
Integrating behaviour and ecology into global biodiversity conservation strategies

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Summary

Insights into animal behaviour play an increasingly central role in species-focused conservation practice. However, progress towards incorporating behaviour into regional or global conservation strategies has been more limited, not least because standardised datasets of behavioural traits are generally lacking at wider taxonomic or spatial scales. Here we make use of the recent expansion of global datasets for birds to assess the prospects for including behavioural traits in systematic conservation priority-setting and monitoring programmes. Using IUCN Red List classifications for >9500 bird species, we show that the incidence of threat can vary substantially across different behavioural categories, and that some types of behaviour—including particular foraging, mating and migration strategies—are significantly more threatened than others. The link between behavioural traits and extinction risk is partly driven by correlations with well-established geographical and ecological factors (e.g. range size, body mass, human population pressure), but our models also reveal that behaviour modifies the effect of these factors, helping to explain broad-scale patterns of extinction risk. Overall, these results suggest that a multi-species approach at the scale of communities, continents and ecosystems can be used to identify and monitor threatened behaviours, and to flag up cases of latent extinction risk, where threatened status may currently be underestimated. Our findings also highlight the importance of comprehensive standardized descriptive data for ecological and behavioural traits, and point the way towards deeper integration of behaviour into quantitative conservation assessments.

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32 1. Introduction

33

34 Conservation biologists and behavioural ecologists have repeatedly called for closer links between their
35 respective fields on the grounds that behavioural insights can contribute significantly to the success of
36 conservation action (Clemmons & Buchholz 1997; Caro 1999; Caro & Sherman 2011; Greggor et al. 2016).
37 However, this cross-disciplinary integration has progressed slowly, in part because the methods and central
38 questions of behavioural ecology do not align closely with the needs of conservation practitioners (Greggor et
39 al. 2016). For example, much of behavioural ecology focuses at the level of the individual, and identifies
40 selective mechanisms acting on genes or organisms, whereas conservation typically operates at the level of
41 populations (Caro 2007). This misalignment is perhaps most pronounced at macroecological scales where
42 global analyses are playing a vital role in conservation science and policy (e.g. Newbold et al. 2015) but
43 generally include only the most basic behavioural information.

44 One reason for the low profile of behaviour in comprehensive broad-scale analyses is because it is
45 difficult and costly to measure standardised behavioural traits across species, space and time (Anthony &
46 Blumstein 2000). The major contributions of behavioural research to conservation have dealt with factors such
47 as individual movements, sensory ecology, animal personality or cultures, and the extent to which they
48 mediate various kinds of human pressures, including disturbance, habitat loss and hunting (Greggor et al.
49 2016, Brakes et al. 2019). The key behavioural metrics under this framework are context-dependent, highly
50 plastic both within and between individuals, and typically estimated through detailed observation and
51 experimentation. They are often inappropriate for quantitative assessments at the wider level of communities
52 or ecosystems because they are (1) only available for a small fraction of species, and (2) not readily
53 incorporated into species-level analyses. For instance, the case-dependent intricacies of how behaviour
54 influences effective population size (N_e) are useful to conservation (Anthony & Blumstein 2000), but we are
55 decades away from having these data available for comprehensive global studies.

56 Global or regional conservation assessments are largely restricted to comprehensive species-level
57 datasets accessible at the relevant scale (see figure 1). Most macroecological analyses have therefore tested
58 whether species conservation status is predicted by human impacts, biogeographical factors such as latitude
59 or range size, and environmental factors such as climate or habitat (Bennett & Owens 1997, Owens & Bennett
60 2000, Cardillo et al. 2004, Cardillo et al. 2005, Lee & Jetz 2011, Keinath et al. 2017), or reversed the process to
61 predict the conservation status of poorly known species (Jetz & Freckleton 2015, Santini et al. 2019). Using
62 freely available GIS layers, these socio-economic, biogeographical and environmental variables can be
63 extracted for specimen localities or geographical range polygons, which in some vertebrate groups are
64 reasonably accurate. The other main components of macro-scale assessments have been demographic factors,
65 including population size and density, and rates of population decline, all of which are theoretically related to
66 extinction risk (Keinath et al. 2017; Santini et al. 2019). In general, only crude population estimates are
67 included in global-scale analyses because very few attempts have been made to quantify population sizes and
68 trends across entire global ranges (Tobias & Seddon 2002, Tobias & Brightsmith 2007). Previous studies have
69 shown that both extrinsic biogeographic and demographic factors are correlated with extinction risk, leading
70 to their widespread inclusion in regional and international conservation status assessments.

71 Perhaps the most influential global assessment is the IUCN Red List (IUCN 2001), an indicator of
72 biodiversity status and change linked to international convention targets (Butchart et al. 2005). The
73 conservation status categories systematically generated by the Red Listing process are enshrined in legislation
74 and widely used in macroecological research (Rodrigues et al. 2006). Previous assessments of predictors of

75 Red List status have generally focused on standard biogeographic or climatic variables, without delving far
76 into behavioural or ecological factors. Indeed, the only ecological and behavioural traits incorporated into
77 most global models of conservation risk are body mass, diet and habitat preferences (Lee & Jetz 2011;
78 Newbold et al. 2015, Keinath et al. 2017). To convert these variables into species-level traits, body mass is
79 typically averaged from small numbers of published estimates, while diet and habitat are classified into broad
80 categories on the basis of published descriptions in secondary literature (Wilman et al. 2014). By contrast,
81 many other behavioural or ecological variables have not been comprehensively estimated at global scales and
82 are often difficult to convert into species-level traits (figure 1).

83 The most relevant behavioural traits to conservation assessment include those that mediate sensitivity
84 to habitat loss, fragmentation, and climate change (Greggor et al. 2016). Factors relating to dispersal behaviour
85 are particularly pertinent because they impinge on the ability of species to cross unsuitable habitat and thus
86 maintain interconnected metapopulations after habitat fragmentation (Lees & Peres 2009). Dispersal-related
87 traits may also regulate the ability of species to track shifting geographical ranges in response to climate
88 change (Early & Sax 2011, Howard et al. 2018), and predict susceptibility to threats like wind farms (Thaxter et
89 al. 2017). In addition, behavioural dimensions of species interactions may be important determinants of
90 responses to a variety of threats. For example, studies focused at the level of species pairs or communities find
91 evidence that interspecific competition leads to population declines or local extinction following habitat loss
92 and fragmentation (Bregman et al. 2015, Grether et al. 2017) while reproductive interference may threaten
93 populations of closely related species interacting or hybridising when climate-driven range shifts lead to
94 secondary contact (Hochkirch et al. 2007, Greggor et al. 2016). However, while standardised estimates of
95 dispersal ability and interspecific competition are available for restricted samples of species, they are not
96 readily available at macroecological scales, except in the form of extremely coarse categories (e.g. whether an
97 organism can fly or not; Keinath et al. 2017).

98 Other variables potentially relevant to conservation status can be placed on a continuum from
99 primarily ecological to primarily behavioural (figure 1). At the ecological end are aspects such as microhabitat
100 preferences, while other factors such as foraging mode, migration, sexual selection, territoriality, reproductive
101 strategy and nesting behaviour have an increasingly behavioural dimension. Previous research suggests that
102 species sensitivity to land-use or climate change can be related to microhabitat (e.g. in the form of vertical
103 stratum of vegetation), foraging behaviour (e.g. gregarious foraging), and reproductive strategy (e.g. breeding
104 system) (Kokko & Brooks 2003, Bueno et al. 2018). Similarly, territorial strategy is linked to species sensitivity
105 to habitat fragmentation (Ulrich et al. 2017), suggesting that elevated interspecific competition via behavioural
106 mechanisms can increase threats associated with land-use and climate change (Jankowski et al. 2011, Grether
107 et al. 2017). Until recently, such inferences were based on relatively restricted species sampling, but this
108 constraint is changing as the compilation and dissemination of global trait datasets gathers pace.

109 To assess whether recent progress in data availability can pave the way for behavioural perspectives
110 to be explicitly included in global conservation strategies, we compiled information on a variety of ecological
111 and behavioural traits for all bird species, including estimates of sexual selection (Dale et al. 2015; Cooney et
112 al. 2017), breeding system (Jetz & Rubenstein 2011), foraging strategy (Pigot et al. 2016, Felice et al. 2019),
113 territorial behaviour (Tobias et al. 2016), and nest placement (Stoddard et al. 2017). We then ran multivariate
114 models to evaluate the extent to which behaviour predicts IUCN Red List status at macroecological scales and
115 in relation to a range of standard biogeographical and environmental variables. Unlike many studies focused
116 on explaining variation in tolerance to human-induced environmental changes (Tuomainen & Candolin 2011,
117 Sol et al. 2013), the aim is not to examine how behaviour influences sensitivity to particular threats,

118 particularly as this would require a different analytical approach. Instead, our goal is to assess the current
119 landscape of behavioural data availability and the prospects for more nuanced conservation assessments and
120 priority-setting.

121

122 2. Methods

123

124 (a) Data

125

126 We assembled data on species threat status from the 2016 Red List (IUCN 2016) along with a range of
127 potential drivers of variation in status, including biogeographic, ecological and behavioural traits, as well as
128 the exposure of each species to human impacts. Geographic range size is consistently identified as the
129 strongest predictor of threat status (Lee & Jetz 2011; Jetz & Freckleton 2015). Although this is not surprising
130 given that two of the main Red List criteria (A and B) are partly based on either Extent of Occurrence (EOO) or
131 Area of Occupancy (AOO), it is nonetheless important to include range size when modelling threat predictors
132 and their correlates. We estimated range size (EOO) for each species based on maps of species breeding
133 distributions (BirdLife International, 2012). Human population pressure is also known to influence extinction
134 risk (Cardillo et al. 2004; Scharlemann et al. 2005; Davies et al. 2006). To quantify the exposure of species to
135 human impacts, we first extracted polygon range maps onto an equal area grid (resolution of $110 \text{ km} \approx 1^\circ$ at
136 the equator) and used this grid to sample human population density, human appropriation of net primary
137 productivity (HANPP) and night-time light intensity, an indicator of urbanisation and development. We
138 calculated the mean value of each metric, averaged across all grid cells overlapping with each species range.

139 We collated data on a selection of ecological traits, including mean species body mass (g), habitat type,
140 diet and island dwelling, all of which have been linked to extinction risk (Bennett & Owens 1997; Owens &
141 Bennett 2000; Cardillo et al. 2005; Lee & Jetz 2011; Jetz & Freckleton 2015). We extracted body mass from
142 Wilman et al. (2014). Using literature to score habitat use, we assigned species to broad habitat categories
143 (coastal, terrestrial, freshwater, sea) according to the predominant habitat utilised across their geographic
144 distribution. We assigned species to one of ten dietary categories: aquatic animals, aquatic plants, terrestrial
145 invertebrates, terrestrial vertebrates, terrestrial carrion, nectar, seeds, fruit, other terrestrial plant matter (e.g.
146 leaves), and omnivore, based on the dominant resource present in their diet (see Supplementary material).
147 Data on proportional resource use were first obtained from Wilman et al. (2014), and then modified and
148 updated based on comprehensive literature searches. Our dietary classification differs from Wilman et al.
149 (2014) in that we subdivided each animal or plant-based resource type into separate aquatic and terrestrial
150 categories (see Felice et al. 2019). This helps us to avoid highly heterogenous categories such as invertivores,
151 which spans a wide variety of species from insectivorous warblers to squid-eating albatrosses and crustacean-
152 eating flamingos (Wilman et al. 2014). Our approach separates warblers (diet: "terrestrial invertebrates") into a
153 different category from albatrosses and flamingos (diet: "aquatic animals"). Using the geographical range
154 polygons described above, we classified species as island dwelling if more than 25% of their geographic range
155 occurred on small islands (landmass $< 2000 \text{ km}^2$). Further details of data compilation methods are given in
156 supplementary materials.

157 To assess the association between IUCN threat status and key behavioural traits, we assembled data
158 on foraging strategy, nest placement, breeding system, mating behaviour, the mean clutch size of broods,
159 territoriality and migratory behaviour (figure 2). Following the method described by Felice et al. (2019), we
160 used literature searches to assign species to one of eight foraging strategies ('Aerial screen', 'Bark glean',

161 'Aerial sally', 'Arboreal glean', 'Ground forage', 'Aquatic plunge', 'Aquatic surface' and 'Aquatic dive'). We
162 classified each species according to the predominant behavioural strategy used to acquire resources, and
163 assigned species utilising multiple foraging strategies as generalists (i.e. nine categories in total, see
164 Supplementary material). Nest placement was scored into a simple three-way system: ground, elevated or
165 cavity (see Stoddard et al. 2017 for details). We used a binary score of breeding system based on a published
166 classification of cooperative and noncooperative breeders (Jetz & Rubenstein 2011). Mating behaviour was
167 scored as strict monogamy, monogamy with infrequent (<5% males) polygyny, monogamy with frequent (5-
168 20% males) polygyny, and polygamy (>20% males and females). These categories are based on the index of
169 sexual selection developed by Dale et al. (2015). Clutch size data was based on Jetz et al. (2008). Using data
170 from Tobias et al. (2016), we assigned all species to three categories according to the degree of territoriality:
171 'strong' (territories maintained throughout year), 'weak' (weak or seasonal territoriality, including species
172 with broadly overlapping home ranges or habitually joining mixed species flocks), and 'none' (never
173 territorial or at most defending very small areas around nest sites). Finally, we assigned the migratory
174 behaviour of species as either sedentary, partially migratory (minority of population migrates long distance or
175 most individuals migrate short distances) and migratory (majority of population undertakes long-distance
176 migration) (Tobias et al. 2016).

177 Most variables were available for the vast majority (i.e.>99%) of species but the identity of species
178 with missing values differed across variables. For categorical predictors, we imputed missing values using the
179 modal class for each genus, if the genus contained at least 2 species and the modal class was present across at
180 least 75% of species. If these conditions were not met, we used the same criteria to impute missing values at
181 the family level. After removing all species with any missing values, our final dataset included $n = 9658$
182 species.

183

184 (b) Statistical analysis

185

186 To model the effects of each predictor variable on extinction risk, we treated threat as a binary variable (0, 1)
187 according to the IUCN Red List categories. All species listed as Vulnerable, Endangered, Critically
188 Endangered, Extinct (including Extinct in the Wild) were classified as Threatened; the remainder (Near
189 Threatened, Least Concern and Data Deficient) were classified as non-Threatened. We modelled threat using a
190 generalised linear mixed effects model in the R package 'lme4' (Bates et al. 2015). We implemented a binomial
191 error structure and included taxonomic family as a random effect to control for the phylogenetic non-
192 independence of species when identifying predictors of threat. To ensure our results were robust to way
193 random effects were modelled, we repeated our main analysis using phylogenetic generalised mixed model
194 using the R package 'phylolm' (Ho & Ane 2014).

195 We assessed collinearity between predictor variables by first estimating Pearson correlation
196 coefficients between each pair of continuous variables. We used a threshold of 0.7 as an indicator of potential
197 collinearity. On this basis we excluded HANPP from our analysis because it was strongly correlated with
198 human population density (0.74), which is a standard predictor of extinction risk used in many previous
199 studies. In order to deal with possible associations among categorical predictors we used generalised variance
200 inflation factors (GVIF) accounting for the number of degrees of freedom associated with each predictor. A
201 GVIF value of 5 or 10 is commonly used as a threshold to remove collinear predictors (Dormann et al. 2013).
202 GVIF values for each predictor were always less than two and so all other predictors were retained in our
203 analysis (Table S1). Predictor variables exhibiting right skew were log transformed prior to analysis.

204 In contrast to previous assessments of the predictors of extinction risk in birds (e.g. Lee & Jetz 2011),
205 we are particularly interested in how behaviour and its covariation with other putative drivers of extinction
206 risk alter the incidence of threat. First, to assess the overall association between each predictor and threat, we
207 ran a series of single predictor (i.e. univariate) models. Second, we fitted a full multivariate model including
208 all predictor variables. We assessed the contribution of each predictor by removing, and then reinserting, each
209 term from the model and calculating the change in the Akaike Information Criterion (ΔAIC). Third, to assess
210 the overall effect of behaviour, we ran a model including all ecological predictors along with metrics of human
211 exposure and range size, but excluding all behavioural traits. Finally, to examine how behaviour may mediate
212 the effects of other extinction drivers, we tested for significant interactions between each behavioural trait and
213 each of the core predictors of threat identified in our full model (range size, body size and human population
214 density). We first added and then removed each individual interaction term from our full model to identify
215 those contributing to a significant improvement in model fit ($\Delta\text{AIC} > 2$). We then included all of the significant
216 interaction terms in the full model and performed step-wise model simplification, removing those interaction
217 terms resulting in the smallest change in model support. We stopped when the removal of any interaction
218 term resulted in a $\Delta\text{AIC} > 2$.

219 To examine how the definition of threat may influence the predictors of extinction risk, we repeated
220 our analysis considering only threatened species ($n = 1251$), predicting lower (0 [Vulnerable]) or higher (1
221 [Endangered, Critically Endangered, Extinct]) levels of threat. Given that range size was included as a
222 predictor in our model, we also repeated our analysis removing the 321 species that were listed as threatened
223 due to small or declining geographic range sizes (i.e. criteria B). To assess how the predictors of threat may
224 change across broad habitat types, we repeated analyses on different subsets of our data including all species
225 ($n = 9658$), terrestrial species ($n = 8495$) and aquatic ($n = 767$) species. We excluded habitat type as a predictor
226 when fitting models to terrestrial and aquatic species. In addition, we excluded diet and mating behaviour
227 when fitting models to threatened and aquatic species, respectively, because models including these terms
228 failed to converge.

229

230 Results

231

232 (a) Overall predictors of threat in birds

233

234 Our results identified a number of core predictors of threat status that align closely with previous assessments
235 indicting that variation in threat across all birds arises as a combination of geography, ecology and human
236 impacts (figure 3). Specifically, the strongest predictor of threat status is geographical range size, with
237 additional strong effects of body mass, island dwelling and the mean human population density across the
238 species geographic range, a metric of exposure to human impact. In both univariate and multivariate models,
239 the incidence of threat decreases with geographic range size (figure 4a) and increases with body size (figure
240 4b, table S2). When tested in isolation, the incidence of threat is higher on islands. However, in the full
241 multivariate model accounting for other factors including range size, this effect is reversed, with a lower
242 incidence of threat on islands (figure 4d, table S2). We note that this counter-intuitive pattern of a lower risk of
243 threat among island dwelling species when accounting for their smaller geographic range size has previously
244 been reported (Manne et al 1999). Similarly, in a univariate model, we found that threat decreases with human
245 population density, but this switches to a positive effect after accounting for variation in geographic range size
246 in the full multivariate model (figure 4c, table S2). In contrast to the positive effect of human population

247 density on threat, threat was only weakly and inconsistently related to night light density (figure 3, table S2).
248 Finally, while there was no consistent relationship between habitat type and threat, we found significant
249 variation in the likelihood of threat across dietary categories, with the highest threat among scavengers,
250 aquatic predators and vertivores compared to invertivores and primary consumers (i.e. frugivores, granivores,
251 nectarivores and herbivores) (figure 4e).

252 In addition to these established predictors, we also identified a significant effect of behaviour on extinction
253 risk (figure 3). Although the improvement in explanatory power is modest (marginal R^2 excluding versus
254 including behaviour = 0.48 versus 0.51 respectively), a full multivariate model including all predictors is
255 significantly better supported than a model excluding behavioural traits (delta AIC = 60). All of these key
256 results relating to the core predictors of threat and the role behaviour were robust to the exclusion of species
257 listed as threatened on the basis of small or declining range size and when modelling the non-independence of
258 species on the basis phylogenetic relatedness rather than taxonomy (table S2, figure S1, S2).

259

260 (b) The effects of behavioural traits on threat

261

262 The strongest behavioural predictor of threat in birds was migratory behaviour (figure 3), whereby long-
263 distance migration confers a higher risk of threat (figure 4i). We note that, in a univariate model, long distance
264 migrants are significantly less threatened than partial migrants or sedentary species (figure 3c, table S2). This
265 contrasting finding arises because on average migrants have larger breeding ranges than sedentary species
266 (figure S3a). Thus, while our multivariate model shows that migratory behaviour promotes threat, migrants
267 are nonetheless less likely to be threatened overall because of their large geographic ranges. In addition, we
268 found that the effect of migratory behaviour is also mediated by body size. Specifically, threat increases more
269 rapidly with body size among sedentary compared to partially migratory species (figure 4b). Another key
270 predictor was clutch size, which was inversely related to the incidence of threat. Although not supported as a
271 main effect in the full multivariate model (figure 3), we detected a significant interaction between clutch size
272 and range size, indicating that large clutch size increases threat among species with restricted geographic
273 distributions but reduces threat among large-ranged species (figure 4a).

274 In contrast to migratory behaviour, some behavioural traits were unrelated to threat, regardless of
275 whether they were considered in isolation or in the full multivariate model. In particular, we found no
276 support for an effect of nest placement (figure 4k) or breeding system (figure 4h) in our models (figure 2, table
277 1). In other cases, threat exhibited significant associations with behaviour, but with effects that varied
278 depending on whether we accounted for other putative drivers of extinction risk (table S2). When tested in
279 isolation, weakly territorial species are less likely to be threatened than non-territorial species but this effect of
280 territoriality is not supported in the full multivariate model accounting for other predictors of threat (figure 2,
281 4j). Conversely, when tested in isolation, we found no effect of mating behaviour on threat (figure 3b, Table
282 S2), while in the full multivariate model, the likelihood of threat is significantly higher among polygamous
283 than monogamous species (figure 2, 4g). This suggests that polygamy may enhance the risk of extinction but
284 that its effects are masked due to covariation with other factors that decrease threat. Indeed, polygamous
285 species have smaller body size on average than monogamous species, potentially explaining why the effect of
286 mating behaviour is only evident in a multivariate model including body size (figure S3b).

287 Models including or excluding foraging behaviour received almost equal support (figure 2), but an
288 effect of foraging behaviour was nevertheless statistically significant (table S2). The incidence of threat is
289 relatively high in species using aquatic plunging and diving behaviours. In addition, while threatened status

290 is currently low among bark climbing and aerial screening birds, our models show that these foraging
291 strategies may nevertheless promote threat (Figure 4f). In contrast, our models show that threat is lower
292 among foraging generalists suggesting that behavioural niche breadth may buffer species from extinction
293 (figure 4f). In addition to these main effects, we found that threat generally increases with human population
294 density but that within some foraging strategies this relationship was weak or even reversed (figure 4c),
295 suggesting that foraging behaviour may mediate the effects of exposure to higher human population density.

296

297 (c) Behavioural predictors across different threat levels and environments

298

299 Our results suggest that the role of behaviour in predicting threat varies across different thresholds of
300 extinction risk in birds (figure 3). In particular, we found that while migratory behaviour is a core predictor of
301 whether species are threatened or not, it does not predict the level of threat (i.e. whether a species is
302 Vulnerable versus Endangered, Critically endangered or Extinct). As a result, a model excluding all
303 behavioural traits is more strongly supported than a full model incorporating all predictors (table S2). The
304 only behavioural trait that is strongly supported as a predictor of threat level is foraging behaviour (figure 2).
305 Finally, we found that the core predictors of threat and the effects of behaviour varied depending on the
306 environment (figure S1). As with our overall analysis, our models highlighted the primary role of migratory
307 behaviour and weaker effects of foraging and mating behaviour among terrestrial species (figure S4). This is
308 expected given that the majority of all birds are terrestrial. In contrast, foraging strategy was the only
309 behaviour significantly associated with threatened status of aquatic species (figure S5), which was instead
310 primarily driven by range size, human exposure and island dwelling (figure S1).

311

312

313 Discussion

314

315 We have shown that global-scale ecological and behavioural datasets predict variation in IUCN Red List
316 status of birds. Some behavioural traits were only significant predictors when behaviour was analysed
317 independently (e.g. territoriality), becoming non-significant when other core predictors of threat were
318 included in the model. Conversely, other behavioural traits (e.g. mating behaviour) were not significant
319 predictors when tested in isolation, and their effect was only evident when accounting for correlations with
320 factors such as body size, geographical range size and human impacts. These findings are consistent with
321 previous reports that most ecological and behavioural traits have relatively weak associations with
322 conservation status when incorporated into regional or global models as a species-level trait (Lee and Jetz
323 2011, Newbold et al. 2015, Keinath et al. 2017). However, although we find little evidence that the recent
324 expansion of behavioural datasets can revolutionise conservation strategies at these wider scales, our results
325 nonetheless show that behavioural traits act as modifiers that can improve explanatory power in conservation
326 assessments, and thus presumably in other predictive exercises (e.g. range shift modelling).

327 The traits with strongest influence on conservation status were foraging strategy and migration.

328 Although migratory species are less threatened overall than sedentary species, this trend is driven by the
329 larger breeding range size of migratory species and, having accounted for this, we found the migratory
330 behaviour promotes extinction risk. This is expected because migrants are sensitive to human pressures not
331 only in their breeding distribution but also along their migratory routes and in their wintering range
332 (Hardesty-Moore et al 2018). We also show that this effect of migration interacts with body size to determine

333 threat. Specifically, threat increases with body size more rapidly among sedentary compared to partially
334 migratory species, perhaps indicating that poorly dispersing large bodied species are particularly at risk. In
335 the case of foraging, we found that significant relationships between behaviour and conservation status were
336 mainly driven by a subset of strategies. For example, bird species foraging by diving or plunging from air to
337 water are highly threatened and these strategies appear to promote extinction risk. Other foraging strategies
338 that appear to promote threat include aerial screening and bark gleaning but the level of threat is currently
339 lower in these categories. One possibility is that species utilising these foraging strategies have been less
340 exposed to human pressure but this seems unlikely given that we found little or no effect of human
341 population density on threat in these groups (figure 4c). A more likely explanation, therefore, is that there are
342 other as yet unknown traits associated with these foraging strategies that reduce sensitivity. A number of
343 other species-level behaviours, including variation in breeding system, territoriality, and nest placement, had
344 little predictive power in explaining variation in IUCN Red List status regardless of how they were entered
345 into models. This does not necessarily indicate that such factors are unimportant to conservation, as it is well
346 known that they play a role in some contexts (e.g. nest design and placement has important implications for
347 predation risk in modified landscapes; Wilcove 1985). However, our models show that these effects are
348 relatively minor and often overwhelmed by other non-behavioural factors at global scales.

349 Behaviour has proved difficult to integrate into global conservation assessment frameworks,
350 including the IUCN Red List criteria. Our results do not point to any straightforward method of achieving this
351 integration, at least in birds. However, the accuracy of Red List assessments might be improved by using life
352 history and behaviour to scale terms in the criteria which are difficult to assess or define, such as “number of
353 mature individuals”, “future rate of decline” and “severe fragmentation” (IUCN 2001). These factors are
354 typically judged with a considerable degree of inference (see Tobias & Seddon 2002, Tobias & Brightsmith
355 2007). The IUCN Red List Guidelines (IUCN Red List Standards and Petitions Committee 2018) on how to
356 assess parameters such as these could usefully be augmented with further guidance in relation to ecological
357 and behavioural factors such as mating systems, sex ratios, reproductive rate and predation pressure,
358 dispersal ability, gap-crossing ability and ecological specialism. Moreover, for Red List assessors considering
359 what constitutes “severe fragmentation”, future versions of the criteria may be improved with guidelines on
360 how best to account for dispersal ability, gap-crossing ability and ecological specialism.

361

362 (d) Challenges

363

364 Previous case studies have highlighted the many vital contributions behavioural insights can offer
365 conservation, including more broadly when identifying behavioural factors that predict tolerance to
366 environmental change (Tuomainen & Candolin 2011, Sol et al. 2013). However, our findings highlight the key
367 challenge of applying behavioural data over larger spatial and taxonomic scales, namely that behavioural
368 traits can have a major influence in particular species or contexts, yet only reduced effect in global analyses.
369 This occurs for two main reasons. First, behavioural traits are often highly flexible, varying within and
370 between individuals and over time, according to factors such as age, season and context. This makes them
371 relatively difficult to estimate by averaging across entire species or populations. Second, behaviour is often not
372 consistently or independently associated with extinction risk in the same way as, for example, low population
373 size, small geographic range and slow reproductive output (Cardillo 2005, Lee and Jetz 2011).

374 This point can be illustrated by year-round territoriality, a system of resource defence most
375 widespread in tropical birds (Tobias et al. 2016). Intense year-round territorial behaviour can increase the risk

376 of extinction in some contexts, such as mountaintop species driven to extinction through costly agonistic
377 interactions with lower elevation replacements moving upslope in response to climatic warming (Jankowski et
378 al. 2011, Freeman et al. 2018). The costs of territoriality are asymmetric, producing both lower-elevation
379 winners and upper-elevation losers. Moreover, the pattern of non-overlapping elevational ranges for highly
380 territorial species holds largely true for some species pairs and localities (Freeman et al. 2019), but not others
381 (Boyce & Martin 2019), particularly in lowland systems where species do not tend to occupy rare climatic
382 niches or to share parapatric range boundaries with close ecological competitors. Given that the relationship
383 between territoriality and extinction risk is bidirectional and context-dependent, it makes sense that we find
384 no overall link between territoriality and IUCN Red List status.

385 An important viewpoint to bear in mind is that the models presented here treat behaviour as an
386 independent species-level trait whereas the influence of behaviour is often dependent on inter-relationships
387 among species. Staying with the example of territoriality, the key factor is not so much whether a particular
388 species aggressively defends territories year-round, but whether it directly competes with a closely related
389 taxon that does the same. Thus, future versions of global models or associated conservation assessments
390 should consider scoring behavioural interactions rather than behaviour per se. Advancing towards this goal is
391 particularly urgent given that species interactions are sensitive to environmental effects. Both climate and
392 land-use change can potentially influence the behaviour of multiple interacting species, as well as their
393 phenology, physiology and relative abundance, and we ideally need to quantify a range of behavioural
394 interactions and responses to understand how environmental changes affect interaction-based ecosystems
395 (Tylianakis et al., 2008; Meise et al., this issue). Again, the key challenge is that the role of behaviour in
396 heterotrophic systems can be complex and highly flexible (Ness & Bressmer 2005), creating difficulties for
397 multi-species models. Nonetheless, we may improve predictions by incorporating behaviour in more
398 sophisticated ways using interaction-based models, starting at local scales and expanding to larger scale
399 ecological networks when data become available.

400 A related point is that, although we have largely focused on how particular behaviours may influence
401 extinction risk, such factors may yet prove to be less important than behavioural flexibility itself (Sol et al.
402 2016). Individual organisms with the ability to modify their behaviour through adaptability (i.e. plasticity)
403 may be better able to survive when confronted with novel environmental conditions and selection pressures
404 imposed by anthropogenic change. Defining and developing general indices of behavioural flexibility and
405 innovation remains a challenge (Audet & Lefebvre 2017), but may nevertheless be broadly predictable by
406 morphometric traits that are increasingly available at large scales (Sol et al. 2005). For instance, differences in
407 relative brain size across species is positively associated with rates of behavioural innovation in birds, an effect
408 that may explain the apparently greater success of large brained species in colonising and persisting in more
409 unpredictable environments (Sayol et al. 2006, Sol et al. 2008), including cities, the most highly altered of
410 human environments (i.e. the 'cognitive buffer' hypothesis) (Sol et al. 2013).

411 412 (e) Opportunities

413
414 Although they extend the number of behavioural traits compiled across a major global radiation, our analyses
415 are limited by the patchy availability of trait datasets and thus remain highly incomplete (figure 1). A major
416 omission is dispersal behaviour, which we only include as a simple score of migration. Dispersal has long
417 been considered relevant to the conservation of fragmented populations and the optimum design of reserve
418 networks (Caro 1999). However, despite the likely importance of dispersal to understanding biodiversity

419 responses to habitat loss and fragmentation, most broad-scale models (e.g. Newbold et al. 2013, Bregman et al.
420 2014) lack estimates of dispersal behaviour simply because they are generally not available as a standardised
421 organismal trait at macroecological scales. This problem may be addressed by the fast-moving field of
422 movement ecology, with GPS trackers and loggers deployed over increasing numbers of species (Kays et al.
423 2015), and data compilation accelerated by new satellite tracking systems, such
424 as ICARUS (<https://icarusinitiative.org>). Given that it could take decades for these technological innovations
425 to generate comprehensive dispersal estimates across major taxonomic groups, one potential stopgap solution
426 is to use morphometric indices of dispersal or flight ability. Dispersal indices, such as hand-wing index in
427 birds, can be estimated by measuring museum specimens to provide a fuller picture of spatial ecology and
428 movement behaviour across multiple species in macroecological analyses (e.g. Pigot & Tobias 2015) and
429 comparative studies of anthropogenic threats (e.g. Thaxter et al. 2017). Such indices, along with further
430 missing data on factors such as reproductive rate and sensitivity to disturbance (figure 1) should be compiled
431 and applied to conservation assessments at global scales.

432 Another area where behavioural indices may prove useful is ecological forecasting. At present,
433 dispersal is usually ignored in global range shift models, or only included on the basis of crude metrics, such
434 as geographical range size (e.g. Hof *et al.* 2018). Similarly, species interactions are difficult to quantify and,
435 while most range shift forecasting models acknowledge the limitation, they are generally not included in
436 analyses. Future models should explore the possibility of estimating the strength of species interactions using
437 either pairwise morphometric trait divergence or scores of territorial behaviour, both of which have been
438 shown to limit geographical range overlap in pairs of avian sister species (Pigot & Tobias 2013, Freeman et al.
439 2019). Theoretically, suites of behavioural traits and associated morphometric indices can be incorporated into
440 species distribution modelling in much the same way proposed for detailed physiological traits (Chown 2012).

441 The associations we detect between behaviour and conservation status (figure 3) suggest that future
442 research could use similar techniques to identify “threatened behaviours” or suites of behaviours. Using
443 global analyses to look beyond species conservation and instead to identify behaviours that are rare or
444 declining might be a useful step towards targeting conservation action towards maintaining behavioural trait
445 diversity. Similarly, the completion of rich behavioural trait datasets for entire taxonomic groups would pave
446 the way towards multi-dimensional community-based analyses of behavioural diversity (BD) metrics,
447 adopting methods from the functional diversity (FD) literature (Petchey & Gaston 2002, Villéger et al. 2008).
448 Setting strategic conservation priorities based on rare behaviours or BD may have important implications for
449 ecosystem function, particularly when focusing on behavioural traits linked to key ecological processes, such
450 as trophic interactions (pollination, seed dispersal, etc.). In addition, there are opportunities for including
451 behaviours in models designed to pinpoint likely future shifts in conservation status by estimating latent
452 extinction risk (Cardillo et al. 2006). The way these models work is to predict threat status for any taxon based
453 on a wide range of attributes and then compare predictions with their observed threat status, thus flagging up
454 any species currently ‘flying under the radar’ (i.e. likely more threatened, and thus a higher conservation
455 priority, than indicated by their current conservation status).

456 (f) Conclusions

457
458
459 Over recent years, there have been repeated calls for behavioural ecologists to increase their focus on
460 conservation, not least because their study organisms are being driven to extinction by anthropogenic change
461 (Caro & Sherman 2011). Previous authors have suggested that bridging the gulf between these fields might be

462 achieved by applying the experimental or mechanistic approaches predominant in behavioural ecology to
463 conservation research (Linklater 2004), or else returning to more descriptive forms of behavioural ecology
464 potentially relevant to conservation (Caro 2007). However, neither of these approaches are exactly suited to
465 the needs of global conservation assessments which call for simple standardised classifications of basic
466 behavioural traits at ambitious scales, including natural history observations and morphometric
467 measurements. Our analyses show how global behavioural classifications are now within reach for some
468 major taxa, highlighting the need for continued sampling of basic descriptive information for massive samples
469 of species and pointing the way forward to a deeper integration of the resultant datasets into conservation
470 assessments at the scale of clades, communities and ecosystems.

471

472 Additional Information

473 **Data Accessibility**

474 Most datasets used in the analyses are openly available in published sources cited in the methods. Where we
475 have used primary data these are provided in the Supplementary Material.

476

477 **Authors' Contributions**

478 J.A.T and A.L.P developed the concepts and compiled data; A.L.P conducted analyses and produced figures;
479 J.A.T wrote the manuscript with substantial input from A.L.P.

480

481 **Competing Interests**

482 We have no competing interests.

483

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485

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492 References

493 Anthony LL, Blumstein DT. 2000. Integrating behaviour into wildlife conservation: The multiple ways that
494 behaviour can reduce N_c . *Biol. Conserv.* **95**, 303–315.

495

496 Audet JN, Lefebvre L. 2017. What's flexible in behavioral flexibility? *Behavioral Ecology* **28**, 943–947,
497 doi:10.1093/beheco/arx007

498

499 Barton K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
500 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)

501
502 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of*
503 *Statistical Software* **67**, 1–48. [doi:10.18637/jss.v067.i01](https://doi.org/10.18637/jss.v067.i01)
504
505 Bennett PM, Owens IPF. 1997. Variation in extinction risk among birds: Chance or evolutionary
506 predisposition? *Proc. R. Soc. B* **264**, 401–408, doi:10.1098/rspb.1997.0057
507
508 Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. 2011. Integrating animal behavior and conservation
509 biology: a conceptual framework. *Behav. Ecol.* **22**, 236–239.
510
511 Berger-Tal O et al. 2015 A systematic survey of the integration of animal behavior into conservation. *Conserv.*
512 *Biol.* **30**, 744–753.
513
514 Birdlife International, 2012. *Bird species distribution maps of the world. Version 2.0*. Cambridge,
515 UK Arlington, Texas: BirdLife International/NatureServe.
516
517 Boyce AJ, Martin TE, 2019. Interspecific aggression among parapatric and sympatric songbirds on a tropical
518 elevational gradient. *Behav. Ecol.* Online Early <https://doi.org/10.1093/beheco/ary194>
519
520 Brakes P et al. 2019 Animal cultures matter for conservation. *Science* **363**, 1032–1034.
521
522 Bregman TP, Sekercioglu CH, Tobias JA. 2014 Global patterns and predictors of bird species responses to
523 forest fragmentation: Implications for ecosystem function and conservation. *Biol. Conserv.* **169**, 372–383.
524
525 Bregman TP, Lees AC, Seddon N, MacGregor HEA, Darski B, Aleixo A, Bonsall MB, Tobias JA. 2015 Species
526 interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology*
527 **96**, 2692–2704.
528
529 Bueno AS, Dantas SM, Henriques LMP, Peres CA. 2018. Ecological traits modulate bird species responses to
530 forest fragmentation in an Amazonian anthropogenic archipelago. *Divers. Distrib.* **24**, 387–402.
531
532 Butchart SHM, Stattersfield AJ, Bennun LA, Akcakaya HR, Baillie JEM, Stuart SN, Hilton-Taylor C, Mace GM.
533 2005 Using Red List indices to measure progress towards the 2010 target and beyond. *Phil. Trans. R. Soc. B*
534 **1454**, 255–268.
535
536 Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM. 2004. Human population density and
537 extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.
538
539 Cardillo M *et al.* 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241,
540 doi:10.1126/science.1116030
541
542 Cardillo M, Mace GM, Gittleman JL, Purvis A. 2006. Latent extinction risk and the future battlegrounds of
543 mammal conservation. *Proc. Natl. Acad. Sci. USA* **103**, 4157–4161.

544
545 Caro T. 1999. The behavior-conservation interface. *Trends Ecol. Evol.* **14**, 366–369.
546
547 Caro T. 2007. Behavior and conservation: a bridge too far? *Trends Ecol. Evol.* **22**, 394–400.
548
549 Caro T, Sherman PW. 2011. Endangered species and a threatened discipline: Behavioural ecology. *Trends Ecol.*
550 *Evol.* **26**, 111–118.
551
552 Chown SL. 2012. Trait-based approaches to conservation physiology: forecasting environmental change risks
553 from the bottom up. *Phil. Trans. R. Soc. B* **367**, 1615–1627.
554
555 Clemmons JR, Buchholtz R. 1997. Behavioral Approaches to Conservation in the Wild. Cambridge University
556 Press, Cambridge.
557
558 Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017. Sexual selection, speciation, and constraints on
559 geographical range overlap in birds. *Ecol. Lett.* **20**, 863–871.
560
561 Dale J, Dey CJ, Delhey K, Kempnaers B, Valcu M. 2015. The effects of life history and sexual selection on male
562 and female plumage colouration. *Nature* **527**, 367–370.
563
564 Davies RG et al. 2006. Human impacts and the global distribution of extinction risk. *Proc. R. Soc. B* **273**, 2127–
565 2133.
566
567 Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JR, Gruber B, Lafourcade B, Leitão PJ,
568 Münkemüller T, McClean C, Osborne P, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S. 2013.
569 Collinearity: a review of methods to deal with it and a simulation study evaluating their performance.
570 *Ecography*, **36**, 27–46
571
572 Early R, Sax DF. 2011. Analysis of climate paths reveals potential limitations on species range shifts. *Ecol. Lett.*
573 **14**, 1125–1133.
574
575 Felice RN, Tobias JA, Pigot AL, Goswami A. 2019. Dietary niche and the evolution of cranial morphology in
576 birds. *Proc. R. Soc. B* **286**, 20182677.
577
578 Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018. Climate change causes upslope shifts and
579 mountaintop extirpations in a tropical bird community. *Proc Nat Acad Sci USA* **115**, 11982–11987
580
581 Freeman BG, Tobias JA, Schluter D. 2019. Behavior influences range limits and patterns of coexistence across
582 an elevational gradient in tropical bird diversity. *bioRxiv* **2019**, 528950.
583
584 Greggor AL et al. 2015. Research priorities from animal behaviour for maximising conservation progress.
585 *Trends Ecol. Evol.* **31**, 953–964.
586

587 Grether GF, Peiman KS, Tobias JA, Robinson BW. (2017) Causes and consequences of behavioral interference
588 between species. *Trends Ecol. Evol.* **32**, 760–772.
589

590 Hardesty-Moore M, Deinet S, Freeman R, Titcomb GC., Dillon EM, Stears K, Klope M, Bui A, Orr D, Young
591 HS, Miller-ter KA, Hughey LF, McCauley DJ. 2018. Migration in the Anthropocene: how collective navigation,
592 environmental system and taxonomy shape the vulnerability of migratory species *Phil. Trans. R. Soc. B.* **373**,
593 1746.
594

595 Hochkirch A, Groning J, Bucker A. 2007. Sympatry with the devil: reproductive interference could hamper
596 species coexistence. *J. Anim. Ecol.* **76**, 633–642.
597

598 Ho, LST, Ane, C. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models.
599 *Systematic Biology* **63**, 397–408.
600

601 Hof C, Voskamp A, Biber MF, Böhning-Gaese C, Engelhardt EK, Niamira A, Willis SG, Hickler T. 2018.
602 Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate
603 diversity. *Proc. Natl. Acad. Sci. USA* **115**, 13294–13299.
604

605 Howard C, Stephens PA, Tobias JA, Sheard C, Butchart SHM, Willis SG, 2018. Flight range, fuel load, and the
606 impact of climate change on the journeys of migrant birds. *Proc. R. Soc. B* **285**: 20172329.
607

608 IUCN, 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN,
609 Gland, Switzerland and Cambridge, UK.
610 <http://app.iucn.org/webfiles/doc/SSC/RedList/redlistcatsenglish.pdf>.
611

612 IUCN 2016. The IUCN Red List of Threatened Species. Version 2016-2 <http://www.iucnredlist.org>.
613 Downloaded on 15 July 2016.
614

615 IUCN Red List Standards and Petitions Committee 2018. Red List Guidelines.
616 <https://www.iucnredlist.org/resources/redlistguidelines>
617

618 Jankowski JE, Robinson SK, Levey DJ, 2010. Squeezed at the top: Interspecific aggression may constrain
619 elevational ranges in tropical birds. *Ecology* **91**, 1877–1884.
620

621 Jetz W, Freckleton RP, 2015. Towards a general framework for predicting threat status of data-deficient species
622 from phylogenetic, spatial and environmental information. *Phil Trans R Soc B* **370**, 20140016.
623

624 Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative
625 breeding in birds. *Curr. Biol.* **21**, 1–7.
626

627 Jetz W, Sekercioglu CH, Bohning-Gaese K, 2008. The worldwide variation in avian clutch size across species
628 and space. *PLoS Biol.* **6**, 2650–2657.
629

630 Kays R, Crofoot MC, Jetz W, Wikelski M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science*
631 **348**, aaa2478.

632

633 Keinath DA et al. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. *Glob.*
634 *Ecol. Biogeog.* **26**, 115–127.

635

636 Kokko H, Brooks R, 2003. Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fennici* **40**,
637 207–219.

638

639 Lee T. & Jetz, W. 2011 Unravelling the structure of species extinction risk for predictive conservation science.
640 *Proc. R. Soc. B* **278**, 1329–1338.

641

642 Lees AC, Peres CA, 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments.
643 *Oikos* **118**, 280–290.

644

645 Linklater WL, 2004. Wanted for conservation research: Behavioral ecologists with a broader perspective.
646 *Bioscience* **54**: 352–360.

647

648 Manne L, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands.
649 *Nature* **399**, 258–261.

650

651 Nakagawa S, Schielzeth HA, 2013. A general and simple method for obtaining R² from generalized linear
652 mixed-effects models. *Methods Ecol Evol* **4**, 133–142, doi:10.1111/j.2041-210x.2012.00261.x.

653

654 Nelson XJ, 2014 Animal behavior can inform conservation policy, we just need to get on with the job – or can
655 it? *Curr. Zool.* **60**, 479–485.

656

657 Ness, JH, Bressmer, K, 2005. Abiotic influences on the behaviour of rodents, ants, and plants affect an ant-seed
658 mutualism. *Ecoscience* **12**, 76–81.

659

660 Newbold T, Scharlemann JPW, Butchart SHM, Sekercioglu CH, Alkemade R, Booth H, Purves DW. 2013.
661 Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc R Soc B* **280**,
662 20122131.

663

664 Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50.

665

666 Owens IPF, Bennett PM, 2000. Ecological basis of extinction risk in birds: Habitat loss versus human
667 persecution and introduced predators. *Proc. Natl. Acad. Sci. USA* **97**, 12144–12148, doi:DOI
668 10.1073/pnas.200223397

669

670 Petchey OL, Gaston, KJ. 2002. Functional diversity (FD), species richness and community composition. *Ecol.*
671 *Lett.* **5**, 402–411.

672

673 Pigot A, Tobias JA, 2013. Species interactions constrain geographic range expansion over evolutionary
674 time. *Ecol. Lett.* **63**, 330–338.
675

676 Pigot A, Tobias JA. 2015. Dispersal and the transition to sympatry in vertebrates. *Proc. R. Soc. B* **282**, 20141929.
677

678 Pigot A, Trisos CH, Tobias JA, 2016. Functional traits reveal the expansion and packing of ecological niche
679 space underlying an elevational diversity gradient in passerine birds. *Proc. R. Soc. B* **283**, 20152013.
680

681 Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M, Brooks TM 2006. The value of the IUCN Red List for
682 conservation. *Trends Ecol. Evol.* **21**, 72–76.
683

684 Santini L et al., 2019. Applying habitat and population density models to land cover time series to inform
685 IUCN Red List assessments. *Conserv. Biol.* doi.org/10.1111/cobi.13279.
686

687 F Sayol, J Maspons, O Lapiedra, AN Iwaniuk, T Székely, D Sol (2016) Environmental variation and the
688 evolution of large brains in birds. *Nature Communications* **7**, 13971.
689

690 Scharlemann JPW, Balmford A, Green RE, 2005. The level of threat to restricted-range bird species can be
691 predicted from mapped data on land use and human population. *Biol. Conserv.* **123**, 317–326.
692

693 Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005 Big brains, enhanced cognition, and response of
694 birds to novel environments. *Proc. Natl Acad. Sci. USA* **102**, 5460–5465. (doi:10.1073/pnas.0408145102)
695

696 Sol D, Bacher S, Reader SM, Lefebvre L. 2008. Brain size predicts the success of mammal species introduced
697 into novel environments. *Amer. Nat.* **172**, S63–S71.
698

699 Sol D, Lapiedra O, Gonzalez-Lagos C. 2013. Behavioural adjustments for a life in the city. *Anim. Behav.*, **85**,
700 1101–1112.
701

702 Sol D, Sayol F, Ducatez S, Lefebvre L. 2016. The life-history basis of behavioural innovations. *Phil. Trans. R.*
703 *Soc. B* **371**, 20150187.
704

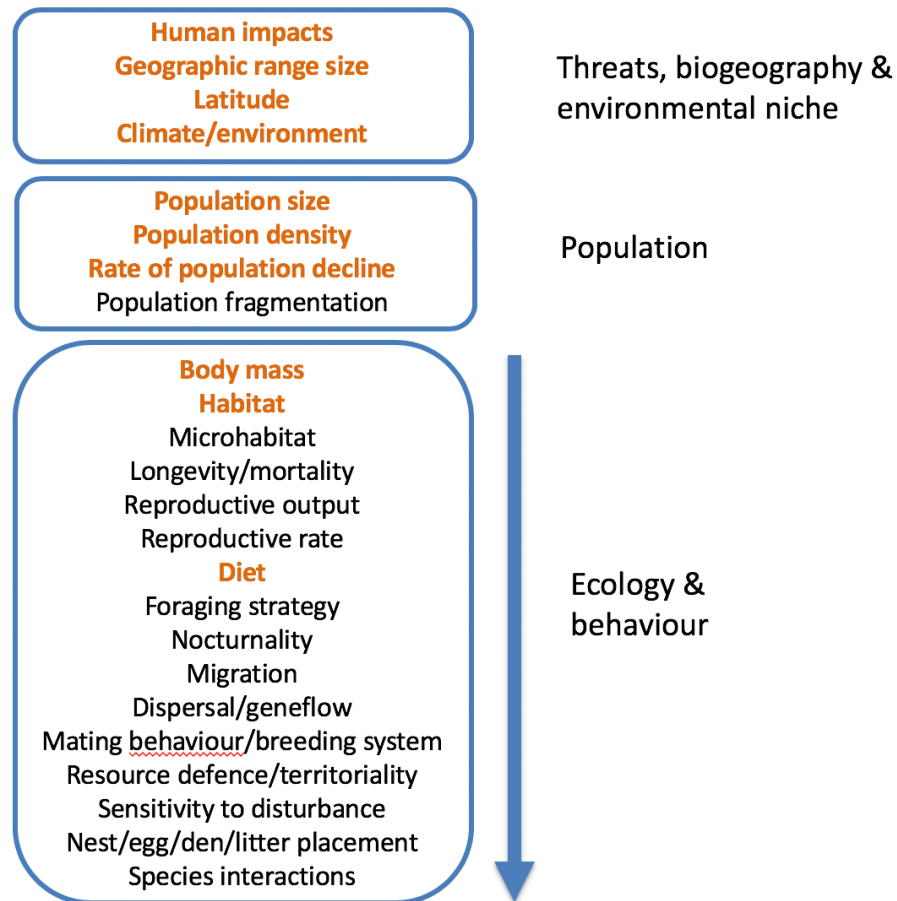
705 Stoddard MC, Yong EH, Akkaynak D, Sheard C, Tobias JA, Mahadevan L. 2017. Avian egg shape: form,
706 function and evolution. *Science* **356**, 1249–1254.
707

708 Thaxter CB et al. (2017) Bird and bat species' global vulnerability to collision mortality at wind farms revealed
709 through a trait-based assessment. *Proc. R. Soc. B* **284**, 20170829.
710

711 Tobias JA, Seddon N, 2002. Estimating population size in the Subdesert Mesite: new methods and implications
712 for conservation. *Biol. Conserv.* **108**, 199–212.
713

714 Tobias JA, Brightsmith D, 2007. Distribution, ecology and conservation status of the Blue-headed Macaw
715 *Primolius couloni*. *Biol. Conserv.* **139**, 126–138.

716
717 Tobias JA, Sheard C, Seddon N, Meade A, Cotton AJ, Nakagawa S, 2016. Territoriality, social bonds, and the
718 evolution of communal signaling in birds. *Frontiers Ecol. Evol.* **4**, 74.
719
720 Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced environmental change. *Biol. Rev.*
721 **86**, 640–657.
722
723 Tylianakis JM, Didham RK, Bascompte J, Wardle DA, 2008. Global change and species interactions in
724 terrestrial ecosystems. *Ecol. Lett.* **11**: 1351–1363.
725
726 Ulrich W, Banks-Leite C, De Coster G, Habel JC, Matheve H, Newmark WD, Tobias, JA, Lens, L 2017.
727 Environmentally and behaviourally mediated co-occurrence of functional traits in bird communities of
728 tropical forest fragments. *Oikos* **127**, 274–284.
729
730 Villéger S, Mason NWH, Mouillot D. 2008. New multidimensional functional diversity indices for a
731 multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.
732
733 Wilcove DS. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**, 1211–
734 1214.
735
736 Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W, 2014. EltonTraits 1.0: Species-level
737 foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027.
738
739



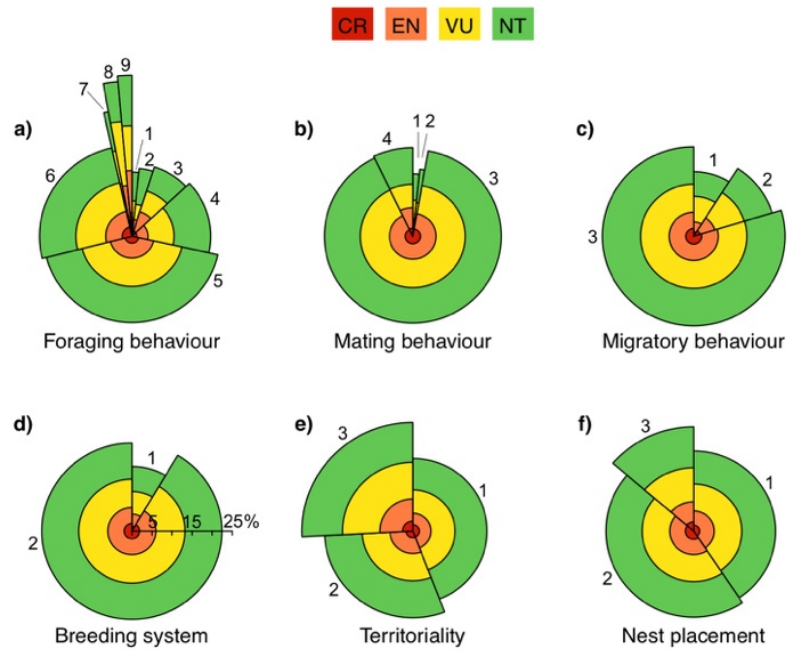
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744 **Figure 1.** Extrinsic and intrinsic factors associated with extinction risk or conservation status at global scales.
 745 Extrinsic factors include anthropogenic threats to species and the biogeographic and environmental context;
 746 intrinsic factors include population and ecological niche dimensions. This diagram summarises the types of
 747 traits that are either available or desirable when constructing models of conservation risk at macroecological
 748 (continental or global) scales; numerous additional factors may impinge on conservation assessments in
 749 particular clades or species. Red text indicates datasets currently available for all species in well studied
 750 groups like birds. Availability of data is currently biased towards environmental, biogeographical and
 751 population attributes, whereas data tend to be unavailable, uncertain or sparse for most ecological variables,
 752 and absent for behavioural variables.

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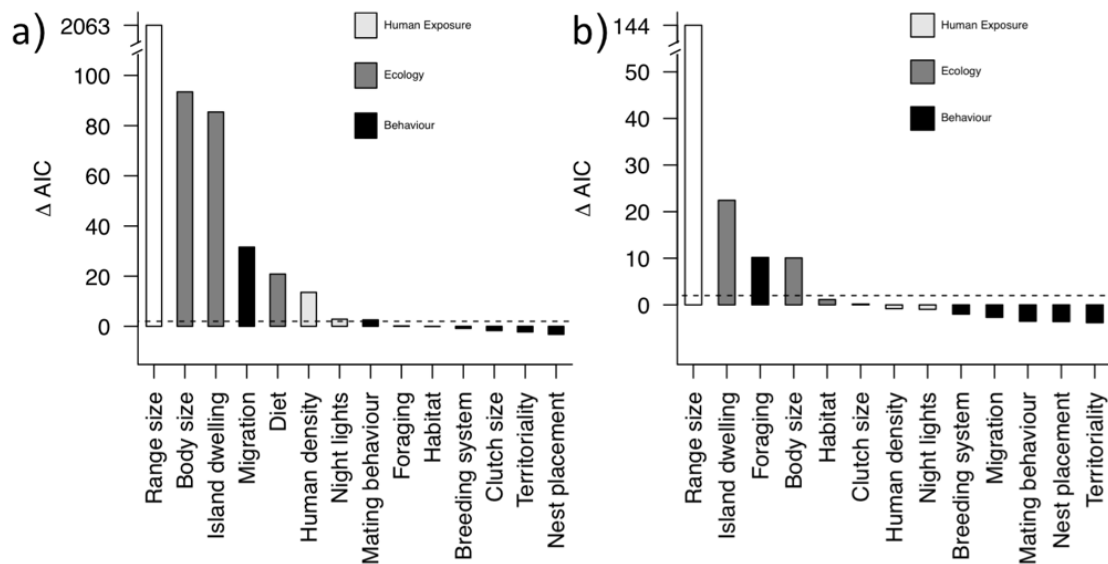
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758 **Figure 2.** The percentage of threatened species in different behavioural categories: a) Foraging behaviour (1
 759 Foraging generalist, 2 Bark gleaning, 3 Aerial screening, 4 Aerial sallying, 5 Arboreal gleaning, 6 Ground
 760 foraging, 7 Aquatic plunge, 8 Aquatic dive, 9 Aquatic surface); b) Mating behaviour (1 Monogamy with
 761 infrequent polygyny, 2 Monogamy with frequent polygyny, 3 Monogamy, 4 Polygyny), c) Migratory
 762 behaviour (1 Migrant, 2 Partial or short-distance migrant, 3 Sedentary); d) Breeding system (1 Cooperative, 2
 763 Non-cooperative); e) Territoriality (1 Weak, 2 Strong, 3 None); f) Nest placement (1 Cavity, 2 Exposed
 764 elevated, 3 Exposed ground). The width of each segment indicates the proportion of all species (n = 9576) in
 765 each behavioural category. Segment heights indicate the % of species threatened in each category. Colours
 766 indicate threat level (Critically endangered [CR], Endangered [EN], Vulnerable [VU] and Near Threatened
 767 [NT]).

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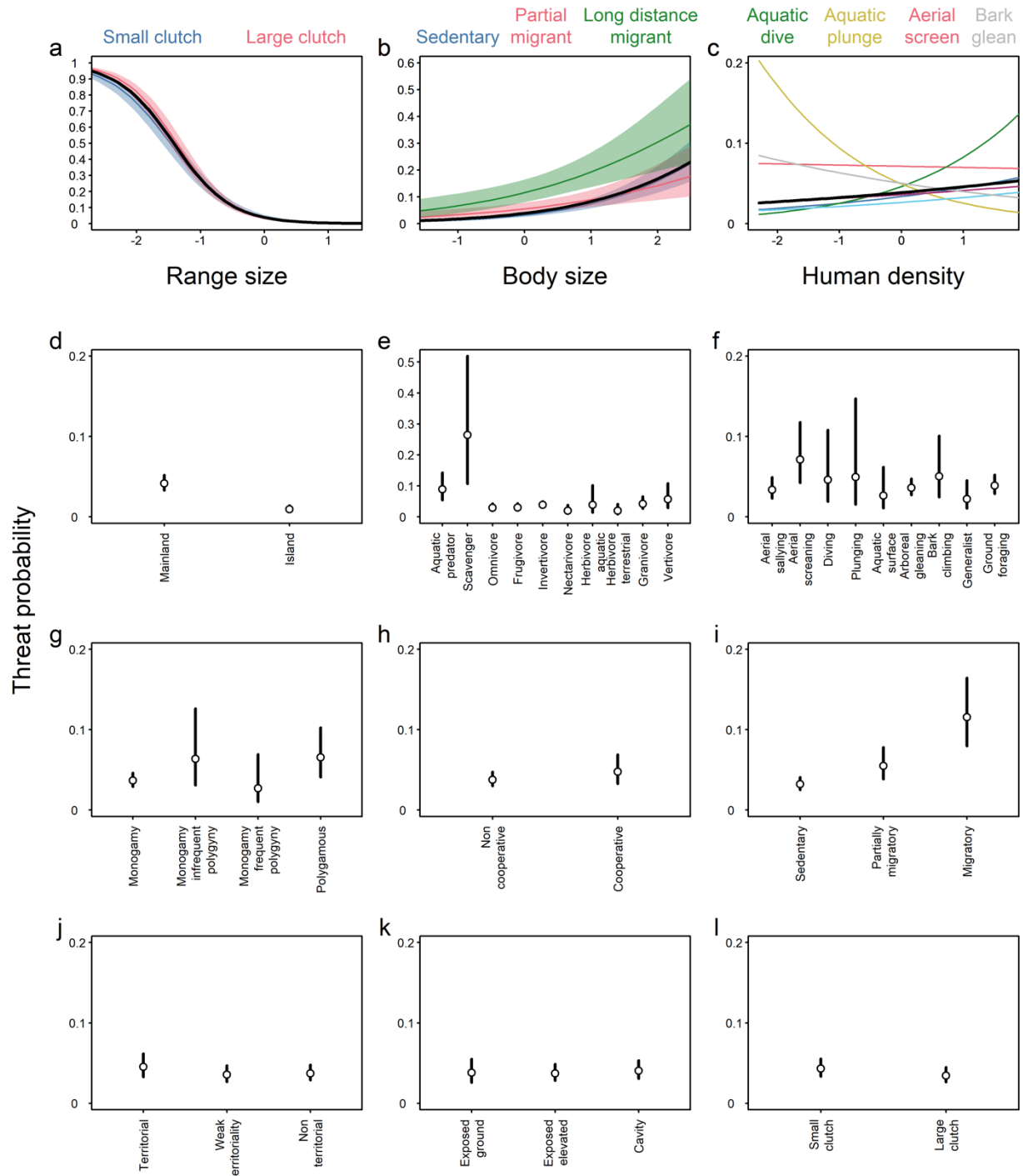
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Figure 3. The relative contribution of anthropogenic, ecological and behavioural predictors to explaining a) threat across all birds (n = 9658) and b) level of threat (i.e. Vulnerable versus Endangered, Critically Endangered or Extinct) among threatened species (n = 1251). The contribution of each predictor is quantified as the difference in AIC between the full model and a model excluding each variable. Predictors are shaded according to variable type. The dashed line indicates a difference of two AIC units indicating strong support for predictor inclusion.



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Figure 4. The influence of behaviour on levels of threat across the world's birds ($n = 9658$). a) Effects of range size mediated by clutch size, b) effects of body size mediated by migratory behaviour, c) effects of human population density mediated by foraging behaviour, d) island dwelling, e) diet, f) foraging behaviour, g) mating behaviour, h) breeding system, i) migratory behaviour, j) territoriality, k) nest placement and l) clutch size. Results are from a generalized linear mixed effects model including all predictor variables and family as a random effect. Clutch size is a continuous variable but is here shown as a binary trait (small or large clutch size) to illustrate the interaction with range size (a). Bars indicate the 95% prediction interval.