

1 **Artificial light at night as a driver to urban colonization by an avian predator**

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16

17 **Abstract**

18 *Context*

19 Urbanization and artificial light at night (ALAN) are major drivers of local biodiversity losses  
20 causing community alterations, disruption of predator-prey interactions, and ultimately,  
21 promotion of cascading effects. However, some species can colonize urban environments.

22 *Objectives*

23 We explore the role of ALAN as a driver of the colonization of urban environments by a  
24 nocturnal avian predator, the burrowing owl *Athene cunicularia*.

25 *Methods*

26 We studied in a suburban locality in La Pampa, Argentina: 1) prey availability with pitfall traps  
27 under streetlights and control sites; 2) diet by analyzing pellets; 3) space use by deploying GPS  
28 data-loggers to breeding owls; 4) nesting habitat selection by comparing environmental  
29 variables at nest and random locations; and 5) productivity by correlating environmental  
30 variables with the number of fledglings.

31 *Results*

32 First, streetlights altered the invertebrate availability, attracting them to illuminated areas.  
33 Second, the owl diet was more similar to the invertebrate taxa trapped at pitfall traps under  
34 streetlights than that in control traps. Third, owl space use was determined by streetlights.  
35 Owls spent more time around light sources, particularly during the nighttime. Fourth, the most  
36 important habitat feature influencing the nesting habitat selection was the distance to  
37 streetlight. Owls selected areas close to streetlights for nesting. Finally, productivity was not  
38 explained by any of our habitat variables.

39 *Conclusions*

40 We demonstrate that ALAN alters the availability of invertebrates and plays a role in the diet,  
41 space use, and occupation of urban burrowing owls. Streetlights increase foraging efficiency  
42 for owls due to the clumping of prey attracted to lights. This predator-prey relationship might  
43 be only supported in suburban environments where low urbanization levels let burrowing owls  
44 nest in bare ground areas, and invertebrates are attracted to ALAN from surrounding wilder  
45 areas.

46 **Keywords**

47 Artificial night lighting, behavior, cascading effects, diet, home range, light pollution, nocturnal  
48 raptor, urban ecology

49 **Running head**

50 Light can facilitate urban colonization

## 51 Introduction

52 Urban environments are predicted to increase in surface and intensity worldwide (Seto  
53 et al. 2012). Currently, around 55% of people live in cities, and by 2030 more than 5 billion will  
54 live in urban areas nearly tripling the global urban land area of 2000 (Seto et al. 2012). One of  
55 the most visible footprints of urbanization is the alteration of natural light levels at night, the  
56 so-called light pollution. A profound transformation of nocturnal landscapes is occurring  
57 worldwide as a consequence of a tremendous increase in the use of artificial light at night  
58 (ALAN)(Falchi et al. 2016). The Earth's area artificially lit increases at a rate of 2.2% per year  
59 (Kyba et al. 2017), and demographic projections and urbanization planning indicate that light  
60 pollution levels will continue to increase unless drastic light management regulations are  
61 implemented, even in protected areas (Kyba et al. 2014; Guetté et al. 2018).

62 Light pollution affects biodiversity in multiple ways (Longcore and Rich 2004; Gaston et  
63 al. 2017; Davies and Smyth 2018), from mass mortality events to subtler effects on animal  
64 behavior and physiology (Stone et al. 2015; Rodríguez et al. 2017; Ayalon et al. 2019; Owens et  
65 al. 2020). These perturbations can produce cascading effects and changes in biological  
66 communities and ecosystems (Davies et al. 2012; Bennie et al. 2015; Knop et al. 2017). ALAN  
67 offers novel predation opportunities (Fleming and Bateman 2018) leading to the disruption of  
68 predator-prey relationships and cascading effects (Longcore and Rich 2004; Davies and Smyth  
69 2018). Diurnal predators could benefit by foraging longer under ALAN (Negro et al. 2000;  
70 DeCandido and Allen 2006; Rutz 2006; Buij and Gschweng 2017). For example, lesser kestrels  
71 *Falco naumanni* nesting on urban colonies may benefit of ALAN by extending their activity to  
72 nocturnal times and reducing the commuting costs of flying between the distant foraging areas  
73 in the surroundings of cities and their urban colonies (Negro et al. 2000). For nocturnal  
74 predators, illumination could be detrimental as foraging times could be reduced, e.g. the  
75 delayed emergence of bats under ALAN (Stone et al. 2015). Also, the nocturnal vision of their  
76 prey could be enhanced or they could spend more time under cover under ALAN, contributing  
77 to reduce predation (Clarke 1983; Scobie et al. 2016). However, nocturnal insectivorous  
78 predators could also benefit from prey attracted to light (Zozaya et al. 2015; Stone et al. 2015;  
79 Komine et al. 2020) or improved visibility by changing from tactile to sight-based foraging  
80 (Dwyer et al. 2013).

81 ALAN is typically studied as a sensory pollutant of cities (Dominoni and Nelson 2018;  
82 Dominoni et al. 2020). Despite being one of the most visible footprints of urbanization (Falchi  
83 et al. 2016), ALAN has usually been overlooked as a driver of colonization and settlement of  
84 birds in urban cities (Isaksson 2018). A larger brain size seems to be the main factor explaining  
85 the species ability to tolerate urban environments, but life history and ecology could also play  
86 a determinant role (Sayol et al. 2020). Moderate levels of urbanization can protect against  
87 predators, favorable temperatures, and food. Urban lighting could be critical to advert  
88 predators at night, but also can provide food resources, for example, congregations of prey  
89 attracted or disorientated by light (Negro et al. 2000; Zozaya et al. 2015; Komine et al. 2020).  
90 Despite these benefits, urban lighting could function as an urban ecological-trap, as  
91 urbanization entails many threats leading to fitness costs, mortality, population declines, and  
92 local extinctions (Grimm et al. 2008).

93 In this paper, we study the role of ALAN in the urban colonization by a nocturnal  
94 predatory bird, the burrowing owl *Athene cunicularia*. This small, territorial raptor nests in  
95 burrows on grasslands, and it is widely distributed throughout North and South America  
96 (BirdLife International 2019). In North America, grassland transformation has led to population

97 declines (BirdLife International 2019). However, in the South America distribution range, the  
98 species has colonized urban areas in recent years, reaching higher densities in urban than in  
99 rural areas (Rebolo-Ifrán et al. 2017; Baladrón et al. 2020). Despite observations of burrowing  
100 owls foraging in illuminated areas (Griffin et al. 2018; Valdez-Gómez et al. 2018), ALAN has  
101 been overlooked in habitat selection studies (Baladrón et al. 2016; Martínez et al. 2017;  
102 Rebolo-Ifrán et al. 2017). ALAN has been considered as a pervasive influence on the habitat  
103 use in North America because prey availability may decrease in illuminated areas (Scobie et al.  
104 2016). Here, we focus on how ALAN influences prey availability, diet, home range, nesting  
105 habitat selection, and productivity of a suburban population. We demonstrate that streetlights  
106 alter invertebrate availability (Davies et al. 2012). Given that the burrowing owl is mainly an  
107 insectivorous species (Sánchez et al. 2008; Solaro et al. 2012; Cavalli et al. 2014), owls benefit  
108 from the ALAN by catching the invertebrates attracted to light. Although exploitation of this  
109 resource could ultimately overcome the constraints of living in urban environments, we  
110 discuss how this novel urban predator-prey relationship could be disrupted in the near future  
111 becoming an ecological trap for this threatened owl species.

## 112 **Methods**

### 113 *Study Area*

114 The study was conducted in La Cuesta del Sur village (36.72° S, 64.27° W), a semi-urban  
115 area (~70 ha) near Santa Rosa city, La Pampa province, central Argentina, during 2017-2018  
116 breeding season. The suburban area is comprised of sparse houses with yards where  
117 burrowing owls excavate their nests within 10–100 m of inhabited buildings. Although streets  
118 are unpaved, sodium vapor streetlights lit the neighborhood at night. Around the village, the  
119 land is dominated by a matrix of agricultural, native forest patches, and a small lagoon (Figure  
120 S1).

### 121 *Invertebrate availability*

122 To assess the availability of invertebrates in relation to light sources, we installed 20  
123 pitfall traps distributed in pairs, i.e. one below post lamps and the other close to that location  
124 under a post without light (Figure S1). Thus, we could compare 10 traps under direct light and  
125 10 traps farther away than 30 meters from any street lamp. We measured richness (number of  
126 orders), biomass (dry biomass in grams), abundance (number of invertebrates per order), and  
127 abundance excluding Formicidae (since social ants were the most abundant invertebrate in  
128 terms of numbers at pitfall traps).

### 129 *Diet*

130 We collected pellets at 19 nest-burrows to identify the main prey items of the  
131 burrowing owl. Pellets were wrapped in aluminum foil, stored in a plastic bag, and dried at  
132 room temperature before analysis. All pellets were broken up by hand under dry conditions,  
133 after which different items were separated. Invertebrate remains were identified to Order or  
134 Family level using a stereo-microscope (8× magnification). Some remains were identified in  
135 comparison to the collections of the *Museo Provincial de Historia Natural* of Santa Rosa, La  
136 Pampa, and the *Centro para el Estudio y Conservación de las Aves Rapaces en Argentina*. The  
137 minimum number of individuals in each pellet was estimated according to the most commonly  
138 found body parts, which represented one individual (heads, mandibles, legs, or other  
139 sclerotized parts). Diet data are shown in two ways: percentage of a particular prey taxon to

140 the total number of identified prey (%P), and percentage of pellets containing a particular prey  
141 taxon, i.e. frequency of occurrence (%FO).

142 To assess the overlap between the pitfall trap contents and diet, we used the  
143 Czekanowski index ( $PS_1$ ):

144 
$$PS_1 = 1 - 0.5 \sum_{j=1}^S |p_{x,i} - p_{y,i}|$$

145 where  $p_{x,i}$  is the proportion of the  $i^{\text{th}}$  diet item consumed by the burrowing owls (diet),  $p_{y,i}$  is  
146 the proportion of the  $i^{\text{th}}$  diet item at traps (under lights or control), and  $S$  is the number of total  
147 prey items. This index ranges from 0 (no overlap) to 1 (complete overlap) and it is well-suited  
148 for comparing proportional data with different numbers of prey items (Kohn and Riggs 1982).

#### 149 *Habitat use and home range*

150 To characterize habitat use, 18 burrowing owls were captured and tagged with GPS-  
151 data loggers (see details on tagging and GPS data loggers in Supplementary Material). All but  
152 one of the owls that was found predated near the nest were recaptured. All data loggers were  
153 operative at the moment of recapture or recovery, but two of them failed to provide useful  
154 data. Once loggers were retrieved, GPS positions were downloaded and imported in *Qgis*  
155 version 3.8.2 (Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>). We  
156 classified the locations as day or night depending on if they were recorded from sunrise to  
157 sunset or from sunset to sunrise, respectively (sunrise and sunset times taken from  
158 <https://www.timeanddate.com/sun/argentina/santa-rosa>).

159 To assess if streetlight surroundings were used more often than other areas, we  
160 compared the number of owl locations in a 30-meter radius of streetlights and random points  
161 locations. We separated these counts considering day or night locations. Random points were  
162 obtained as follow: First, we created kernel density estimations for each tracked bird by using  
163 the heatmap algorithm (Interpolation) at the processing toolbox of *Qgis*. Given the differences  
164 in distribution among the GPS-locations of each bird, we set a search radius (or kernel  
165 bandwidth) and cell size to 40 m and 0.1, respectively. These parameters provided an optimum  
166 density raster in terms of smoothness and sharpness for all tracked birds. The number of rows  
167 and columns of the output raster varied according to the spatial distribution of each bird.  
168 Second, we vectorized the kernel rasters to delete surfaces with 0 or 1 locations (reduced  
169 kernels). Thus, we reduced the chance of random points falling in low-density areas producing  
170 more conservative estimates. Finally, we generated a random point for each reduced-kernel  
171 (Figure S2).

#### 172 *Nesting habitat selection and productivity*

173 Using binoculars and our monitoring of spotted burrowing owls, we looked for nest-  
174 burrows at yards. Each nest-burrow was geo-referenced and described by seven  
175 environmental variables: one binary variable describing the location of the nest, i.e. nest under  
176 a tree or open to sky, four distance measures to the nearest street, light, building, and  
177 inhabited house, and two percentages of mowed grass at two spatial scales (in 20 and 50-m  
178 circles centered on in nests) (see Table S1 for details). Vegetation structure is an important  
179 trait that determines horizontal visibility (Baladrón et al. 2016). The variables nest location and  
180 percentages of mowed grass described such variation. Distances to street, light, building, and  
181 inhabited house described the anthropogenic environment. Nesting habitat characteristics

182 were recorded for 27 active burrowing nest owls and 38 randomly-selected locations within  
183 our study area (Figure S1). We also recorded the productivity (number of fledglings) of each  
184 active nest to test for potential relationships with habitat variables.

#### 185 *Statistical analyses*

186 To compare richness, biomass, and abundance of invertebrates in the paired pitfall  
187 traps, i.e. under streetlights or control, we used Generalized Linear Mixed Models (GLMMs)  
188 with trap location as a two-level factor (under or far away from a streetlight). For biomass, we  
189 used a normal error distribution and identity link, while Poisson error distributions and log link  
190 functions were used for the response variables richness and abundance. Given that pitfall traps  
191 were distributed in pairs, they cannot be treated as independent samples. Therefore, pair  
192 identity was included as a random factor.

193 To study habitat use, we ran a GLMM with binomial error distribution and logit link to  
194 assess the space used in relation to streetlights and random points within the home range of  
195 the owls. As response variable, we used the proportion of GPS-locations within the 30-m  
196 buffer areas centered at streetlights and random points. We created a two-vector variable  
197 containing the counts of success and failure (Zuur et al. 2009). We included two factors with  
198 two levels: period (day or night) and location (Streetlight or random location) and its  
199 interaction. Owl identity was included as a random factor to meet the data independence  
200 assumption.

201 To study nesting habitat selection, we conducted multivariate analyses with  
202 environmental variables (Table S1). We ran Generalized Linear Models (GLMs) with binomial  
203 errors and logit link functions. As response variable, we used a binomial variable (active nest or  
204 random location). To avoid multicollinearity, we excluded those variables with variance  
205 inflation factors (VIFs) higher than two (Zuur et al. 2010). The variables ‘% mowed grass 20’  
206 and ‘Distance to building’ were excluded as they reached VIFs of 8.1 and 4.3, respectively.  
207 Thus, we ran all the potential models with the five remaining explanatory variables. Before  
208 analyses, we standardized continuous explanatory variables (mean = 0; SD = 1), as they were  
209 taken on different scales. We ranked the best possible models based on corrected Akaike’s  
210 information criterion (AICc) and all explanatory variables according to their influence on the  
211 response variable (Burnham et al. 2011). The final selection of models contained those models  
212 within two AICc units from the best model (the lower the AICc, the better the model). We  
213 conducted model averaging with this set of competing models. The explanatory variables were  
214 ranked by importance, i.e. sum of their weight over all competing models (the closer to 1, the  
215 higher importance).

216 To assess the relationship between productivity and environmental variables we ran  
217 negative binomial GLMs with log link functions. As a response variable, we used the number of  
218 fledglings (productivity). The same explanatory variables and multimodel inference as in  
219 previous analyses of nesting habitat selection were used. Variables were also scaled and VIFs  
220 were lower than two.

221 All statistical analyses were conducted in *R* version 3.6 (R Foundation for Statistical  
222 Computing, Vienna, Austria), using the lme4, MuMIn, car, MASS, and EcoSimR packages.

## 223 Results

### 224 *Invertebrate availability*

225 Invertebrate richness, biomass and abundance were higher under streetlights traps  
226 than in control pitfall traps (Figure 1). These differences were statistically significant according  
227 to the GLMMs as 95% Confidence Intervals did not included the zero (Richness: estimate  $\pm$  SE =  
228 0.364  $\pm$  0.152, 95% CI = 0.067, 0.665; Biomass: estimate  $\pm$  SE = 2.019  $\pm$  0.406, 95% CI = 1.190,  
229 2.849; and Abundance: estimate  $\pm$  SE = 0.351  $\pm$  0.020, 95% CI = 0.311, 0.391).

### 230 *Diet*

231 A total of 2719 preys were found in 62 pellets from 19 nest-burrows (mean  $\pm$  SD = 3.3  
232  $\pm$  pellets per nest; range: 1-6). The most abundant and frequent prey taxon were Scarabaeidae  
233 beetles (Table S2). The number of invertebrates at pitfall traps under streetlights was higher  
234 than at control traps (5835 and 4108 invertebrates, respectively). Interestingly, the  
235 Czekanowski index of similarity showed a higher overlap between the invertebrate content of  
236 pitfall traps under streetlights and burrowing owl diet than between the invertebrate content  
237 of control traps and owl diet ( $PS_1$  values = 0.329 and 0.252, respectively).

### 238 *Habitat use and home range*

239 GPS devices logged data for a mean of 3.3  $\pm$  1.2 (mean  $\pm$  SD) days and gathered a total  
240 of 48,952 GPS-locations (mean  $\pm$  SD = 3263.5  $\pm$  1245.5 locations per individual, n = 15). GPSs  
241 recorded 21,172 locations at day and 27,780 locations at night.

242 All home ranges (kernel density estimations) of burrowing owl individuals contained at  
243 least one streetlight (Figure 2). Neighbor owls segregated streetlights by breeding pair  
244 irrespective of the distance between nest-burrows and streetlights (see an example in Figure  
245 S2). Owls were concentrated around streetlights, particularly at night (Figure 2). The GLMM  
246 explaining the number of GPS locations around random points and streetlights within the  
247 home ranges obtained an AICc lower (AICc = 6191.3) than that of the null model, i.e. the model  
248 only containing the intercept (null model: AICc = 11295.5). The interaction 'period x location'  
249 was significant (level 'Night:Random point': estimate  $\pm$  SE = -3.118  $\pm$  0.067; 95% CI = -3.250, -  
250 2.987; Figure 3).

### 251 *Nesting habitat selection and productivity*

252 The multimodel inference indicated that our habitat variables explained nesting  
253 habitat selection of burrowing owls. The null model got a high value of AICc with respect to the  
254 best model (>9 points of AICc) and five competing models obtained AICc values lower than two  
255 in relation to the AICc value of the best model (Table S3). The five competing models were  
256 statistically significant in relation to the null model (Likelihood ratio tests provided all P-values  
257 < 0.004). Four out of the five competing models contained the variable distance to light, which  
258 showed the highest importance (0.84; Table S3). Distance to light was negatively related to the  
259 probability of occupation, i.e. nest-burrows were closer to lights than random points. Although  
260 the averaged 95% confidence interval included the zero, it mostly covered negative values (-  
261 1.945, 0.026; Table S4).

262 Productivity was not related to any habitat variable. The null model reached a lower  
263 AICc value than any model including habitat variables (Table S3). Interestingly, the most

264 important variables were again distance to light and percentage of mowed land, and they  
265 showed the same sign (Tables S3 and S4).

## 266 Discussion

267 Our study demonstrates that ALAN plays a key role in the occupation of urban  
268 environments by burrowing owls, which contrasts with the reported for other owls species  
269 (Marín-Gómez et al. 2020). First, streetlights alter the invertebrate availability (Davies et al.  
270 2012), attracting invertebrates to illuminated areas where they are more abundant. Second,  
271 the owl diet was more similar to the invertebrate taxa trapped at pitfall traps under streetlight  
272 than that in control traps. Third, home range and space use of owls were greatly determined  
273 by streetlights. Owls spent more time around light sources, particularly during the nighttime.  
274 Fourth, the most important habitat feature influencing the nesting habitat selection was the  
275 distance to streetlight, indicating that owls selected areas close to streetlights for nesting.  
276 Finally, although our sample size was quite limited and no significant relationship was found,  
277 the habitat variable best explaining owl productivity was the distance to light.

278 In North America populations, ALAN has been proposed as a sensory disturbance of  
279 space use in a highly modified landscape including cattle ranching, annual crop production,  
280 and petroleum development facilities (Scobie et al. 2016). The latest industry includes oil and  
281 gas wells, compressor stations, and other facilities producing sound, light, and roads (Scobie et  
282 al. 2016). Anthropogenic noise is a sensory disturbance for owls. Noise intensity limits owl  
283 species richness in urban areas (Fröhlich and Ciach 2019; Marín-Gómez et al. 2020). In fact,  
284 burrowing owls avoid roads due to the noise produced by road traffic (Scobie et al. 2014).  
285 Thus, the noise produced by the several types of infrastructures could be masking the ALAN  
286 effect on the habitat use of North American burrowing owls (Scobie et al. 2016). In contrast,  
287 light sources in our study are streetlights in a quiet residential area. Thus, the lower levels of  
288 noise let us detect the effect of ALAN on owl habitat use.

289 Raptor exposure to ALAN and urbanization are expected to increase in the future (Seto  
290 et al. 2012; Alpanidou et al. 2020). Thus, it is essential to improve our understanding on the  
291 potential impact of increasing urban ALAN on raptors (Alpanidou et al. 2020). The new  
292 predation opportunities provided by ALAN have been exploited by many species from different  
293 taxonomic groups (Fleming and Bateman 2018), such as fish (Bolton et al. 2017), amphibians,  
294 reptiles (Perry et al. 2008), bats (Stone et al. 2015), passerine birds (Lebbin et al. 2007), and  
295 diurnal and nocturnal raptors (Negro et al. 2000; DeCandido and Allen 2006; Rutz 2006;  
296 Canário et al. 2012; Buij and Gschweg 2017). Such exploitation of food resources can increase  
297 individual and population fitness, leading to urban colonization. In this line, invasions of the  
298 Asian house gecko (*Hemidactylus frenatus*) and the Cane toad (*Rhinella marina*) could be  
299 facilitated by the attraction of prey to ALAN (Zozaya et al. 2015; Komine et al. 2020). The  
300 attraction of invertebrates to ALAN is a well-known phenomenon, leading to disruption of  
301 predator-prey relationships and cascading effects (Longcore and Rich 2004; Fleming and  
302 Bateman 2018). The burrowing owl has a generalist diet, with a higher preponderance of  
303 insects in urban environments in detriment of small mammals (Cavalli et al. 2014). As in other  
304 diet studies, invertebrates were the most consumed prey item (Sánchez et al. 2008; Cavalli et  
305 al. 2014) and were also more abundant around streetlights (Figure 1). Our model species  
306 adopts a passive sit-and-wait strategy to capture light-attracted invertebrates (Figure S3). The  
307 proximity of streetlights to nests makes the consumption of these invertebrates energetically  
308 favorable and more efficient because foraging and food provisions occur at short distances.  
309 Also, adults hunt while still not losing sight of their nest, which is critical for a better defense of

310 the nest-burrow against predators (Cavalli et al. 2013). The dietary overlap and the space use  
311 at night described here, as well as field observations, demonstrate that burrowing owls benefit  
312 from ALAN by prey attraction. This agrees with a recent review that concludes that prey  
313 availability is an important determinant of the success of urban-nesting raptors (Kettel et al.  
314 2018).

315 However, is this predator-prey relationship stable in the long-term? ALAN is a sink for  
316 invertebrate populations (Owens et al. 2020), even more in this scenario where attracted  
317 invertebrates are preyed by the owls. Therefore, only moderate levels of urbanization could  
318 support this predator-prey interaction, as it will need the attraction of invertebrates from  
319 nearby areas (Grubisic et al. 2018; Fenoglio et al. 2020). Moderate levels of urbanization with  
320 large bare ground areas are needed to let owls built their nest-burrows. Our study area is a  
321 suburban environment that complies with these two requirements. Given that urbanization,  
322 human-modified habitat in suburban areas, and light pollution are expected to increase in the  
323 future (Seto et al. 2012; Kyba et al. 2014, 2017), invertebrate preys at cities are expected to  
324 decrease (Grubisic et al. 2018; Owens et al. 2020; Fenoglio et al. 2020). Thus, this predator-  
325 prey interaction might become an ecological-trap for burrowing owls. In addition, the lighting  
326 industry and conservationists try to design more wildlife-friendly lighting systems by reducing  
327 the attraction of invertebrates (Donners et al. 2018; Longcore et al. 2018). In this sense, a wide  
328 field of research has emerged, particularly focused on intensity, light spectrum, timing, and  
329 shielding (Gaston et al. 2012). Thus, the efforts conducted to reduce invertebrate attraction by  
330 the new lighting systems could accelerate the decline of the owl profitability from this light-  
331 disturbed predator-prey interaction. However, the relatively large brain size (in the percentile  
332 90.8 among 629 bird species examined for brain size) and enhanced cognitive abilities of  
333 burrowing owls could help them to cope with new resources and opportunities (Sayol et al.  
334 2020). In fact, recent studies have demonstrated that urban colonizers are just a fraction of the  
335 rural populations showing differences in genes related to cognitive and emotional behaviors  
336 (Mueller et al. 2018, 2020). Burrowing owls are also able to use tools: they collect mammalian  
337 dung to bait and attract preys (Levey et al. 2004).

338 The low richness and abundance of predators in urban cities can explain the urban  
339 colonization by the burrowing owl (Rebolo-Ifrán et al. 2017). Demographic parameters of  
340 urban populations may improve by predation release (Rebolo-Ifrán et al. 2017), but what is the  
341 main driver underpinning such facts? Apart from food provision, ALAN could provide other  
342 benefits to burrowing owls. Under lighted areas, owls could more easily detect predators than  
343 in darker natural areas. In addition, ALAN could deter predator attacks. In this sense, daily nest  
344 survival rates of urban black birds increased with increasing light exposure (Russ et al. 2017).  
345 Even though predator abundance in urban cities can be lower than in rural areas (Rebolo-Ifrán  
346 et al. 2017), semi-domestic dogs and cats could predate or disturb nesting owls (Cavalli et al.  
347 2016). Although we have not tested this option, an easy experiment could be set up to test for  
348 flight initiation distances between different light levels conditions (Carrete and Tella 2010).

### 349 *Conclusions*

350 Human-induced environment alterations, such as urbanization and ALAN, create novel  
351 opportunities and niches (Fleming and Bateman 2018). Understanding how such opportunities  
352 affect wildlife is essential for its management. Here, we show that ALAN is a key factor to  
353 explain the recent and increasing urban colonization of the burrowing owl in South America  
354 (Rebolo-Ifrán et al. 2017; Baladrón et al. 2020), although the particular life-history traits (small  
355 size and large brain) and its ecology (insectivorous diet) of the species play also a role (Sayol et

356 al. 2020). We demonstrate that owls forage at illuminated areas to predate on prey  
357 concentrated by ALAN. Moreover, owls prefer nesting close to streetlights, perhaps reducing  
358 commuting costs and predation. Thus, the alterations produced by ALAN overcomes urban  
359 threats and pressures, at least for a fraction of the genetic pool of the burrowing owl (Mueller  
360 et al. 2018, 2020).

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375 **Author contributions.** AR, PMO-V, and JHS designed the study. PMO-V, JHS, and AR collected  
376 field data. JHS, AR, and PMO-V provided materials. AR analyzed the data and wrote the  
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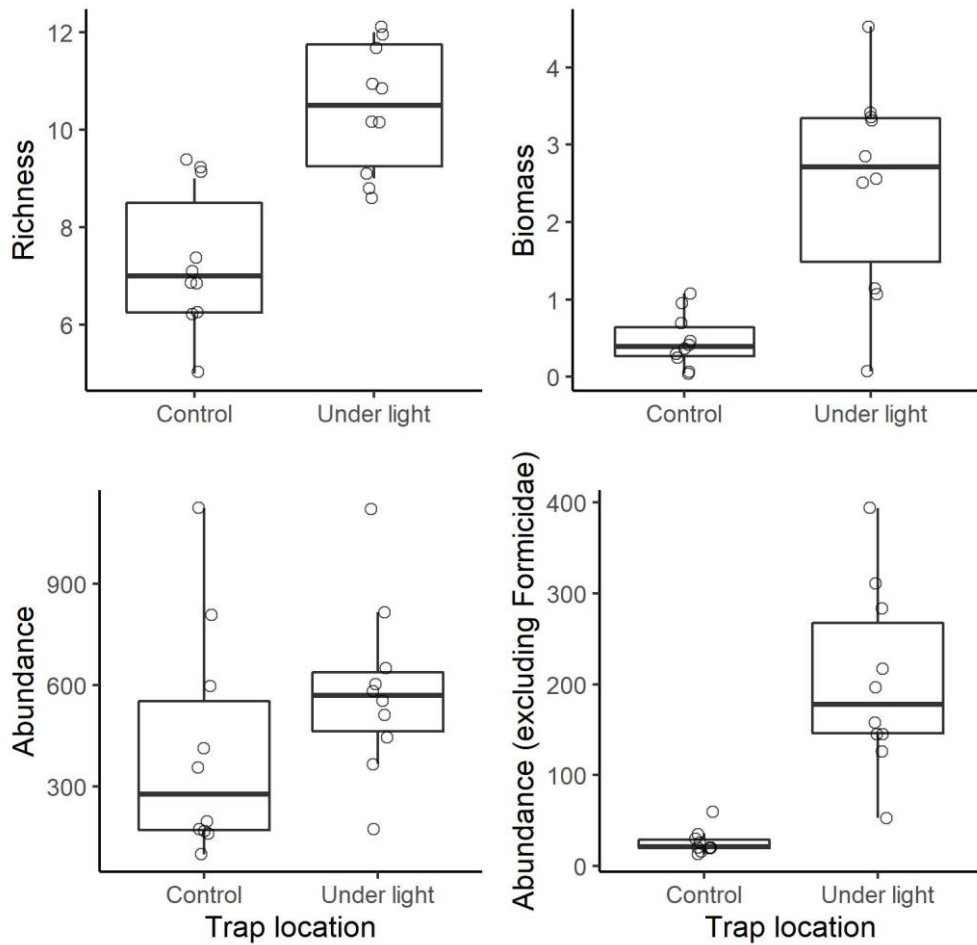
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548 **Figure 1**

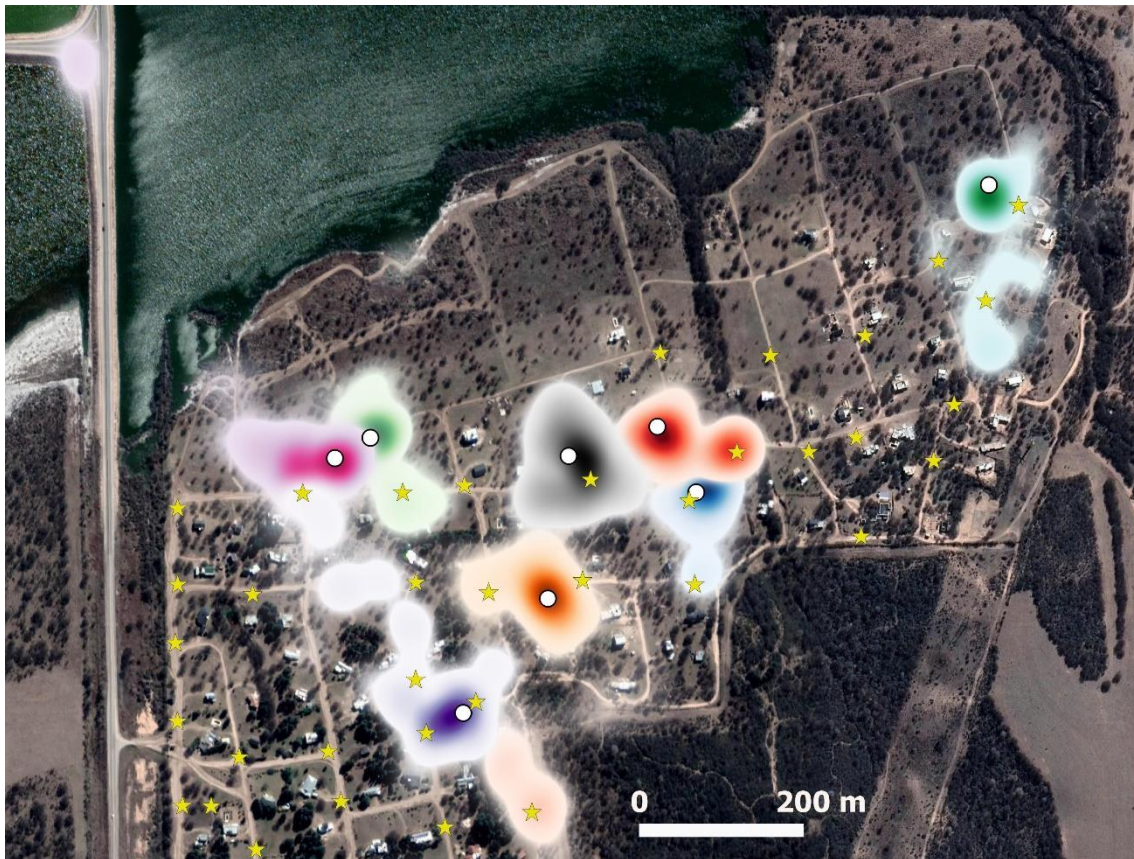
549 **Figure 1.** Boxplots of richness, biomass, number of invertebrates, and number of invertebrates  
550 excluding Formicidae between pitfall traps located under streetlights or control locations. Data  
551 correspond to Order level. Richness = Number of invertebrate orders. Biomass = dry biomass in  
552 grams. Abundance = Number of invertebrates per order. Box plots display five summary  
553 statistics (the median, two hinges, and two whiskers). The thick line within the box represents  
554 the median (the 50th percentile). The lower and upper hinges correspond to the first and third  
555 quartiles (the 25th and 75th percentiles). The whiskers extend to 1.5 \* IQR from the hinge  
556 (where IQR is the inter-quartile range, or distance between the first and third quartiles). Open  
557 circles indicate the value for each pitfall trap (jittered for a better visualization) both for under  
558 streetlights and control locations.



559

560 **Figure 2**

561 **Figure 2.** Kernel density estimations of eight GPS-tracked burrowing owls *Athene cunicularia* in  
562 La Cuesta del Sur village, La Pampa province, Argentina. Kernels for individual owls are  
563 represented by different colors. The higher the color intensity, the higher density of GPS  
564 locations. Nests (white dots) and streetlights (stars) are shown. Note that the individual  
565 represented by the pink color visited the intersection of the road in the middle of the lake  
566 (upper left corner). During the tracking period, artificial illumination was employed at the  
567 intersection because of nocturnal works on the road.

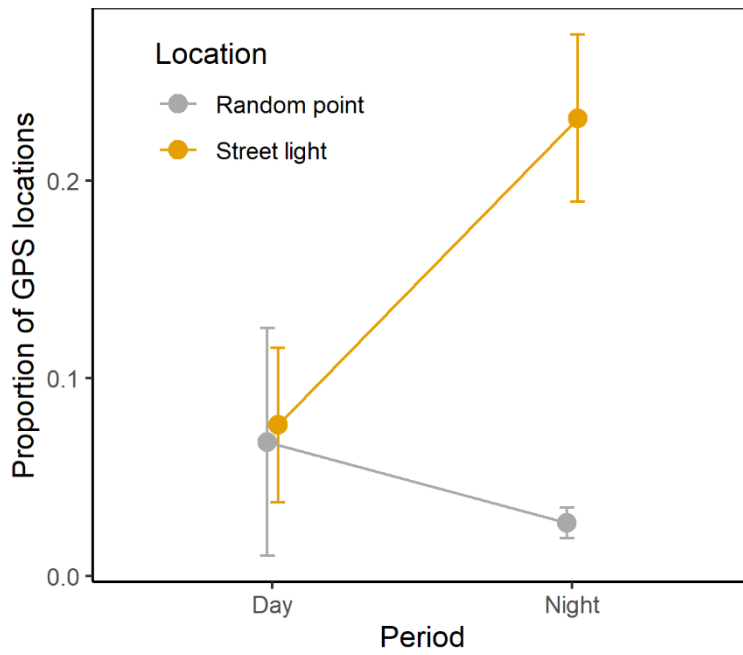


568

569 **Figure 3**

570 **Figure 3.** Mean and standard errors of the proportions of GPS locations of burrowing owls  
571 *Athene cunicularia* by period (day and night) and location (random point and streetlight). The  
572 proportion of GPS locations corresponds to the number of locations within 30 m radius circles  
573 centered in random points and streetlights within the home range of GPS tracked burrowing  
574 owls. One value per each level was obtained for each GPS-tracked owl.

575



576