Flight morphology and visual obstruction predict collision risk in birds

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ABSTRACT

28 Collisions with buildings are a major source of mortality for wild birds, but these instantaneous

events are difficult to observe. As a result, the mechanistic causes of collision mortality are

30 poorly understood. Here, we evaluate whether sensory and biomechanical traits can explain why

some species are more collision-prone than others. We first examined concordance of species

32 vulnerability estimates across previous North American studies to determine whether these

estimates are repeatable, and whether vulnerability is more similar among closely-related species.

34 We found moderate concordance and phylogenetic signal, indicating that some bird species are

consistently more collision-prone than others. We next tested whether morphological traits

36 related to flight performance and sensory guidance explain these differences among species. Our

comparative analysis shows that two traits primarily predict collision vulnerability within

38 passerines: relative beak length and relative wing length. Small passerine species with relatively

short wings and those with relatively long beaks are more collision-prone, suggesting that greater

40 maneuverability and obstructed vision contribute to risk. Together, these findings can help

inform mitigation strategies and predict which species will be most at risk in other regions.

1. INTRODUCTION

Building collisions are the second leading source of direct, human-caused bird mortality in North America, and are estimated to cause between 365–988 million deaths annually in the US [1] and between 16–42 million deaths annually in Canada [2]. Birds are attracted to lighted structures at night [3] or attempt to fly through windows in the daytime [4], only to collide and die upon impact or from injuries later on. Migratory species are especially at risk; the majority of collisions occur during migration, particularly in areas with strong levels of artificial light [3,5]. Additionally, several recent studies have established habitat-related correlates of collision mortality, such as building size and type, glass surface area, light pollution, surrounding land cover, and regional urbanization [6–10]. Behavioural correlates of collisions have also been identified, including nocturnal migration behavior [5,11], insectivory [10,12] and the use of social flight calls [3]. Knowledge of the sensory and biomechanical causes of building collisions is needed to devise effective strategies to prevent these fatalities. However, a major challenge to studying bird collisions with buildings and other anthropogenic structures is that each collision event is instantaneous and difficult to observe and predict.

In the absence of direct observations of collisions, an alternative way to evaluate causes is to consider the physiological traits of species that are most at risk. Not all bird species are equally vulnerable to building collisions; certain species like the white-throated sparrow, black-throated blue warbler, and ruby-throated hummingbird have been found to collide more frequently than expected, given their abundance at the spatial scale over which collisions are counted [1,5,10,11]. Shared traits among these vulnerable species can be a clue to common causes of collisions, and can allow risk to be predicted in other populations that have not been studied [3]. Here, we evaluate whether traits related to sensory guidance and flight performance

predict the vulnerability of bird species to collisions. As a first step, we analyzed the

66   concordance among published species vulnerability estimates from four previous studies of

North American birds [1,3,10,11]. These four studies are based on >106,000 bird fatalities across

68   62 geographic locations, and focus primarily on large buildings, with substantial variation among

studies in terms of landscape type, building type, survey methods, analytical methods, the spatial

70   scale of the analysis, and site-specific environmental features, such as vegetation and artificial

light (see Table S1 for details). This variation is important, because it allows us to identify

72   whether there are repeatable differences in collision risk that are detected across methodologies.

If species traits contribute to collision risk, we expect vulnerability estimates to be both

74   repeatable across different studies, and also more similar among closely-related species, as found

in a previous study of a single metropolitan region [11].

76   Next, we evaluated whether species risk is related to traits that influence vision, sensory

processing, and flight maneuverability, all of which are expected to influence threat detection

78   and avoidance in flight. Our predictions are explained below and listed in (Table 1). Note that

sensory and biomechanical traits may also be correlated with broad classes of foraging and

80   migration behavior, which have been examined in other recent work [7,10]. Our goal is not to

address these ecological factors, but rather we aim to identify which (if any) of the sensory and

82   biomechanical traits in Table 1 contribute to collision risk. This is important for a fundamental

understanding of bird flight as well as identifying the proximate causes of building collisions.

84   Vision is the primary sense that guides bird flight. Hence, the first set of traits we

considered relate to visual guidance. Larger eyes permit greater sensitivity and acuity of vision

86   [13], since they can hold more retinal photoreceptors and receive more light through a larger

pupil [14]. We therefore hypothesized that eye size may influence collision risk, and we

88   predicted that birds with larger eyes, and thus greater visual acuity, may have lower vulnerability

scores. Another trait that impacts frontal vision is the beak; long beaks relative to body size can

90   produce a longer anterior blind area, and consequently, a narrower binocular field [15]. This

blind area may limit the ability for birds to detect oncoming objects or to gauge distance,

92   particularly when objects lie in the frontal plane. Thus, we predicted that species with larger

beaks may be at greater risk of colliding. We also predicted that species with enhanced visual

94   processing due to a larger brain [16] may have lower vulnerability scores, since visual processing

ability could aid birds in detecting an imminent collision. We expect that these predictions would

96   generally apply to diurnal, nocturnal, and artificial light-induced collisions, because birds with

greater visual acuity and less obstructed vision should be better able to correct for visual

98   guidance errors across contexts.

The second set of traits we considered are related to a bird's maneuverability, defined as

100   the ability to change speed and direction [17]. The ability to generate power to perform rapid

evasive maneuvers may allow a bird to avoid collisions more easily. Since enhanced

102   maneuverability is associated with increased flight muscle capacity [18,19], we predicted that

birds with greater pectoral muscle size may be less prone to colliding. Differences in

104   maneuverability across bird species are also influenced by wing shape and aspect ratio, such that

short broad wings are associated with increased power [20]. Variation in wing shape within a

106   population has also been shown to predict mortality due to vehicle collisions. For example, in

cliff swallows, road-killed individuals were found to have significantly longer wings than

108   average in the population, indicating that shorter wings provide an advantage when avoiding

vehicle collisions [21]. Thus, we predicted that species with shorter wing spans would have

110   lower collision risk.

Although we generally predicted that species with greater visual and flight capacity

112   would be less collision-prone (Table 1), an alternative scenario is that they may actually be more

prone to colliding. For example, highly maneuverable birds with shorter wingspans often fly in

114   more cluttered environments [22], and consequently they may have narrower safety margins that

cause them to fly closer to buildings, putting themselves at greater risk. Consistent with this

116   scenario, bird species with greater aerial maneuverability have recently been found to collide

more often with aircraft [23]. Similarly, it is possible that species with greater visual capability

118   have narrower safety margins, and that this could lead to elevated risk. Finally, as outlined in

Table 1, it is the relative size of most traits (adjusted for body mass) that affects flight, and hence

120   we considered mass-adjusted traits in our analysis. Body mass itself may also contribute to

collision risk because it can affect maneuverability, safety margins, and the force of impact

122   during collisions. Therefore, we considered the possibility that differences in body mass may

interact with the traits listed in Table 1 to explain why some species collide more than others.

124 **Table 1. Traits that are expected to influence collision vulnerability**. In most cases, it is the relative size of the trait (adjusted for body mass) that affects flight. The predicted effect is the

126 expected change in vulnerability when the trait value increases.

Trait	Relevance for flight	Predicted effect on collision vulnerability
Absolute eye size	Visual acuity	Decrease
Relative eye size	Visual acuity	Decrease
Relative beak width	Visual obstruction	Increase
Relative beak length	Visual obstruction	Increase
Relative skull size	Sensory processing	Decrease
Relative wing length	Maneuverability	Increase
Relative keel size	Maneuverability	Decrease

128 **2. MATERIAL AND METHODS**

(a) Species collision vulnerability

130 We compiled estimates of species collision vulnerability from four previous studies that

surveyed bird collision fatalities in North America, and that focused primarily on large buildings

132 during spring and fall migration seasons [1,3,10,11] (see Table S1 for details of each study). Two

of the studies were conducted at a continent-wide scale, while the other two focused on single

134 metropolitan areas; all four studies differed substantially in monitoring protocol and coverage.

Each study reported species vulnerability estimates based on an analysis of collision frequency

136 relative to abundance at the spatial scale over which collisions were counted. Hence, a species

reported to have high vulnerability is one that was found to have died in collisions near buildings

138 more often than expected, given its abundance. In total, we gathered 397 vulnerability estimates

for 164 species (128 passerines with 2.7 estimates per species on average, and 36 non-passerines

140 with 1.6 estimates per species). We standardized the estimates by scaling each study to have a

mean vulnerability of 0 and a standard deviation of 1, to facilitate comparison across studies. A

142   complete list of all species and their standardized vulnerability estimates is provided in the

supplement.

144   We analyzed the concordance of the standardized vulnerability estimates by examining

Pearson's correlations and repeatability using R 3.6.2 [24]. To estimate repeatability, we fit a

146   mixed-effects model of the estimates with species as a random effect and study (four levels) as

the fixed effect in the lme4 1.1-21 package [25], and we calculated repeatability as the

148   proportion of variance attributed to species ID [26]. We used parametric bootstrapping to obtain

the 95% CIs for repeatability. To determine whether vulnerability is more similar among closely

150   related species, we first calculated species-average vulnerability by taking the mean of the

available standardized estimates (note that if a species was not common at a particular study's

152   geographic location, it would not have an estimate). We used the phylogeny from

http://BirdTree.org [27,28] to calculate phylogenetic lambda of species-average vulnerability

154   scores using the phytools 0.6-99 package [29]. Lambda is a measure of phylogenetic signal that

ranges from zero to one. A lambda value near one indicates that vulnerability is highly similar

156   for closely related species, whereas a value near zero indicates that vulnerability is independent

of phylogenetic relatedness.

158

(b) Morphological measurements

160   We collected data on morphological traits representative of each species from skeletal specimens

available at the Canadian Museum of Nature. We aimed to measure four to five adult-sized

162   individuals per species, including both sexes, where available. Our measurements included 393

specimens from 89 species ($4.4 \pm$ SD 1.2 individuals per species), with variation due to the

164   number of intact specimens in the collection. Most of the studied species breed across the North

American continent (see supplement for details). For each individual specimen, we recorded

166   body mass from the specimen metadata where available, and photographed the scleral rings, the

skull from the dorsal view, and the humerus and ulna using a digital SLR camera (Canon EOS

168   M50 with EF-M 28 mm lens) mounted on a copy stand. As an indication of flight muscle

capacity, we measured the keel along the diagonal axis from the anterior ventral point to the

170   posterior ventral point using digital calipers (± 0.01 mm). The length of the keel is highly

correlated with the mass of the primary flight muscles [30,31], which provide the main source of

172   power for flight maneuvers [19].

We measured eye size, beak length and width, skull size, and wing length from digital

174   images using ImageJ 1.52a [32]. All pixel measurements in ImageJ were converted to cm using a

5 cm scale that was included in every photograph. As a measure of eye size, we measured the

176   inner diameter of each scleral ring – a ring of overlapping bony plates inside the sclera of the eye

[33]. Scleral ring diameter is highly correlated with eye size and provides a proxy of spatial

178   visual acuity [34]. For any specimen with both scleral rings intact, we averaged the left and right

diameters. As a measure of visual obstruction, we measured the length and width of the beak

180   from the dorsal view of the skull. Beak width was measured at the base of the beak where it

meets the skull, and beak length was measured as the length of the skull plus the beak. As a

182   proxy for brain size variation across species, we measured the width of the skull at its widest

point. External head size and skull volume have been shown to reliably predict inter-individual

184   variation in brain mass [35,36]. Hence, the width of the skull is expected to be a reliable measure

of species differences in our sample. As our measure of wing length, we took the length of each

186   humerus and ulna as the longest straight-line distance (chord). For the humerus, this

measurement extended from the tip of the shoulder joint to the inside of the elbow notch. If an

188   individual had two matching bones intact (e.g., left and right humerus), we averaged the two

measures. Some specimens (and species) were missing traits (e.g., due to broken bones); details

190   of the sample sizes per trait are provided in Fig. S1.

For each of the traits described above, we computed the species-average trait value

192   relative to body mass, according to our hypotheses in Table 1. This is important because the

species studied vary widely in body mass (Fig. S1), and the capacity of a given anatomical trait

194   to influence flight also depends on body mass. To compute each relative trait value, we first fit a

linear model of the log-transformed trait values relative to log-transformed body mass, across all

196   individual specimens (Fig. S1), and extracted the model residuals. For the specimens that did not

have body mass available in the metadata (26% of 393 individuals), we used the mean species

198   mass for adults from the Birds of the World online database [37]. Finally, we took the mean

value of the residuals for each species as the relative species trait value (see the supplement for a

200   detailed explanation). Hence, a species with a large relative keel size has a larger keel than

expected for its body mass. The only trait where we also considered absolute magnitude was eye

202   size (Table 1).

Because relative humerus length was closely correlated with relative ulna length (r =

204   0.81, p < 0.0001, n = 88 species), we combined these two traits into one measure of species

relative wing length by taking the average. We also verified that both humerus and ulna length

206   are highly correlated with species wing chord, a common measure of the distal part of the wing (r

= 0.90 and 0.92 respectively, all p < 0.0001, see supplement for details). Prior to further analysis,

208   we checked variance inflation factors for all of the relative trait values and body mass, and

confirmed that the variance inflation factors were relatively low (all < 2.3).

210

(c) Collision vulnerability in relation to morphological traits

212   To evaluate whether visual and flight-related traits predict collision vulnerability, we modelled

the standardized vulnerability estimates using Bayesian phylogenetic mixed-effects regression in

214   the package MCMCglmm 2.29 [38]. The models included a random effect of species to account

for repeated measures, as well as the phylogenetic structure to account for non-independence

216   among related species [19,39]. The use of a repeated measures analysis ensured that species with

more estimates were accorded greater weight in the analysis. We fit a series of candidate models

218   to consider hypothesized effects of sensory and biomechanical traits; these candidate models are

listed in Table S2. Each candidate model included fixed effects of either one, two, or none of the

220   skeletal traits listed in Table 1. Additional fixed effects accounted for the source study

(categorical variable with four levels), a species' log-transformed body mass (continuous

222   variable), and a binary factor describing whether a species was a nocturnal migrant that used a

social flight call. Previous evidence has shown that nocturnal migration with social flight call use

224   is an important predictor of urban collision risk [3].

We built two model sets. The "All birds" model set analyzed passerines and non-

226   passerines together (n = 205 vulnerability estimates for 85 species), whereas the "Passerine only"

analysis was limited to the order Passeriformes (n = 164 vulnerability estimates for 59 species).

228   There were no non-passerines < 40 g in our morphometric analysis, and only two passerines >

100 g. This makes it difficult to distinguish effects that are due to small size vs. membership in

230   the passerine clade. Hence, running both model sets provided a check on whether our

conclusions were robust to taxonomic and size-based sampling. The "All birds" models included

232   additional fixed effects for membership in the passerine order and the potential interaction

between each trait and body mass (i.e., size-dependence of trait effects). Because we used model

234   comparison, the analyses only included species for which complete trait data were available. We

used DIC (deviance information criterion) to compare Bayesian models fit with MCMC.

236   Each model was run for 500,000 iterations after a burn-in period of 3,000, and posterior

results were thinned to include every 500th sample. We verified convergence using the Gelman-

238   Rubin statistic and confirmed that posterior autocorrelation values were < 0.1. As a means of

visualizing the main results, we refit the top models from the MCMCglmm analysis with lme4

240   1.1-21 [25] using taxonomic family and species as nested random effects. After confirming that

the coefficients from this lme4 analysis were consistent with the posterior MCMCglmm model,

242   we plotted the results using partial residual plots from the visreg 2.5-0 package [40].

244   **3. RESULTS**

(a) Consistency and phylogenetic distribution of collision risk

246   Published estimates of bird species collision vulnerability were moderately repeatable (R = 0.32

[95% CI 0.20 to 0.43]) and positively correlated (average r of 0.33; Fig. 1a). Examining the

248   composite vulnerability score (all studies combined), we find that closely related species tend to

have similar collision risk (Fig. 1b), with a moderate phylogenetic signal (lambda = 0.54, p <

250   0.001).

252   *(b) Collision vulnerability and morphology*

The best-fit models of species collision vulnerability indicated that two skeletal traits were

254   associated with increased risk: relatively long beaks and relatively short wings (Fig. 2; Tables

S3-S4). In the "All birds" analysis, the effect of beak and wing length was limited to small and

256   medium-sized species (Table S5), which are almost exclusively the passerines in our dataset. The

258 best-fit "Passerine only" model led to the same conclusion. Both model sets also identified body mass as an important predictor, with smaller species generally being more collision prone (Fig. S3 and Tables S4-S5). Consistent with a previous study [3], collision risk was also found to be

260 higher for nocturnal migrants that use social flight calls (Fig. S3).

262 **4. DISCUSSION**

Several recent studies have established that bird species differ in vulnerability to building

264 collisions [1,5,10,11]. We show here that despite pronounced differences across studies in terms of geographic scale and monitoring protocols, estimates of species vulnerability are moderately

266 repeatable and associated with phylogeny (Fig. 1).

In addition to factors that have previously been studied [3,10,11], our findings indicate

268 that visual obstruction may be one of the contributing factors to collision risk. Vulnerability was positively associated with beak length for small passerine birds (Fig. 2a). Examples of species

270 with relatively long beaks that are consistently identified as collision-prone include the white-breasted nuthatch, brown creeper, and gray catbird (Table S7). This general result suggests that

272 long beaks that obstruct the frontal visual field [15] may also impair the ability of small birds to avoid collisions. With impaired vision, a bird might be more apt to misinterpret window

274 reflections as vegetation or open sky, or be more prone to guidance errors caused by artificial light. Smaller birds also have visual systems with lower spatial resolution [14,41,42], and a long

276 beak obstructing their frontal visual field might exacerbate this issue.

Our results point to maneuverability as another contributing factor to collision risk,

278 because small passerine species with relatively short wings were found to be more collision-prone (Fig. 2b). Examples of short-winged species include the white-throated sparrow, fox

280   sparrow, and rose-breasted grosbeak, all of which are estimated to have high collision risk (Table

S7). Given that short, broad wings allow for increased power and maneuverability [20], this

282   finding suggests that more maneuverable species are more collision-prone. This result also

contradicts our initial prediction in Table 1, but is consistent with another recent study finding

284   that more maneuverable bird species are more likely to strike aircraft [23]. Highly maneuverable

species often fly in cluttered environments such as forest and dense vegetation [22]. They may

286   thus have narrower safety margins that cause them to venture closer to buildings in urban and

suburban environments, both during the day and at night when errors may be caused by artificial

288   light.

Our results indicate that small body size is generally associated with increased risk, even

290   within passerines (Fig. S3). We propose that this is because small body size is also associated

with narrow safety margins during flight. Small birds are often observed to enter denser

292   vegetation and other cluttered airspaces as an escape strategy (e.g., when chased by predators

and/or competitors) [43]. They may also depend on high-risk airspaces for foraging opportunities.

294   Hence, buildings and window barriers may create ecological traps for the smallest and most

maneuverable bird species. In line with our general results, hummingbirds are estimated to be the

296   most collision-prone group of bird species [1], and they also have extremely small body sizes,

high maneuverability, and long beaks. Although we were not able to collect morphometric data

298   from hummingbirds, our results point to their common traits as generally collision prone.

There are many other traits relevant to flight control that should be investigated in future

300   collision studies. For example, not all birds look forward when they fly [44]. Collision avoidance

may thus depend on the orientation of the eyes as well as the position of the eyes relative to the

302   beak [45]. Similarly, the temporal resolution of vision (number of changes perceived per second)

is another important trait that may influence the ability of a bird to rapidly detect and avoid

304   obstacles [46]. It is important to note that a vast number of collisions – particularly among

passerines – occur during nocturnal and crepuscular times when birds can be disoriented or

306   attracted by artificial light sources [3]. Monitoring studies that examine collisions at those times

can help determine whether certain visual systems are more sensitive to guidance errors caused

308   by artificial light, and how we might prevent bird strikes under these conditions.

Previous studies have provided great insight into the features of urban and suburban

310   environments that pose risk, such as artificial light at night, glass surface area, and proximity to

vegetation [3,6–8,11,12]. Our results show how morphology can also explain why some species

312   are more collision-prone than others, owing to their small size, visual obstruction, and

maneuverability. Our findings also have implications for predicting the impacts of building

314   development on bird populations outside of North America, where monitoring data may be

deficient. Mitigation strategies are often costly, and understanding which morphological and

316   flight-related traits lead to collisions will help target these strategies towards a particular trait or

species group. For example, it will be important to ensure that the placement, spacing,

318   colouration, and size of features used in products designed to make glass more bird-friendly are

large and frequent enough that small birds with obstructed vision can detect them [47].

320   An important caveat is that our results are correlative, and a complete understanding of

the proximate causes of collisions still requires directly observing these events. Additionally,

322   nearly all of the fatalities used in our analysis occurred in urban settings during migration.

Although urban collisions are better sampled, residential buildings in suburban habitats are

324   estimated to cause a substantial proportion of total bird collision mortality across the continent

[1,2,48]. Residential buildings may elicit different visual guidance errors and affect different

326   species than urban and campus buildings [1]. There is an urgent need for studies of the proximate

mechanisms of non-fatal collisions, and collisions in suburban environments. In the future, our

328   results suggest that experimental tests of mitigation strategies should be targeted towards small,

maneuverable species with obstructed vision in order to have the greatest benefit.

330

332   **FIGURE LEGENDS**

        Figure 1. Estimates of bird species vulnerability to collisions are repeatable. (a) The
334   heatmap shows Pearson's correlation coefficients comparing estimates from four previous
        studies. Most correlations were positive and moderately strong. Sample sizes (i.e., numbers of
336   species) are shown within each cell; see the list of References [#] and Table S1 for details. (b)
        Distribution of species-average standardized collision vulnerability across the avian phylogeny
338   (n = 164 species). Dark blue indicates species with low composite vulnerability (colliding less
        often than expected, based on abundance), whereas red indicates high vulnerability. The dotted
340   line denotes the passerines. See Fig. S2 for additional taxonomic information.

342   **Figure 2. Collision risk for small passerines is associated with maneuverability and visual
        obstruction.** Partial residual plots show the relationship between collision vulnerability and
344   morphological traits that were retained in the best-fit model ("Passerine only"). Each data point
        represents a residual vulnerability estimate after accounting for the effects of nocturnal migration
346   calling behaviour and body mass (n = 59 species; see Fig. S3 for additional data). Within
        passerines, relatively elongated beaks (a) and short wings (b) are associated with elevated rates
348   of collisions. The full results of this analysis are provided in the supplement. Beak and wing
        length are also found to predict risk for small species in the "All birds" model (Table S5).

18

350   DATA ACCESSIBILITY
        All data and R scripts are available at: https://figshare.com/s/0de0dc5ff609a2d19c15
352   The repository will be made public when the final version of the study is published.

354   AUTHOR CONTRIBUTIONS
        RD and EJ conceived the study, collected the data, analyzed the data, and wrote the manuscript.
356   JAE, SRL, and BMW contributed vulnerability estimates and edited the manuscript.

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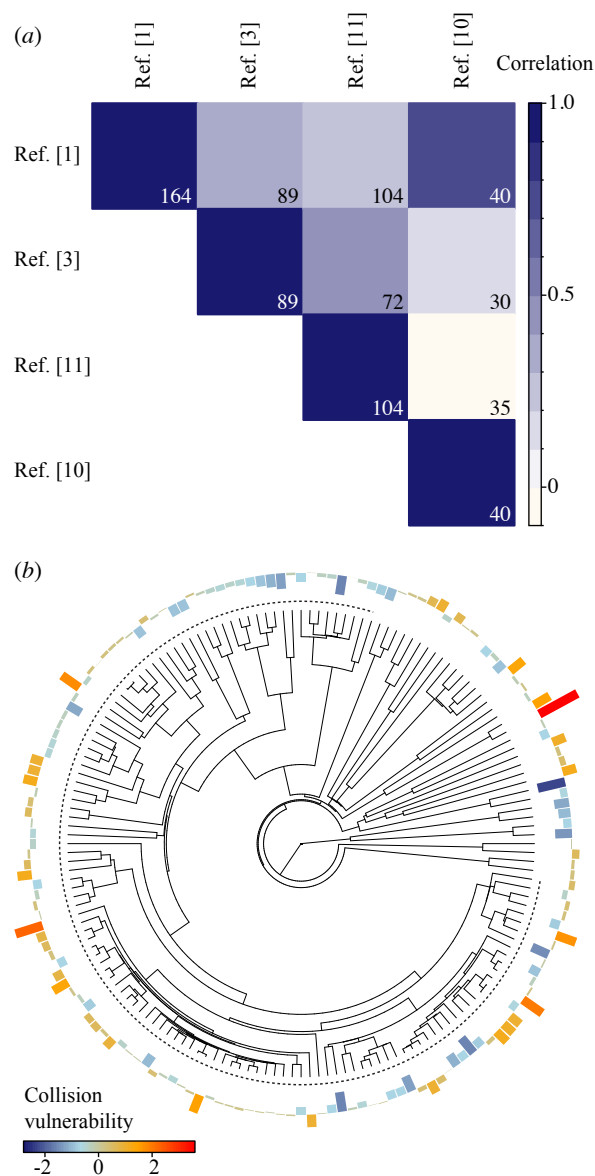
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Figure 1

(a)

(b)

Collision vulnerability

Figure 2