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# Morphological differences along a chronological gradient of urbanisation in an endemic insectivorous bird of New Zealand

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1 **Morphological differences along a chronological gradient of urbanisation in an endemic**  
2 **insectivorous bird of New Zealand**

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4  
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14  
15 **Abstract**

16 Urbanisation constitutes one of the most rapid human-induced environmental changes,  
17 developing at the expense of natural and semi-natural habitats. It often implies alterations of  
18 many abiotic and biotic factors and contributes to create new environmental conditions,  
19 including temperature, food resources, competition and predation. Despite increasing  
20 empirical evidence of intra-specific divergence in phenotypic traits (e.g., physiological,  
21 behavioural or morphological) between urban and rural individuals, such patterns have often  
22 remained disconnected from the underlying mechanisms involved. In the current study, we  
23 tested for divergence in functional morphological traits that are related to feeding ecology  
24 (i.e., bill morphology, body mass and condition) and/or to the locomotory performance in

25 escaping from predators (i.e., wing, tarsus and tail morphology, body mass and condition)  
26 along a chronological gradient of urbanisation (old urban, recent urban and rural areas),  
27 using the New Zealand fantail, an endemic insectivorous passerine species. We found  
28 divergences in phenotypic traits related to bill morphology along the urban-rural gradient:  
29 birds inhabiting the old urban area had stubbier bills (i.e., shorter, deeper and wider bills)  
30 than those inhabiting the recent urban and rural areas. We did not detect any difference in  
31 locomotion-related morphological traits. Our results suggest the urbanisation-induced  
32 alteration in food resources may drive morphological divergence in bird populations. We  
33 emphasized the need for mechanistic and experimental studies, with a particular focus on  
34 resource-based mechanisms, to identify more precisely the morphological responses of  
35 urban populations to changes in food composition, and the resulting implications for  
36 communities in urban ecosystems.

37 **Keywords:** bill morphology, insectivorous bird, locomotion-related traits, New Zealand  
38 fantail, resource-related traits, urbanisation gradient

### 39 **Introduction**

40 Human impact on natural environments has been considerably increasing around the planet,  
41 triggering major changes in many ecosystems (Sanderson et al. 2002; Steffen et al. 2004;  
42 Venter et al. 2016). The subsequent human-driven disturbances constitute major driving  
43 forces leading to ecological and evolutionary phenotypic changes in wildlife populations, at a  
44 rate outpacing the changes observed in natural contexts (Hendry et al. 2008; Darimont et al.  
45 2009; Gaynor et al. 2018). Urbanisation is one of the most evident human-induced rapid  
46 environmental changes, developing at the expense of natural or semi-natural (e.g., rural)  
47 areas and wildlife habitats (Marzluff et al. 2001; Steffen et al. 2004; Sih et al. 2011; Gil and  
48 Brumm 2014). The urbanisation process contributes to create new environmental conditions

49 (see Kowarik 2011), such as increases of temperatures, human-induced disturbances and  
50 alterations, introductions of non-native species, resulting in new patterns of access to  
51 resources such as supplementary feeding (Fuller et al. 2008; Galbraith et al. 2015) and of  
52 predation pressure (Marzluff et al. 2001; Shochat et al. 2006; Gil and Brumm 2014). Such  
53 human-induced alteration of environmental factors and ecological processes put the urban  
54 development as one of the main threats to biodiversity (Maxwell et al. 2016). Understanding  
55 responses of animals to urbanisation and to the subsequent changes in ecological processes  
56 is thus crucial for evolutionary ecology and conservation in urban ecosystems (Chace and  
57 Walsh 2006).

58         To date, extensive work has explored the effects of urbanisation on the functional  
59 composition of communities, and especially for avian assemblages (Chace and Walsh 2006;  
60 Marzluff 2017; Oliveira Hagen et al. 2017; Pithon et al. 2021). However, there is less  
61 information about the intra-specific response to urbanisation (Liker et al. 2008; Caizergues et  
62 al. 2018), which may be critical in predicting species colonisation or their long-term  
63 persistence in urban ecosystems (Sih et al. 2011). Recently, Caizergues et al. (2018)  
64 demonstrated the existence of an urban morphotype in the great tit *Parus major*, with urban  
65 individuals being smaller (lower body size, shorter wing, tarsus and tail lengths) than their  
66 rural conspecifics (see also Liker et al. 2008 for similar patterns in the house sparrow *Passer*  
67 *domesticus*). However, the strength and direction of such differences appear to vary  
68 substantially between areas and/or species (Evans et al. 2009; Seress and Liker 2015; Sepp et  
69 al. 2018), likely reflecting variation in the local ecological forces involved (Shochat et al.  
70 2006). Therefore, studies addressing phenotypic changes in the light of mechanisms that  
71 underlie the urbanisation process, which have so far often remained disconnected in the  
72 literature (Chace and Walsh 2006; Shochat et al. 2006; Sol et al. 2013; Alberti et al. 2017), are

73 needed. The current study thus focuses on morphological traits, particularly suitable to  
74 investigate phenotypic responses to urbanisation process (Yeh 2004; Shochat et al. 2006;  
75 Liker et al. 2008), because of the rapid adaptive or plastic changes they may imply (e.g., in  
76 ten generations in Amiot et al. 2007; see also Bitton and Graham 2015).

77         Alterations of food resources and predation pressure are two major forces underlying  
78 the urbanisation process based on bottom-up and top-down effects respectively (Shochat  
79 2004; Chace and Walsh 2006; Shochat et al. 2006; Chamberlain et al. 2009; Seress and Liker  
80 2015). First, urban areas often provide a higher food availability and predictability through  
81 supplementary feeding, communal waste and compost (Fuller et al. 2008; Galbraith et al.  
82 2015; Seress and Liker 2015). Such increase in anthropogenic food and alteration in food  
83 item composition may lead to changes in the diet of birds along rural-urban gradients (e.g.,  
84 Mennechez and Clergeau 2001; Scott et al. 2015). Feeding ecology is closely related with the  
85 bill morphology in birds (Smith and Girman 2000): higher bill depth and width are positively  
86 linked to the bill bite force (Herrel et al. 2005) and to the feeding efficiency according to the  
87 hardness of food items (Durell et al. 1993; Smith and Girman 2000). Therefore, the  
88 urbanisation-induced changes in the diet of birds may constitute a major force expected to  
89 trigger changes in bill traits. The higher food availability and predictability in urban areas may  
90 also paradoxically contribute to reduce the body mass or condition of urban birds (Shochat  
91 2004; Demeyrier et al. 2017; Caizergues et al. 2018) as a result of the non-necessity to  
92 constitute fat reserves (Cuthill et al. 2000) and of the higher concentration of competitors  
93 resulting in a lower *per capita* amount of food items (Shochat 2004; Seress and Liker 2015).

94         Urban areas also favour the proliferation of predators (increased human-commensal  
95 and/or non-native predator species, humans perceived as predators by animals: Frid and Dill  
96 2002; Chace and Walsh 2006; Fischer et al. 2012). Predation pressure may thus induce

97 morphological adjustments (Gosler et al. 1995), adaptations (Swaddle and Lockwood 1998),  
98 or exert a selection in birds based on the morphological traits that are directly related to the  
99 aerodynamics or locomotory performance in escaping from predators (see Møller et al.  
100 2009, 2013; van den Hout et al. 2010). For instance, wing shape may affect the take-off angle  
101 and would affect the relative risk of predation for birds, while tarsus length would be  
102 negatively linked to the relative risk of predation (longer tarsus facilitating the take-off leap)  
103 (Swaddle and Lockwood 1998, 2003). High body mass or wing loading also impair flight  
104 abilities such as manoeuvrability (Dietz et al. 2007; van den Hout et al. 2010), take-off  
105 velocity and angle (Kullberg et al. 1996; Møller 2015), and reduce the flight speed (Burns and  
106 Ydenberg 2002; Lindström et al. 2003), thus altering the antipredator response (Gosler et al.  
107 1995; Lindström et al. 2003; Møller 2015). Body mass may also be affected in urban areas  
108 because of changes in predation pressure through the trade-off starvation-predation risk,  
109 which should favour a lower investment in antipredator strategies and a higher investment in  
110 energy gain when predation risk relaxes (Gosler et al. 1995; MacLeod et al. 2006).

111 In the current study, we investigated morphological divergence in the New Zealand  
112 (NZ) fantail *Rhipidura fuliginosa*, a bird species recently subjected to urbanisation. This  
113 endemic insectivorous species is one of the most common and best-known passerine species  
114 of New Zealand. It seems to survive well the urbanisation and is commonly observed in the  
115 remnant forest patches of urbanised areas (Robertson 2007). Because of its recent  
116 colonisation by European societies (early 19<sup>th</sup> century, Duncan and Young 2000), New  
117 Zealand offers an interesting context to study the response of birds to rapid novel  
118 environmental conditions, such as urbanisation. Particularly, the recent introduction of  
119 human-commensal mammalian predators (i.e., mainly ship rats *Rattus rattus*, domestic and  
120 feral cats *Felis catus*, and common brushtail possums *Trichosurus vulpecula*, van Heezik et al.

121 2008; Aguilar and Farnworth 2013) by Europeans, originally absent in New Zealand, offers an  
122 interesting context to address our questions (see also Chace and Walsh 2006).

123         Based on a synchronic comparison of three areas depicting a chronological gradient  
124 of urbanisation (old urban, recent urban and rural areas) in the Auckland region of New  
125 Zealand, we (i) tested whether birds living under different degree of urban development  
126 show morphological differences, and (2) interpreted the results through a functional and  
127 mechanism-orientated standpoint. Since urbanisation was shown to affect the composition  
128 of invertebrate communities in New Zealand (see Toft et al. 2019), we may reasonably  
129 assume that composition of food items differs along the urbanisation gradient, as well as the  
130 predation pressure, as indicated by the daily nest predation rates increasing from rural to  
131 urban study areas (Table 1, see also van Heezik et al. 2010). Therefore, we tested the  
132 hypothesis that birds differed in morphological traits that are related to feeding ecology (bill  
133 morphology, body mass and condition) and/or to the locomotory performance in escaping  
134 from predators (i.e., wing, tarsus and tail morphology, body mass and condition) (see Table  
135 2). Urban birds were expected to have stubbier bills than their rural conspecifics (Badyaev et  
136 al. 2008; Evans et al. 2009) as a result of a putative urbanisation-induced alteration in food  
137 resources, and/or longer wings, tail and tarsus that increase escape flight abilities (see Table  
138 2), as a result of the putative increased predation pressure. Morphological differences were  
139 expected to be particularly pronounced between bird populations inhabiting the most  
140 contrasted study areas, i.e., the preserved rural area and the old urban area.

141

## 142 **Material and methods**

### 143 Study areas

144 The study was conducted from 2011 to 2014 in the North Shore district of the Auckland

145 region, New Zealand (36.471°S 174,452°E). The study area is divided in three areas (Fig. 1),  
146 depicting a chronological gradient of urbanisation since the early 1900s (*old urban, recent*  
147 *urban* and *rural* areas). All these areas have preliminarily undergone a common historical  
148 fragmentation of native forest, induced by agricultural development. Thus, they are all  
149 composed of isolated remnant patches of mature native broadleaf-podocarp forest. These  
150 patches vary from 1.74 to 113.6 ha (Myers 2005). Between-area divergences have emerged  
151 with their differential history of urban development, through chronological settlements of  
152 built-up areas around the pre-existing patches of native forest, without any further habitat  
153 destruction (Myers 2005). Daily human visitation was assessed in each study area as an index  
154 of human disturbance. First, for each patch, we calculated the number of people present  
155 during the sampling session, divided by the total number of people reported in this patch  
156 over all sampling sessions (i.e., at least 10). Then, an index was calculated for each study  
157 area, as a mean of the values calculated for each single-patch within the area. Daily nest  
158 predation rate (as a proxy of predation risk) was also assessed during the nesting period  
159 between 2011 and 2014. Estimations were made using the Mayfield method (Mayfield  
160 1961), providing an unbiased estimate for nests found at different developmental stages.  
161 Nests were located and monitored from September to late January 2011-2014 to optimize  
162 predation rate estimation.

163

#### 164 *Old urban area*

165 The *old urban area* has been exposed to urban development since the early 1900s (Auckland  
166 Regional Council 2010a). This area is predominantly characterized by dense industrial and  
167 residential areas (431-1695 dwelling/km<sup>2</sup>, Grimes et al. 2006). Patches of native forest,  
168 associated with open vegetated spaces of short vegetation cover and low density of mature



169 trees, are part of the urban matrix. In this study area, forest patches were exposed to the  
170 higher level of human visitation reported (Table 1). Birds were also exposed to a high  
171 predation pressure, as indicated by the high nest predation rate (Table 1). In this area, the  
172 main predators were non-native and human-commensal mammals such as domestic and  
173 feral cats (Aguilar and Farnworth 2013), ship rats and the common brushtail possum. Native  
174 predators (morepork *Ninox novaeseelandiae* and swamp harriers *Circus approximans*) were  
175 less present in this area.

176

#### 177 *Recent urban area*

178 The *recent urban area* differs from the previous one by its recent exposure to urban  
179 development (<25 years, Auckland Regional Council 2010a). It is characterized by a mix of  
180 recent urban infrastructures (i.e., both residential and industrial) with a lower dwelling  
181 density (2-431 dwelling/km<sup>2</sup>, Grimes et al. 2006). Vegetation is characterized by the remnant  
182 patches of native forest, associated with open vegetated spaces of mature trees and shrubs.  
183 Forest patches were exposed to a lower level of human visitation but have similar nest  
184 predation rates compared to the old urban area (Table 1).

185

#### 186 *Rural area*

187 The *rural area* is part of the Tawharanui Regional Park established in 1973. It is characterized  
188 by pastures, patches of mature native forest and restored wetlands. Agricultural activity is  
189 mainly oriented toward extensive farming (sheep and beef) for maintenance of open  
190 grassland habitats (Auckland Regional Council 2010b). Management is based on wildlife  
191 conservation through the restoration of native habitats and integration of biodiversity in  
192 farming practices. However, it is an open recreational park with campground, beach access

193 and walkways in native forest remnants, resulting in intermediate level of human visitation  
194 (Table 1). The establishment of predator-exclusion fence in 2004 associated with pest  
195 control, has resulted in a lower density of predation from terrestrial mammals (Table 1),  
196 though avian predators remain present (e.g., morepork and swamp harrier). This fence has  
197 also contributed to reduce the area access for humans to a single road or aquatic access.

198

#### 199 Data collection

200 Birds were captured at multiple sampling sites spread within the forest patches that cover  
201 each of the study areas (i.e., old urban, recent urban and rural areas), to ensure that  
202 morphological measurements are representative of subpopulations inhabiting each study  
203 area (number of sampling sites within the old urban area = 13; recent urban = 10; rural = 9).  
204 Captures were conducted using mist-nets, deployed from 6 am to 12 pm, from September to  
205 late February during the period 2011-2014. Once captured, each bird was measured and  
206 ringed with an alphanumeric metal ring purchased from the New Zealand Department of  
207 Conservation. Seven morphological traits were measured. Bill length (from the bill base to  
208 the tip), bill width and height (at the base), and tarsus length (length of the tarsometatarsal  
209 bone) were measured with a precision of 0.1 mm. Tail length (from the distal end of the  
210 uropygial gland to the tip of the largest rectrix), wing chord length (from the carpal joint to  
211 the tip of the longest primary feather or feather sheath) were measured with a precision of  
212 0.5 mm. Bird body mass was measured with a precision of 0.01 g using a high-precision  
213 balance. Bird sex was determined using molecular sexing, following the method of  
214 Fridolfsson and Ellegren (1999), from blood samples collected from the brachial vein. A total  
215 of 27, 11 and 34 mature individuals were captured and measured respectively in the old  
216 urban, recent urban and rural areas.

217

218 Index calculation

219 To determine the body condition of birds, we first calculated a synthetic index of body size  
220 using the first axis (PCI) of a principal component analysis performed on the wing, tarsus and  
221 tail lengths (see Chastel and Kersten 2002; Geslin et al. 2004). The first axis explained 56.27%  
222 of the overall variance in body size. Then, a body condition index was calculated as the  
223 residual mass from a linear regression performed between body mass and body size index  
224 (see Jakob et al. 1996; Chastel and Kersten 2002; Geslin et al. 2004). Finally, we also  
225 calculated ratios of bill sizes (as proxies of bill shape) and a ratio of body mass/wing chord as  
226 a proxy of wing loading.

227

228 Statistical analyses

229 To test for between-area (old urban, recent urban and rural) differences in morphological  
230 traits, we used a multivariate analysis of variance (MANOVA). A first MANOVA was  
231 performed testing for the interacting effects of area and sex on morphological traits. There  
232 was no interaction between area and sex on morphological traits (MANOVA;  $F_{2,39} = 0.929$ ,  $p =$   
233  $0.565$ ). Sex was thus excluded from the final design of the MANOVA. Statistical significance of  
234 the F-statistic was assessed using a Pillai test. Then, ANOVAs were performed to identify the  
235 significant morphological metrics contributing to between-area differences. When needed,  
236 Tukey's multiple comparison tests were finally performed to reveal significant differences  
237 between modalities (i.e., areas). Since we expected differences in body mass along the  
238 urbanisation gradient that needed to be tested (see predictions in introduction), and  
239 because some dependent variables already integrate body mass in their calculation (e.g.,  
240 wing loading, body condition index), body mass was first implemented as a dependent

241 variable rather than as a covariate in the analyses. The potential influence of the body mass  
242 of the birds on our results was then assessed as a complementary multivariate analysis of  
243 covariance, performed on the morphological traits that have previously showed significant  
244 between-area differences (see Online Resource 1). All analyses were performed using R  
245 software (R Core Team 2019).

246

## 247 **Results**

248 The multivariate analysis of variance showed between-area differences in morphological  
249 traits (MANOVA;  $F_{2, 57} = 2.651$ ,  $P = 0.001$ ). All bill traits (i.e., bill length, depth and width)  
250 differed between areas (Fig. 2, Table 3). In the old urban area, birds had shorter (by 16–19%),  
251 but deeper (+ 11–13%) and wider (+ 11–17%) bills, than birds inhabiting the recent urban  
252 and rural areas (Fig. 2a–c, Tables 3, 4). Bill ratios (as proxy of bill shape) also varied between  
253 areas (Fig. 2d–e, Table 3). The significantly greater ratios of bill depth / bill length (+ 40%) and  
254 bill width / bill length (+ 43–54%) observed in birds inhabiting the old urban area were  
255 suggestive of stubbier bill shape in this population, relatively to recent urban and rural  
256 populations (Fig. 2d–e, Tables 3, 4). All these differences remained consistent when  
257 controlling for the body mass of the birds (Online Resource 1). No between-area difference  
258 was detected for the ratio of bill depth / bill width (Fig. 2f, Table 3). Overall, patterns of  
259 morphological differences in bill traits remained consistent, with differences observed  
260 between the old urban area and the two others (recent urban and rural), while no  
261 differences were detected between the recent urban and rural areas (Table 4). Finally, we did  
262 not detect any difference in bird condition indices nor in locomotory morphology (i.e., wing  
263 chord, tail and tarsus length) (Table 3).

264

265 **Discussion**

266 We found between-area differences in morphological traits in the insectivorous NZ fantail  
267 species, along a gradient of urbanisation. Our results thus support that the anthropogenic  
268 process of urbanisation can induce intra-specific phenotypic changes in bird populations.  
269 Particularly, we found empirical evidence of divergence in bill size and bill ratios along the  
270 urban-rural gradient, while we did not detect any difference in bird condition or locomotion-  
271 related traits (i.e., wing-, tarsus- and tail-related metrics). We discussed these results through  
272 a mechanism-orientated and functional approach.

273

274 *Morphological divergence and resource-based mechanisms*

275 We found differences in bill size and ratios along the urbanisation gradient, that remained  
276 consistent when controlling for the body mass of the birds (see Online Resource 1). In the old  
277 urban area, birds had stubbier bills (i.e., shorter, deeper and wider bills, and higher ratios of  
278 bill depth/length and bill width/length) than in the two other areas (i.e., recent urban and  
279 rural). These results are consistent with Evans et al. (2009) showing that urban blackbirds  
280 *Turdus merula*, tended to have stubbier bills than rural ones. Given that bill size and shape  
281 are closely related to feeding ecology in birds (Smith and Girman 2000; Corbin 2008), such  
282 changes in bill traits may result from urbanisation-induced changes in food resources  
283 (Shochat 2004; Shochat et al. 2006; Seress and Liker 2015).

284         Deeper and wider bills are known to favour a greater bite force (Herrel et al. 2005;  
285 Badyaev et al. 2008), and could therefore reflect a shift in the between-area composition of  
286 the available food items (Durell et al. 1993; Badyaev et al. 2008). Badyaev et al. (2008)  
287 showed that urban house finches *Carpodacus mexicanus* mainly feed on harder and larger  
288 seeds and adapted towards deeper and wider bills procuring a greater bite force, compared

289 to individuals living in semi-natural areas (Hulscher and Ens 1991; Durell et al. 1993). This  
290 hypothesis is also supported by the clear shift reported in the composition of insects  
291 communities between old growth forests and suburban areas in New Zealand (Toft et al.  
292 2019), but also by a potential urbanisation-induced increase in invertebrate body size (e.g.,  
293 spiders in Lowe et al. 2014) likely favouring stubbier-billed individuals. Stubbier bills could  
294 also be more advantageous in urban areas with a hard ground surface (Cuthill et al. 1992;  
295 Evans et al. 2009). Kleindorfer et al. (2006) demonstrated that lowland Darwin's small ground  
296 finches *Geospiza fuliginosa* feeding mainly seeds on the ground by picking and/or chipping  
297 had shorter and deeper bills than highland individuals feeding more on insects in short  
298 vegetation by gleaning and/or sliding. Disparity in bill morphology in the NZ fantail could,  
299 therefore, result from a shift of substrate use and foraging strategies, from hawking, gleaning  
300 and flushing in native environments (Gill 1980; Gill et al. 1983), to sallying and picking in  
301 urban areas. This hypothesis is supported by Møller (2009) showing that birds persisting in  
302 urban areas display high rates of feeding or foraging innovations. Bill divergence may also be  
303 explained by temperature differences (thermoregulation hypothesis, see LaBarbera et al.  
304 2017), higher in urban than in rural areas (according to the urban heat island effect, see  
305 Shochat et al. 2006; Kowarik 2011). However, we are less confident in this hypothesis as an  
306 increased urban temperature would have favoured lower bill depth and width (LaBarbera et  
307 al. 2017), which contrasts with our results. Since birds were measured over the years 2011–  
308 2014, morphological traits may have varied over the study period. However, we believe that  
309 this did not alter our results and conclusions, since we did not detect any influence of time  
310 for most of the morphological trait measurements (Online Resource 2), except for bill depth  
311 (though this is not the case for bill ratios) for which a very slight effect was detected (i.e.,  
312 coefficient = -0.08 mm, while the precision of bill measurements was 0.1 mm).

313           Although differences in body mass might also be expected as a result of an alteration  
314 of food resources (Cuthill et al. 2000; Dulisz et al. 2016; Salleh Hudin et al. 2016; Caizergues  
315 et al. 2018), we did not detect any difference in body mass or body condition. This could  
316 result from the maintenance of a balanced trade-off in food acquisition-predation risk,  
317 consistent with the predicted higher abundance of food resources counterbalanced by the  
318 higher level of predation risk observed in urban areas.

319

### 320 *Morphology and predation pressure*

321 Although differences in locomotory morphology (i.e., wing-, tarsus- and tail-related traits)  
322 might have been expected along the urbanisation gradient as a result of alterations in  
323 predation risk (Swaddle and Lockwood 1998; Shochat et al. 2006; Møller et al. 2009, 2013),  
324 we did not detect any difference between study areas. It does not imply that birds did not  
325 respond to the changes in predation risk, but that they may display other regulatory  
326 responses such as adjustments in their internal state (i.e., physiological and psychological  
327 states, see Nathan et al. 2008) rather than biomechanical adjustments (see van der Veen and  
328 Lindström 2000; Møller 2009; Møller and Ibáñez-Álamo 2012; Møller et al. 2013). For  
329 instance, Witter et al. (1994) suggested that birds would adjust their decision-making in  
330 escape behaviour according to their morphology at a given time (see also Sol et al. 2018).  
331 This hypothesis is also supported by the many other behavioural responses reported in New  
332 Zealand passerines to predation risk from introduced mammals (e.g., adjustment of parental  
333 investment in Massaro et al. 2008; adjustment of nest site selection in Lawrence et al. 2017).  
334 Alternatively, the high predation risk detected in the current study for nests in urban areas  
335 does not necessarily relate to high predation risk for adults, as nest and adult predation  
336 often imply different predator species (Marzluff et al. 2001; Seress and Liker 2015). Adults

337 could, therefore, be subjected to a relaxed predation pressure in urban areas, thus reducing  
338 top-down effects (see Shochat 2004; Seress and Liker 2015).

339 Overall, our results are not typical of the urban morphotype described in other bird  
340 species, which have generally smaller locomotion-related traits (shorter wing, tarsus and tail  
341 lengths) than their rural conspecifics (Liker et al. 2008; Dulisz et al. 2016; Caizergues et al.  
342 2018). This could result from a locality-specific process of urbanisation, influencing  
343 ecological processes differentially between Europe and New Zealand (see Evans et al. 2009).  
344 Indeed, New Zealand context differs by the predation pressure which seems to be higher in  
345 urban than rural areas (see also Chace and Walsh 2006). Secondly, native birds are naive  
346 about introduced mammalian predators (but also introduced competitors) thus affecting the  
347 mechanisms involved in response to predation (see Sih et al. 2010). Thirdly, the urbanisation  
348 process of Auckland has occurred by keeping intact the native forest remnant patches in  
349 urban areas (see Ramalho and Hobbs 2012 for a review on such urbanisation modes). These  
350 remnants forest patches may play a key role (e.g., conservation in indigenous invertebrates,  
351 Toft et al. 2019), buffering the effect of urbanisation, thus reducing pressures acting on  
352 morphological traits (Chace and Walsh 2006; Kowarik 2011).

353

#### 354 *Conclusion and perspectives*

355 To conclude, morphological divergence in bill traits between birds inhabiting the old urban  
356 area versus the recent urban and rural areas, provides empirical evidence of a morphological  
357 response to the urbanisation process, potentially supported by resource-based explanations.  
358 The absence of morphological divergence between recent urban (< 25 years) and rural areas  
359 may indicate that morphological response is not linearly related with time since urbanisation  
360 (see also Evans et al. 2009). It therefore suggests that a time-lag of 25-60 years is necessary



361 to enter in the phase of phenotypic adjustment to urbanisation (see Evans et al. 2010). Such  
362 rapid responses in bill morphology to urbanisation, already suggested in Evans et al. (2009).  
363 They are also consistent with morphological responses of invasive species to novel  
364 environments and local conditions in food resources (Amiot et al. 2007), and could thus be  
365 critical for the ecology and evolution of species subjected to rapid environmental changes  
366 (Benkman 1993; Møller 2009; Sih et al. 2011). While human-induced alterations of resources  
367 may influence interspecific interactions and cause cascading effects on ecological networks  
368 (Thompson 1998; Auer and Martin 2013), the observed morphological responses in bill traits  
369 may have major implications on trophic interactions and ecological dynamics of  
370 communities. Further mechanistic studies, consisting in well-replicated experimental  
371 assessment of the urbanisation-induced changes in resource composition, and subsequent  
372 effects on the diet and morphology of urban birds, is critically needed. They should  
373 contribute to better understand implications of urbanisation processes for ecological  
374 communities.

375

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607 **Table 1** Estimates of daily human visitation (proxy of anthropogenic disturbance) and daily  
 608 nest predation rate on the three study areas (old urban, recent urban and rural areas).

609

Area	Daily human frequentation	Daily nest predation rate
Old urban	0.436	0.022
Recent urban	0.181	0.021
Rural	0.275	0.014

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612 **Table 2** Expected divergence in morphological traits as a response to urbanisation, and the  
 613 underlying mechanisms involved.

Morphological traits	Mechanisms involved	References
<i>Bill morphology</i> - Bill length - Bill width - Bill depth - Bill ratio	Bill size and shape are proxy of the bill bite force and related to the bird feeding ecology (e.g., diet)	(Durell et al. 1993; Smith and Girman 2000; Herrel et al. 2005)
<i>Bird condition</i> - Body mass - Body condition index	Availability and predictability of food resources influence the bird body mass/condition. Body mass depends on the predation risk, mediated by the trade-off starvation-predation risk Body mass is negatively related to flight ability in response to predation risk	(Cuthill et al. 2000; Caizergues et al. 2018)  (Gosler et al. 1995; MacLeod et al. 2006)  (Witter et al. 1994; Kullberg et al. 1996; Møller 2015)
<i>Wing</i> - Wing chord - Wing loading	Wing loading is negatively and wing length positively related to escape flight abilities	(Burns and Ydenberg 2002; Yom-Tov et al. 2006)
<i>Tail</i> - Tail length	Tail length is positively related to escape lift and flight maneuverability	(Thomas and Balmford 1995)
<i>Tarsus</i> - Tarsus length	Longer tarsus should favour take-off leap and reduce the risk of predation	(Swaddle and Lockwood 1998)

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**Table 3** Analyses of variance testing for between-area (old urban, recent urban and rural areas) differences in morphological traits, and group mean estimates. The measurements of the bill, wing, tail and tarsus are expressed in millimetres. Body mass is expressed in grams. Significant p-values are indicated in bold.

Morphological trait	Old urban (N=27)		Recent urban (N=11)		Rural (N=34)		Area comparison	
	Mean	SD	Mean	SD	Mean	SD	F	P
<i><u>Bill morphology</u></i>								
Bill length (L)	9.56	1.73	11.81	0.44	11.42	0.82	22.192	<b>&lt;0.001</b>
Bill depth (D)	2.62	0.26	2.35	0.18	2.32	0.19	6.490	<b>0.004</b>
Bill width(W)	3.66	0.68	3.06	0.36	3.22	0.35	10.819	<b>&lt;0.001</b>
D/L ratio	0.28	0.06	0.20	0.02	0.20	0.02	20.097	<b>&lt;0.001</b>
W/L ratio	0.40	0.11	0.26	0.03	0.28	0.04	24.355	<b>&lt;0.001</b>
D/W ratio	0.71	0.14	0.78	0.11	0.72	0.09	1.471	0.241
<i><u>Body condition</u></i>								
Body Mass (Wt)	7.83	0.50	7.72	0.51	7.93	0.71	1.147	0.328
Body condition index	-0.076	0.476	-0.031	0.551	0.071	0.556	0.599	0.554
<i><u>Locomotory morphology</u></i>								
Wing chord (Wg)	71.52	2.54	69.54	2.38	71.36	2.91	1.634	0.207
Wt/Wg ratio	0.109	0.006	0.108	0.006	0.110	0.006	0.512	0.603
Tail length	94.11	5.26	93.27	4.29	94.56	6.05	0.009	0.991
Tarsus length	21.30	1.03	21.29	0.99	21.51	0.83	0.644	0.530

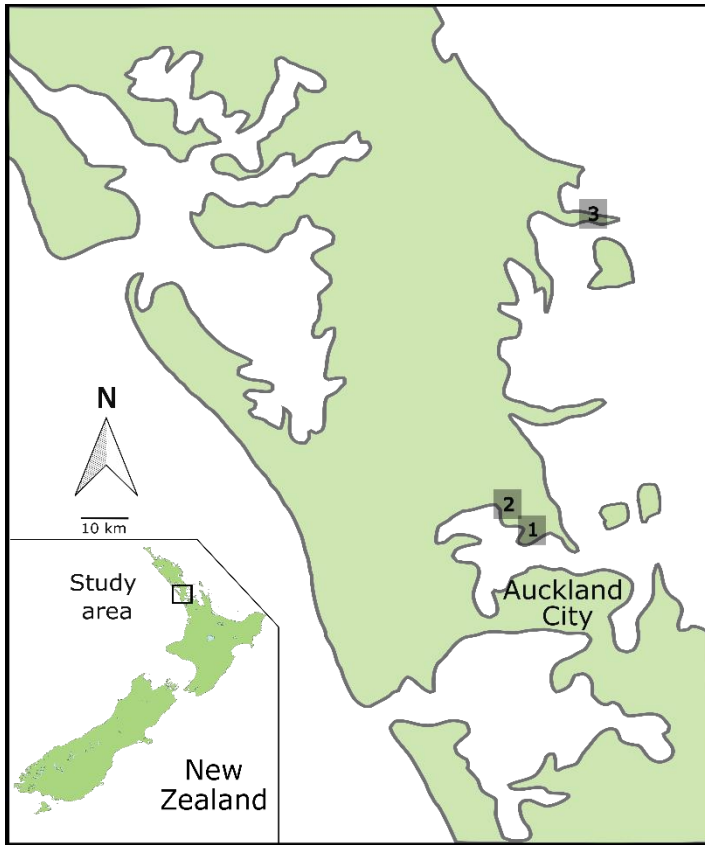
**Table 4** Tukey post-hoc multicomparisons testing for significant pairwise differences between each modality (i.e., areas). Significant p-values are indicated in bold.

Morphological trait	Contrast	Mean diff.	Group mean		<i>P</i>
			inf	sup	
Bill length (L)	Old Urban-Rural	-1.863	-2.62	2.92	<b>&lt;0.001</b>
	Old Urban-Recent Urban	-2.263	-3.31	-1.22	<b>&lt;0.001</b>
	Rural-Recent Urban	-0.400	-1.42	0.62	0.616
Bill depth (D)	Old Urban-Rural	0.212	-0.07	0.35	<b>0.001</b>
	Old Urban-Recent Urban	0.177	-0.02	0.37	0.083
	Rural-Recent Urban	-0.035	-0.22	0.15	0.898
Bill width (W)	Old Urban-Rural	0.437	0.12	0.75	<b>0.004</b>
	Old Urban-Recent Urban	0.602	0.15	1.05	<b>0.006</b>
	Rural-Recent Urban	0.164	-0.27	0.6	0.637
D/L ratio	Old Urban-Rural	0.073	0.05	0.10	<b>&lt;0.001</b>
	Old Urban-Recent Urban	0.079	0.04	0.12	<b>&lt;0.001</b>
	Rural-Recent Urban	0.006	-0.03	0.04	0.929
W/L ratio	Old Urban-Rural	0.117	0.07	0.16	<b>&lt;0.001</b>
	Old Urban-Recent Urban	0.144	0.08	0.21	<b>&lt;0.001</b>
	Rural-Recent Urban	0.026	-0.04	0.09	0.595
D/W ratio	Old Urban-Rural	-0.012	-0.08	0.06	0.906
	Old Urban-Recent Urban	-0.066	-0.17	0.03	0.266
	Rural-Recent Urban	-0.053	-0.15	0.04	0.394

Figure captions:

**Figure 1** Location and satellite images (Land Information New Zealand 2019) of the three study areas in the the North Shore district of the Auckland region, New Zealand (36.471°S 174,452°E).

**Figure 2** Bill morphology of the New Zealand fantail, along a chronological gradient of urbanisation (old urban, recent urban and rural areas). Bill traits considered are simple morphological traits (i.e., bill length, depth and width) and ratios as proxy of bill shape (D/L: bill depth/length; W/L: bill width/length; D/W: bill depth/width).



**Figure 1**



**3** Rural area

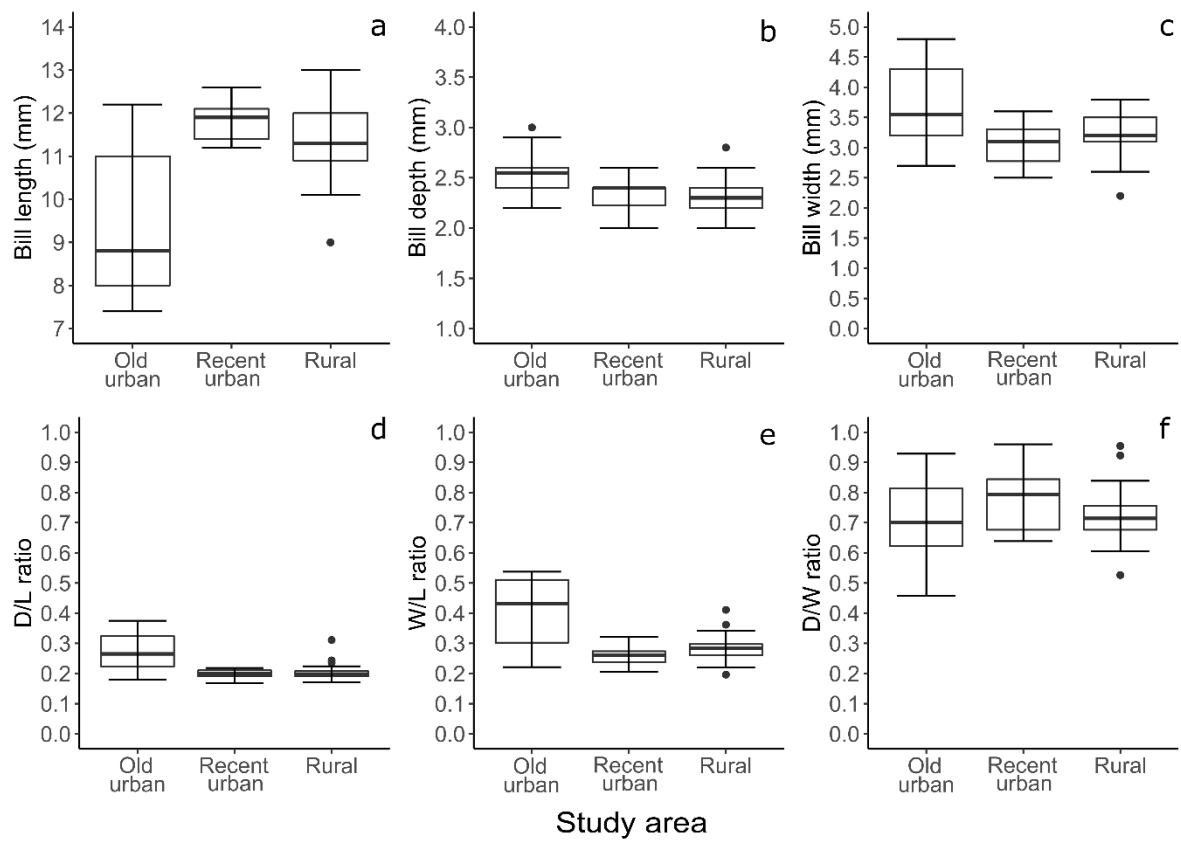


**2** Recent urban area



**1** Old urban area





**Figure 2**