796.9</b>	<b>0.00</b>	<b>0.304</b>
<b>GLMM 18</b>	<b>6</b>	<b>1797.0</b>	<b>0.10</b>	<b>0.290</b>
<b>GLMM 17</b>	<b>7</b>	<b>1798.6</b>	<b>1.74</b>	<b>0.128</b>
<b>GLMM 16</b>	<b>6</b>	<b>1798.7</b>	<b>1.79</b>	<b>0.124</b>
<b>GLMM 12</b>	<b>7</b>	<b>1800.0</b>	<b>3.13</b>	<b>0.064</b>
<b>GLMM 15</b>	<b>7</b>	<b>1800.2</b>	<b>3.33</b>	<b>0.057</b>
<b>GLMM 9</b>	<b>9</b>	<b>1803.1</b>	<b>6.25</b>	<b>0.013</b>
GLMM 11	10	1804.3	7.44	0.007
GLMM 20	11	1804.6	7.73	0.006
GLMM 4	5	1806.5	9.57	0.003
GLMM 19	6	1808.1	11.23	0.001
GLMM 0	4	1808.3	11.44	0.001
GLMM 5	5	1810.2	13.29	0
GLMM 2	6	1811.0	14.12	0
GLMM 14	7	1811.7	14.81	0

GLMM 1	6	1812.1	15.16	0
GLMM 3	10	1812.8	15.86	0
GLMM 7	11	1813.1	16.19	0
GLMM 13	7	1814.0	17.07	0
GLMM 8	8	1814.5	17.60	0
GLMM 10	9	1815.3	18.45	0

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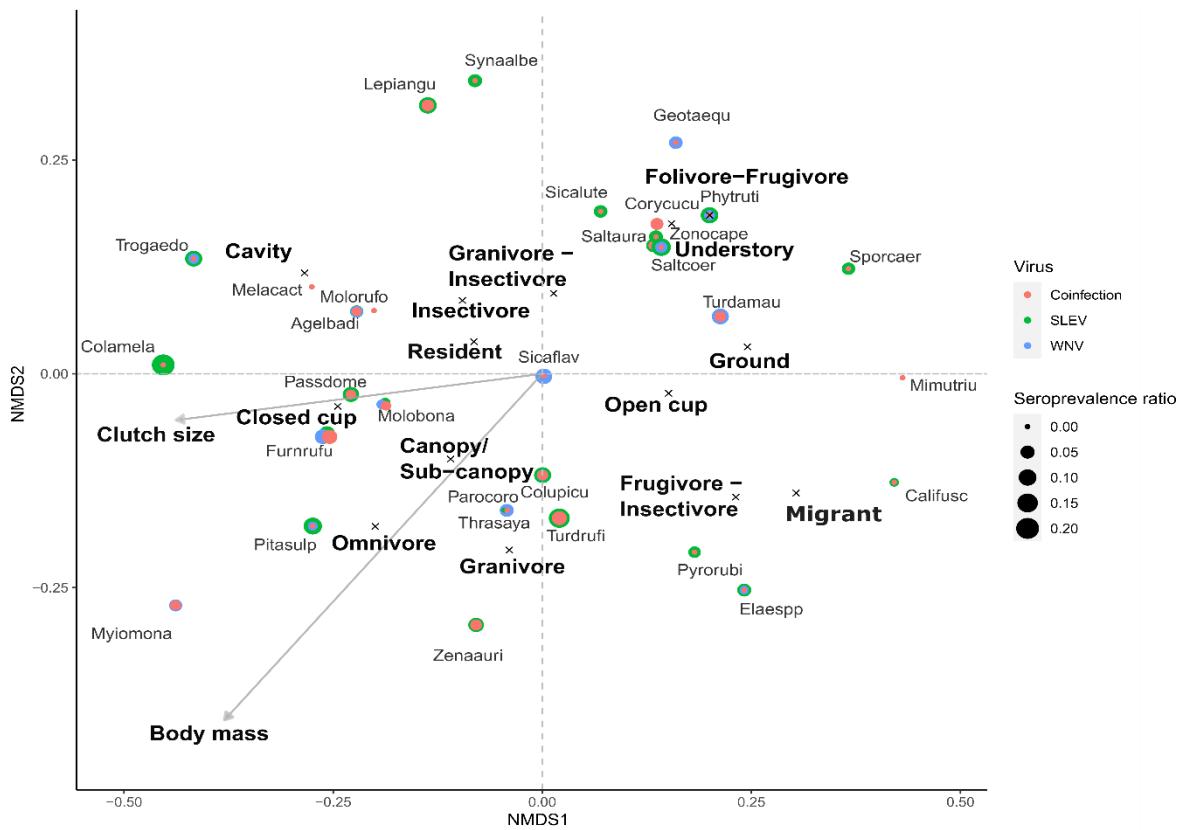


294

295 Figure 1. Map of sampled Argentinean provinces. Within each province, the number of sampled birds,  
296 species tested, sample sites and years sampled are included.

297

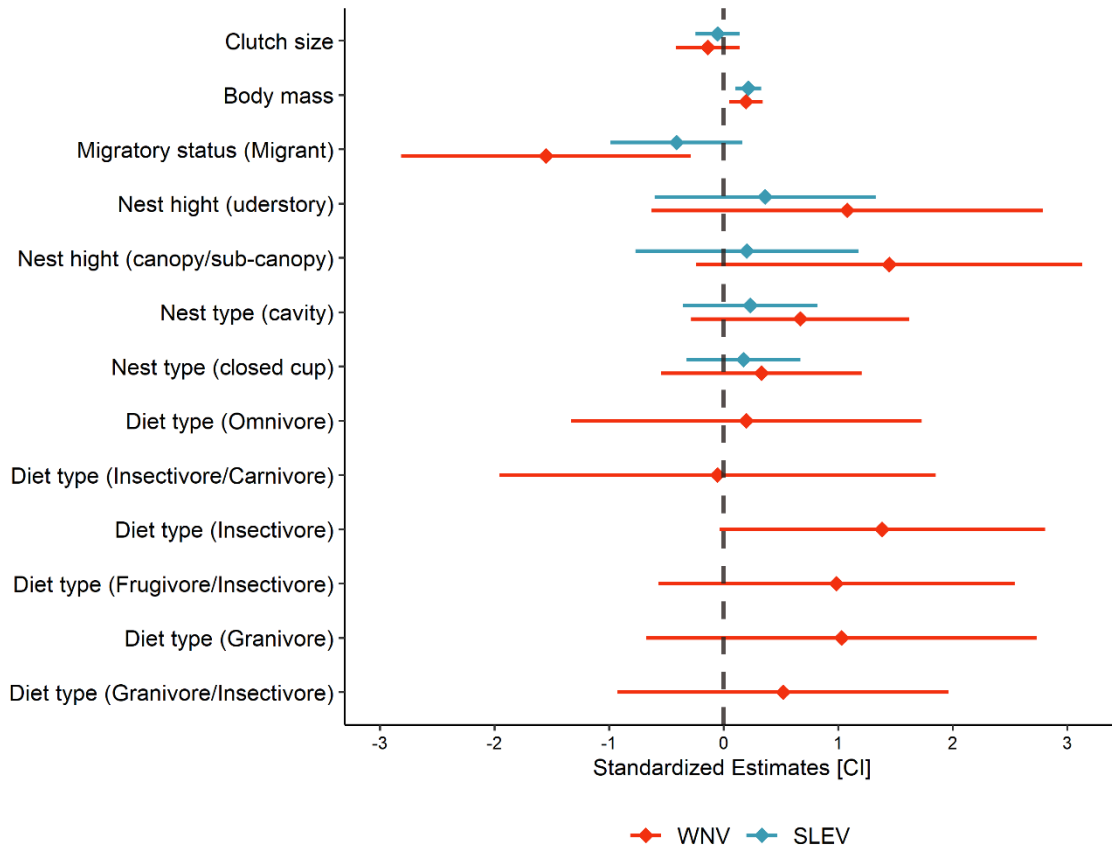
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299

300 Figure 2. Visualization of birds' species according their seroprevalence and their ecological and life  
301 history traits. Non-metric multidimensional scaling (NMDS) plot of life history and ecological traits (via  
302 Gower dissimilarities distance) between sampled species with more than 20 individuals tested for  
303 West Nile virus (WNV) and Saint Louis Encephalitis virus (SLEV) neutralizing antibodies (n = 33).  
304 Concentric circles show if the evaluated species included individuals that were positive for WNV,  
305 SLEV antibodies or showed coinfections between both viruses and the circle size indicates the  
306 magnitude of the seroprevalence.

307



308

309 Figure 3. Effect sizes of the selected ecological and life-history traits variables on West Nile virus  
310 (red) and Saint Louis Encephalitis virus (blue) exposure risk. Standardized effect sizes (rhombus  
311 symbols) and 95% CI (lines) from model-averaged parameter estimates from the subset of candidate  
312 models. Body mass and migratory status had significant effects on WNV risk, whereas only body  
313 mass had significant effects on SLEV risk. In both cases, body mass is positively associated, and  
314 for WNV, residents were more exposed than migrants were.

315

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324 Data, scripts, code, and supplementary information availability: Data and R-codes are available in  
325 figshare repository (Giayetto et al. 2023; DOI: <https://doi.org/10.6084/m9.figshare.21978875.v1>). The  
326 method section and description provide all necessary information about the dataset.

327 Statement of authorship: GO, NFN and DA designed the research, GO collected data, GO and MAP  
328 performed the statistical analysis, all authors analysed the output data. GO wrote the first draft of  
329 the manuscript and all authors contributed with the manuscript revision.

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