

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 far 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 classification for >9500 bird species, we show that the incidence of threat can vary substantially across different behavioural syndromes, and that some types of behaviour—including particular foraging, mating and migration strategies—are significantly more threatened than others. When all factors are included in a combined model, behavioural traits have a weaker effect than well-established geographical and ecological factors, including range size, body mass and human population pressures. We also show that the association between behavior and extinction risk is partly driven by correlations with these underlying factors. 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 forward to a deeper integration of behaviour into quantitative conservation assessments.

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34 1. Introduction

35

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

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

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

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

77 Red List status have generally focused on standard biogeographic or climatic variables, without delving far
78 into behavioural or ecological factors. Indeed, the only ecological and behavioural traits incorporated into
79 most global models of conservation risk are body mass, diet and habitat preferences (Lee & Jetz 2011;
80 Newbold et al. 2015, Keinath et al. 2017). To convert these variables into species-level traits, body mass is
81 typically averaged from small numbers of published estimates, while diet and habitat are classified into broad
82 categories on the basis of published descriptions in secondary literature (Wilman et al. 2014). By contrast, the
83 availability of many other behavioural or ecological variables is highly patchy at global scales, and limited by
84 the difficulty of converting into species-level traits (figure 1).

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

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

111 To assess whether recent progress in data availability can pave the way for behavioral perspectives to
112 be explicitly included in global conservation strategies, we compiled information on a variety of ecological
113 and behavioural traits for all bird species, including estimates of sexual selection (Dale et al. 2015; Cooney et
114 al. 2017), breeding system (Jetz & Rubenstein 2011), foraging strategy (Pigot et al. 2016, Felice et al. 2019),
115 territorial behaviour (Tobias et al. 2016), and nest placement (Stoddard et al. 2017). We then ran multivariate
116 models to evaluate the extent to which behaviour predicts IUCN Red List status at macroecological scales and
117 in relation to a range of standard biogeographical and environmental variables. Our goal is to assess the
118 current landscape of behavioural data availability and the prospects for more nuanced conservation
119 assessments and priority-setting.

120

121 2. Methods

122

123 (a) Data

124

125 We assembled data on species threat status from the 2016 Red List (IUCN 2016) along with a range of
126 potential drivers of variation in status, including biogeographic, ecological and behavioural traits, as well as
127 the exposure of each species to human impacts. Geographic range size is consistently identified as the
128 strongest predictor of threat status (Lee & Jetz 2011; Jetz & Freckleton 2015). We estimated range size for each
129 species based on expert opinion extent of occurrence maps of species breeding distributions (BirdLife
130 International, 2012). Human population pressure is also known to influence extinction risk (Cardillo et al.
131 2004; Scharlemann et al. 2005; Davies et al. 2006). To quantify the exposure of species to human impacts, we
132 first extracted polygon range maps onto an equal area grid (resolution of 110 km \approx 1° at the equator) and used
133 this grid to sample human population density, human appropriation of net primary productivity and night-
134 time light intensity, an indicator of urbanisation and development. We calculated the mean value of each
135 metric, averaged across all grid cells overlapping with each species range.

136 We collated data on a selection of ecological traits, including mean species body mass (g), habitat type,
137 diet and island dwelling, all of which have been linked to extinction risk (Bennett & Owens 1997; Owens &
138 Bennett 2000; Cardillo et al. 2005; Lee & Jetz 2011; Jetz & Freckleton 2015). We assigned species to one of ten
139 dietary categories: aquatic animals, aquatic plants, terrestrial invertebrates, terrestrial vertebrates, terrestrial
140 carrion, nectar, seeds, fruit, other terrestrial plant matter (e.g. leaves) and omnivore, based on the dominant
141 resource present in their diet (see Supplementary material). Data on proportional resource use were first
142 obtained from Wilman et al. (2014), and then modified and updated based on comprehensive literature
143 searches. Our dietary classification differs from Wilman et al. (2014) in that we subdivided each animal or
144 plant-based resource type into separate aquatic and terrestrial categories (see Felice et al. 2019). This helps us
145 to avoid highly heterogeneous categories such as invertivores, which spans a wide variety of species from
146 insectivorous warblers to squid-eating albatrosses and crustacean-eating flamingos (Wilman et al. 2014). Our
147 approach separates warblers (diet: "terrestrial invertebrates") into a different category from albatrosses and
148 flamingos (diet: "aquatic animals"). Using literature to score habitat use, we assigned species to broad habitat
149 categories (coastal, terrestrial, freshwater, sea) according to the predominant habitat utilised across their
150 geographic distribution. We included habitat type as a predictor in our main models but also used this
151 variable along with a measure of forest dependency (obtained from BirdLife International:
152 <http://datazone.birdlife.org/home>) to subset our data and perform additional analysis focusing on terrestrial
153 species (n = 8433) or those with medium to high forest dependency (n = 5646). 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 km²). 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. Following the method described by Felice et al. (2019), we used
160 literature searches to assign species to one of seven foraging strategies. We classified each species according to
161 the predominant behavioural strategy used to acquire resources, and assigned species utilising multiple
162 foraging strategies as generalists (see Supplementary material). Nest placement was scored into a simple

163 three-way system: ground, elevated or cavity (see Stoddard et al. 2017 for details). We used a binary score of
164 breeding system based on a published classification of cooperative and noncooperative breeders (Jetz &
165 Rubenstein 2011). Mating behaviour was scored as strict monogamy, monogamy with infrequent (<5% males)
166 polygyny, monogamy with frequent (5-20% males) polygyny, and polygamy (>20% males and females). These
167 categories are based on the index of sexual selection developed by Dale et al. (2015). Clutch size data was
168 based on Jetz et al. (2008). Using data from Tobias et al. (2016), we assigned all species to three categories
169 according to the degree of territoriality: 'strong' (territories maintained throughout year), 'weak' (weak or
170 seasonal territoriality, including species with broadly overlapping home ranges or habitually joining mixed
171 species flocks), and 'none' (never territorial or at most defending very small areas around nest sites). Finally,
172 we assigned the migratory behaviour of species as either sedentary, partially migratory (minority of
173 population migrates long distance or most individuals migrate short distances) and migratory (majority of
174 population undertakes long-distance migration) (Tobias et al. 2016).

175 Most variables were available for the vast majority (i.e.>99%) of species but the identity of species
176 with missing values differed across variables. For categorical predictors, we imputed missing values using the
177 modal class for each genus, if the genus contained at least 2 species and the modal class was present across at
178 least 75% of species. If these conditions were not met, we used the same criteria to either impute missing
179 values at the family level. After removing all species with any missing values, our final dataset included $n =$
180 9576 species.

181

182 (b) Statistical analysis

183

184 To model the effects of each predictor variable on extinction risk, we treated threat as a binary variable (0, 1)
185 according to the IUCN Red List categories. All species listed as Vulnerable, Endangered, Critically
186 Endangered, Extinct (including Extinct in the Wild) were classified as Threatened; the remainder (Near
187 Threatened, Least Concern and Data Deficient) were classified as non-Threatened. We modelled threat using a
188 generalised linear mixed effects model, with a binomial error structure and including taxonomic family as a
189 random effect to control for the phylogenetic non-independence of species when identifying predictors of
190 threat. Predictor variables exhibiting right skew were log transformed prior to analysis.

191 In contrast to previous assessments of the predictors of extinction risk in birds (e.g. Lee & Jetz 2011),
192 we are particularly interested in how behaviour and its covariation with other putative drivers of extinction
193 risk alter the incidence of threat. First, to assess the overall association between each predictor and threat, we
194 fitted a series of single predictor (i.e. univariate) models. Second, we generated a series of multivariate models
195 and calculated relative model fit according the Akaike Information Criterion (AIC). We assessed the relative
196 importance of each behavioural trait relative to other predictors by excluding each variable in turn from the
197 full model and calculating the difference in AIC (delta AIC). We then assessed the overall contribution of
198 behavioural traits in predicting threat by calculating the AIC and r^2 of a full model including all predictor
199 variables, and comparing with a model excluding behavioural traits. Finally, we also calculated the AIC and r^2
200 of a model including only behavioural traits.

201 When comparing univariate and multivariate models, we were particularly interested in testing how
202 covariation between behavioural traits and ecological, geographical or socio-economic variables may modify
203 the association between threat and behaviour. We identify three possible scenarios. First, when behaviour is
204 weakly related to threat, we may nevertheless find strong variation in the incidence of threat across
205 behavioural categories because of differences in other factors that drive variation in threat (i.e. ecology,

206 geography or human impacts), an example of an ‘enhanced’ effect. Second, the opposite pattern may emerge,
207 if behaviour has a significant effect on threat, but this effect is ‘masked’ by countervailing effects of ecological,
208 geographical or human impacts. Finally, the apparent effect of a given behaviour on threat could even be
209 ‘reversed’, when taking into account covariation with other factors.

210 To examine how the definition of threat may influence the predictors of extinction risk, we repeated
211 our analysis considering only threatened species ($n = 1216$), predicting lower (0 [Vulnerable]) or higher (1
212 [Endangered, Critically Endangered, Extinct]) levels of threat. To assess how the predictors of threat may
213 change across broad habitat types, we repeated our analysis on different subsets of our data including all
214 species ($n = 9576$), terrestrial species ($n = 8433$) and forest dependent species ($n = 5646$).

215

216 Results

217

218 Our results identified a number of core predictors of threat status that align closely with previous assessments
219 indicating that threat arises as a combination of geography, ecology and human impacts (Fig. 2). Specifically,
220 the strongest predictor of threat status is geographical range size, with additional strong effects of body mass,
221 island dwelling and the mean human population density across the species geographic range, a metric of
222 exposure to human impact. In both univariate and multivariate models, the incidence of threat decreases with
223 geographic range size and increases with body size (Table S1). When tested in isolation, the incidence of threat
224 is higher on islands than on the mainland and in areas of low human population density (Table S1). However,
225 in the full multivariate model, these effects are reversed, with a higher incidence of threat in areas of greater
226 human population density, but a lower incidence of threat on islands (Table S1, see also Manne et al 1999).
227 In addition to these core predictors, we also identified an effect of behaviour on extinction risk. A multivariate
228 model including behavioural traits alone explains 7% of the variance in threat status. A full multivariate
229 model including all predictors is significantly better supported than one excluding behavioural traits (delta
230 AIC = 36) although the improvement in explanatory power is small (R^2 excluding versus including behaviour
231 = 0.49 versus 0.51 respectively). Behavioural traits receiving strong support for inclusion in the full
232 multivariate model (delta AIC >2) were mating behaviour (monogamous or polygamous mating) and
233 migration (Fig. 2). Behavioural traits receiving weak or no support for inclusion in the model (delta AIC <2)
234 were foraging mode, breeding system, territoriality, nest placement and clutch size. The effects of behaviour
235 were similar regardless of whether we conducted our analysis across all birds, only terrestrial species (Fig.
236 S1a) or those restricted to forests (Fig. S1b). This is perhaps not surprising, given that forest dependent species
237 comprise more than half of all birds. We note, however, that the role of behaviour in predicting threat does
238 depend on the way in which threat is defined. Specifically, while behaviour is a significant predictor of
239 whether a species is threatened or not (delta AIC = 36), it does not predict the level of threat (i.e. whether a
240 species is Vulnerable versus Endangered, Critically endangered or Extinct) (delta AIC = -15, Fig. S2).

241 Some behavioural traits were unrelated to threat, regardless of whether they were considered in
242 isolation or in the full multivariate model. In particular, we found no effect of nest placement or breeding
243 system in our models (Fig. 3, Table S1). In other cases, threat exhibited significant associations with behaviour,
244 but with effects that varied depending on whether we accounted for other putative drivers of extinction risk
245 (Fig. 3a, Table S1). In the case of foraging behaviour, we find that the incidence of threat varies substantially
246 across foraging categories. For instance, >30% species that feed either by diving or by aerial attacks in aquatic
247 habitats are threatened compared to <10% species that are foraging generalists or bark probing specialists in
248 terrestrial habitats (Fig. 3a). However, our full multivariate model shows that most of this variation in the

249 incidence of threat is driven by covariation between foraging behaviours, ecological traits and exposure to
250 human impacts (Fig. 4). In particular, species feeding at sea and with large body size are more threatened than
251 land-based and small bodied species (Fig. S3). Having accounted for these confounding variables, only species
252 feeding by aerial attacks in aquatic habitats have significantly higher levels of threat (i.e. an example of an
253 'enhanced' effect) (Fig. 4, Table S1). A similar effect was also found for clutch size (Table S1). While the
254 incidence of threat declines with increasing clutch size, this association is not significantly supported when
255 accounting for confounding variables in the full multivariate model (Table S1).

256 Mating behaviour provides a possible example of a 'masking' effect. When tested in isolation, we
257 found that polygamous species are no more likely to be threatened than monogamous species (Fig. 3b, Table
258 S1). However, after accounting for the confounding effects of other predictors in the full multivariate model,
259 we found that the probability of being threatened is significantly higher among polygamous than
260 monogamous species (Fig. 4, Table S1). This effect of mating behaviour is masked when considered in
261 isolation because polygamous species on average have a smaller body size than monogamous species, and this
262 smaller body size nullifies the effect of mating behaviour on threat (Fig. S3). This suggests that polygamy may
263 enhance the risk of extinction but that its effects may have been masked due to covariation with other factors
264 that decrease extinction risk.

265 In a univariate model, we found that proportionately fewer migrants are threatened compared to
266 partial migrants or sedentary species (Fig. 3c, Table S1). This may suggest that migration, or perhaps
267 associated greater vagility, buffers species from extinction. However, in our full model we found the opposite
268 effect of migration on the likelihood of being threatened, whereby migrants are more likely to be threatened
269 than sedentary species (Fig. 4). These contrasting findings arise because migratory tendency is strongly
270 correlated with range size, with migrants have larger breeding ranges on average than sedentary species (Fig.
271 S3), and thus a lower incidence of threat. However, having statistically accounted for the negative effects of
272 range size on threat, migrants are more likely to be threatened than sedentary species (Fig. 4, Table S1). This
273 suggests that undertaking long distance migration makes species more at risk of extinction but that this is
274 unable to overcome the effects of other covarying factors that instead lead to a higher prevalence of threat
275 among sedentary species (i.e. an example of a 'reversed' effect).

276 277 **Discussion**

278
279 We have shown that global-scale ecological and behavioural datasets predict variation in IUCN Red List
280 status of birds, but that these relationships are largely explained by underlying correlations with well-
281 established macroecological variables. Some behavioural traits were only significant predictors when
282 behaviour was analysed independently, becoming non-significant when correlations with factors such as body
283 size, geographical range size and human impacts were included. Conversely, other behavioural traits were not
284 significant predictors in behaviour-only models, and their effect was only evident when socio-economic and
285 biogeographic variables were included. These findings are consistent with previous reports that most
286 ecological and behavioural traits have relatively weak associations with conservation status when
287 incorporated into regional or global models as a species-level trait (Lee and Jetz 2011, Newbold et al. 2015,
288 Keinath et al. 2017). However, although we find little evidence that the recent expansion of behavioural
289 datasets can contribute substantially to refining conservation strategies at these wider scales, our results also
290 show that behavioural traits act as modifiers that can improve explanatory power in conservation assessments
291 and other predictive exercises.

292 The traits with strongest influence on conservation status were foraging strategy, mating behaviour
293 and migration. Even in these cases, we found that significant relationships between behaviour and
294 conservation status were only detected for certain strategies. For example, bird species foraging by diving
295 from air to water were significantly more threatened than otherwise predicted. Moreover, a number of
296 species-level behaviours, including variation in breeding system, territoriality, and nest placement, had little
297 predictive power in explaining variation in IUCN Red List status regardless of how they were entered into
298 models. This does not necessarily indicate that such factors are unimportant to conservation, as it is well
299 known that they play a role in some contexts (e.g. nest design and placement has important implications for
300 predation risk in modified landscapes; Wilcove 1985). However, our models show that these effects are minor
301 and often overwhelmed by other non-behavioural factors at global scales.

302 These results do not support the integration of behaviour into global conservation assessment
303 frameworks, including the IUCN Red List criteria. However, the accuracy of Red List assessments might be
304 improved by using life history and behaviour to scale terms in the criteria which are difficult to assess or
305 define, such as “number of mature individuals” and “future rate of decline” (IUCN 2001). These factors are
306 typically judged with a large dose of guesswork (see Tobias & Seddon 2002, Tobias & Brightsmith 2007).
307 Guidelines on how to scale judgements in relation to ecological and behavioural factors such as mating
308 systems, sex ratios, reproductive rate and predation pressure could be useful in fine-tuning predictions of
309 “number of mature individuals” and “future rate of decline”. Moreover, for Red List assessors considering
310 what constitutes “severe fragmentation”, future versions of the criteria may be improved with guidelines on
311 how best to account for dispersal ability, gap-crossing ability and ecological specialism.

312
313 (a) Challenges

314
315 Our findings highlight one of the key challenges of applying behavioural data over larger spatial and
316 taxonomic scales, namely that behavioural traits can have a major influence in particular species or contexts,
317 yet only reduced effect in global analyses. This occurs for two main reasons. First, behavioural traits are
318 inherently flexible within and between individuals and therefore poorly represented by averaging across
319 entire species or populations. Second, behaviour is often not consistently or independently associated with
320 extinction risk in the same way as, for example, low population size, small geographic range and slow
321 reproductive output (Cardillo 2005, Lee and Jetz 2011).

322 This point can be illustrated by year-round territoriality, a system of resource defence most
323 widespread in tropical birds (Tobias et al. 2016). Intense year-round territorial behaviour can increase the risk
324 of extinction in some contexts, such as mountaintop species driven to extinction through costly agonistic
325 interactions with lower elevation replacements moving upslope in response to climatic warming (Jankowski et
326 al. 2011, Freeman et al. 2018). The costs of territoriality are asymmetric, producing both lower-elevation
327 winners and upper-elevation losers. Moreover, the pattern of non-overlapping elevational ranges for highly
328 territorial species holds largely true for some species pairs and localities (Freeman et al. 2019), but not others
329 (Boyce & Martin 2019), particularly in lowland systems where species do not tend to occupy rare climatic
330 niches or to share parapatric range boundaries with close ecological competitors. Given that the relationship
331 between territoriality and extinction risk is bidirectional and context-dependent, it makes sense that we find
332 no overall link between territoriality and IUCN Red List status.

333 An important viewpoint to bear in mind is that the models presented here treat behaviour as an
334 independent species-level trait whereas the influence of behaviour is often dependent on inter-relationships

335 among species. Staying with the example of territoriality, the key factor is not so much whether a particular
336 species aggressively defends territories year-round, but whether it directly competes with a closely related
337 taxon that does the same. Thus, future versions of global models or associated conservation assessments
338 should consider scoring behavioural interactions rather than behaviour per se. Advancing towards this goal is
339 particularly urgent given that species interactions are sensitive to environmental effects. Both climate and
340 land-use change can potentially influence the behavior of multiple interacting species, as well as their
341 phenology, physiology and relative abundance, and we ideally need to quantify a range of behavioural
342 interactions and responses to understand how environmental changes affect interaction-based ecosystems
343 (Tylianakis et al., 2008). Again, the key challenge is that the role of behavior in heterotrophic systems can be
344 complex and highly flexible (Ness & Bressmer 2005), creating difficulties for multi-species models.
345 Nonetheless, we may improve predictions by incorporating behaviour in more sophisticated ways using
346 interaction-based models, starting at local scales and expanding to larger scale ecological networks when data
347 become available.

348 A related point is that, although we have largely focused on how particular behaviours may influence
349 extinction risk, such factors may yet prove to be less important than behavioural flexibility itself (Sol et al.
350 2016). Individual organisms with the ability to modify their behaviour through adaptability (i.e. plasticity)
351 may be better able to survive when confronted with novel environmental conditions and selection pressures
352 imposed by anthropogenic change. Defining and developing general indices of behavioural flexibility and
353 innovation remains a challenge (Audet & Lefebvre 2017), but may nevertheless be broadly predictable by
354 morphometric traits that are increasingly available at large scales (Sol et al. 2005). For instance, differences in
355 relative brain size across species is positively associated with rates of behavioural innovation in birds, an effect
356 that may explain the apparently greater success of large brained species in colonising and persisting in more
357 unpredictable environments (Sayol et al. 2006, Sol et al. 2008), including cities, the most highly altered of
358 human environments (i.e. the ‘cognitive buffer’ hypothesis) (Sol et al. 2013).

359 360 (b) Opportunities

361
362 Although they extend the number of behavioural traits compiled across a major global radiation, our analyses
363 are limited by the patchy availability of trait datasets and thus remain highly incomplete (figure 1). A major
364 omission is dispersal behaviour, which we only include as a simple score of migration. Dispersal has long
365 been considered relevant to the conservation of fragmented populations and the optimum design of reserve
366 networks (Caro 1999). However, despite the likely importance of dispersal to understanding biodiversity
367 responses to habitat loss and fragmentation, most broad-scale models (e.g. Newbold et al. 2013, Bregman et al.
368 2014) lack estimates of dispersal behaviour simply because they are generally not available as a standardised
369 organismal trait at macroecological scales. This problem may be addressed by the fast-moving field of
370 movement ecology, with GPS trackers and loggers deployed over increasing numbers of species (Kays et al.
371 2015), and data compilation accelerated by new satellite tracking systems, such
372 as ICARUS (<https://icarusinitiative.org>). Given that it could take decades for these technological innovations
373 to generate comprehensive dispersal estimates across major taxonomic groups, one potential stopgap solution
374 is to use morphometric indices of dispersal or flight ability. Dispersal indices, such as hand-wing index in
375 birds, can be estimated by measuring museum specimens to provide a fuller picture of spatial ecology and
376 movement behaviour across multiple species in macroecological analyses (e.g. Pigot & Tobias 2015) and
377 comparative studies of anthropogenic threats (e.g. Thaxter et al. 2017). Such indices, along with further

378 missing data on factors such as reproductive rate and sensitivity to disturbance (figure 1) should be compiled
379 and applied to conservation assessments at global scales.

380 Another area where behavioural indices may prove useful is ecological forecasting. At present,
381 dispersal is usually ignored in global range shift models, or only included on the basis of extremely crude
382 metrics, such as geographical range size (e.g. Hof *et al.* 2018). Similarly, species interactions are difficult to
383 quantify and, while most range shift forecasting models acknowledge the limitation, they are generally not
384 included in analyses. Future models should explore the possibility of estimating the strength of species
385 interactions using either pairwise morphometric trait divergence or scores of territorial behaviour, both of
386 which have been shown to limit geographical range overlap in pairs of avian sister species (Pigot & Tobias
387 2013, Freeman *et al.* 2019). Theoretically, suites of behavioural traits and associated morphometric indices can
388 be incorporated into species distribution modelling in much the same way proposed for detailed physiological
389 traits (Chown 2012).

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

405 406 (c) Conclusions

407
408 Over recent years, there have been repeated calls for behavioural ecologists to increase their focus on
409 conservation, not least because their study organisms are being driven to extinction by anthropogenic change
410 (Caro & Sherman 2011). Previous authors have suggested that bridging the gulf between these fields might be
411 achieved by applying the experimental or mechanistic approaches predominant in behavioural ecology to
412 conservation research (Linklater 2004), or else returning to more descriptive forms of behavioural ecology
413 potentially relevant to conservation (Caro 2007). However, neither of these approaches are exactly suited to
414 the needs of global conservation assessments which call for simple standardised classifications of basic
415 behavioural traits at ambitious scales, including natural history observations and morphometric
416 measurements. Our analyses show how broad-scale behavioural classifications are now within reach for some
417 major taxa, highlighting the need for continued sampling of basic descriptive information for massive samples
418 of species and pointing the way forward to a deeper integration of the resultant datasets into conservation
419 assessments at the scale of clades, communities and ecosystems.

420

421 Additional Information

422 Data Accessibility

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

425

426 Authors' Contributions

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

429

430 Competing Interests

431 We have no competing interests.

432

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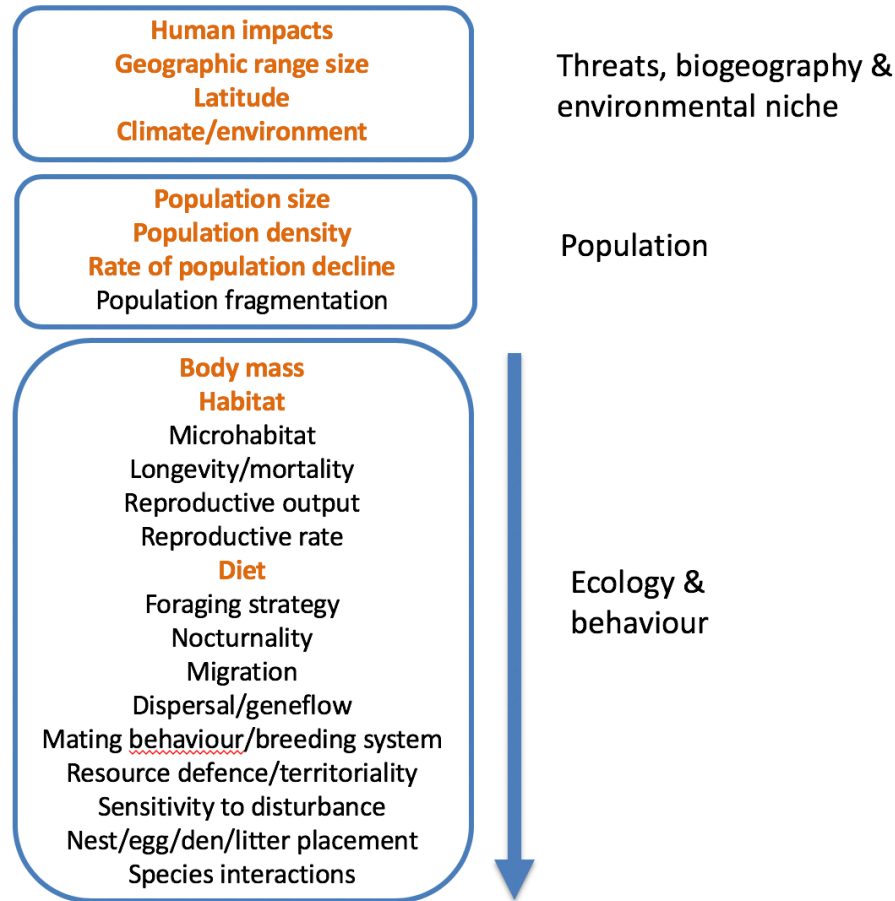
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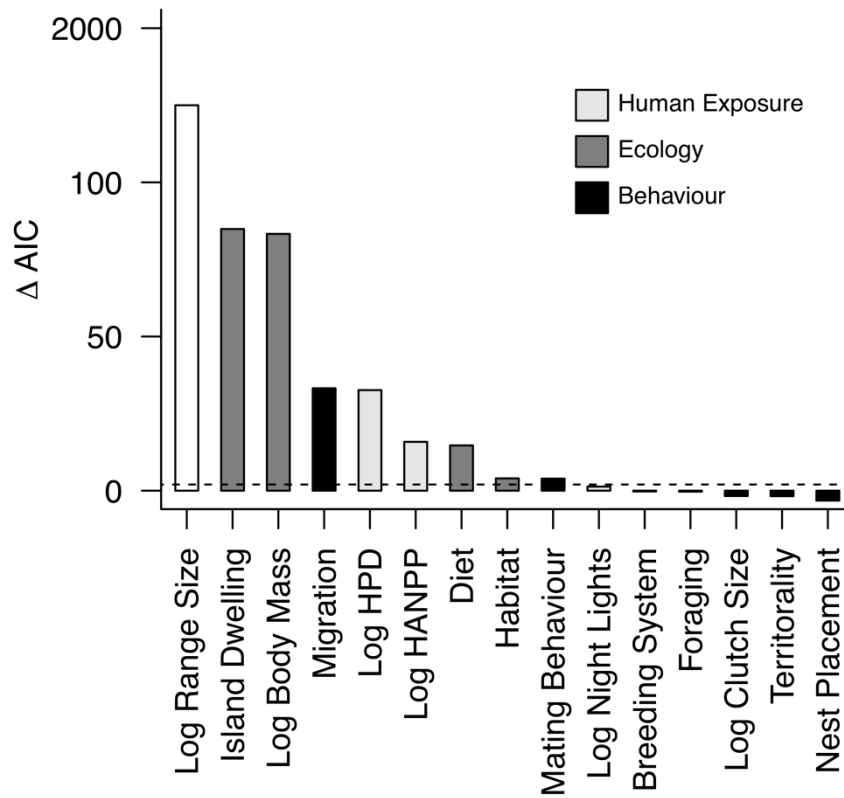
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672 **Figure 1.** Extrinsic and intrinsic factors associated with extinction risk or conservation status at global scales.
673 Extrinsic factors include anthropogenic threats to species and the biogeographic and environmental context;
674 intrinsic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

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686 **Figure 2.** The relative contribution of anthropogenic, ecological and behavioural variables to explaining threat

687 status. Variable contributions are quantified as the difference in AIC between the full model and a model

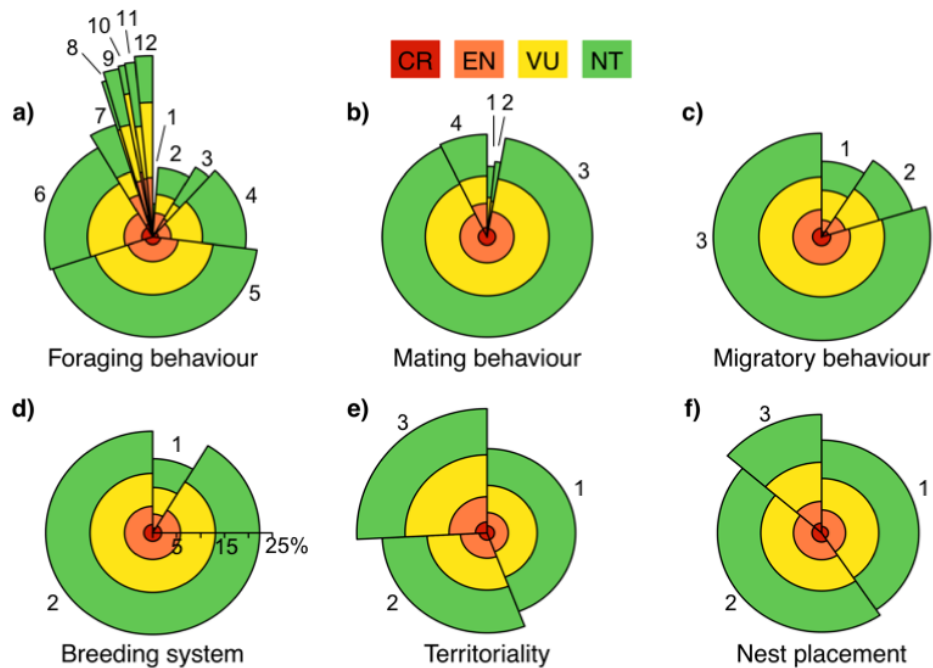
688 excluding each variable. Variables are colored according to variable type. The dashed line indicates a

689 difference of 2 AIC units indicating strong support for variable inclusion.

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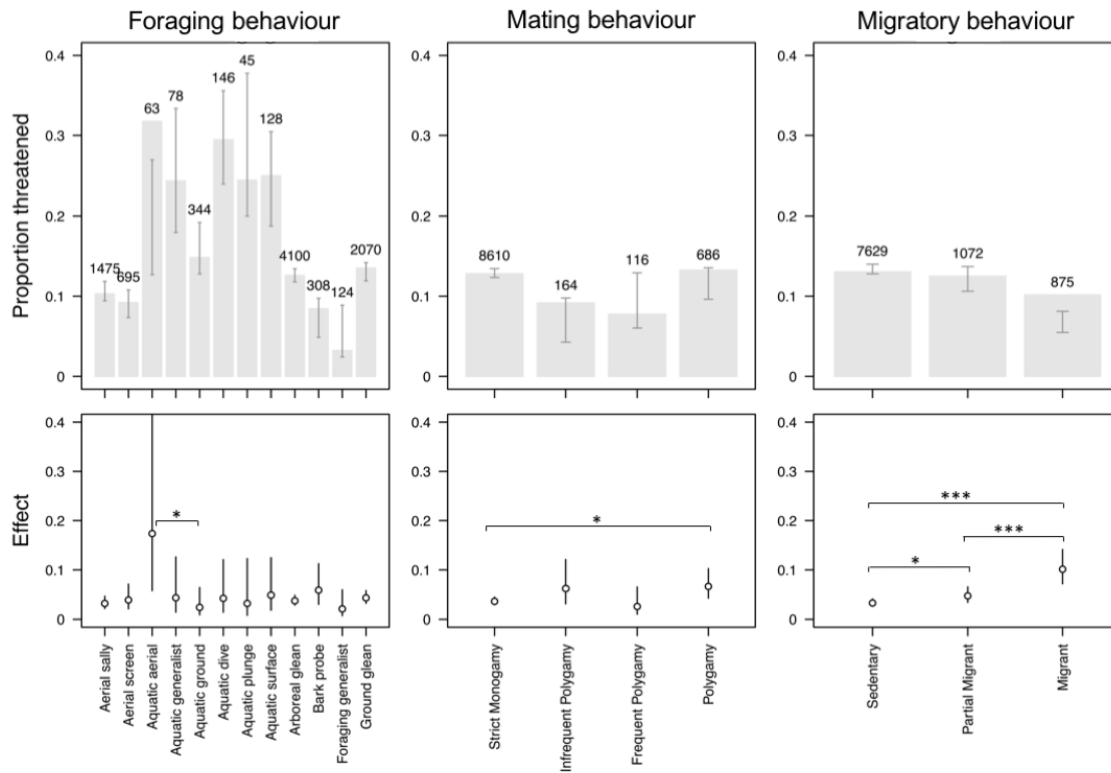
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697 **Figure 3.** The % of threatened species in different behavioural syndromes: a) Foraging behaviour (1 Foraging
 698 generalist, 2 Aerial screen, 3 Bark glean, 4 Aerial sally, 5 Arboreal glean, 6 Ground forage, 7 Aquatic ground, 8
 699 Aquatic plunge, 9 Aquatic surface, 10 Aquatic aerial, 11 Aquatic generalist, 12 Aquatic dive), b) Mating
 700 behaviour (1 Monogamy with infrequent polygyny, 2 Monogamy with frequent polygyny, 3 Monogamy, 4
 701 Polygyny), c) Migratory behaviour (1 Migrant, 2 Partial migrant, 3 Sedentary), d) Breeding system (1
 702 Cooperative, 2 Non-cooperative), e) Territoriality (1 Weak, 2 Strong, 3 None), f) Nest placement (1 Cavity, 2
 703 Exposed elevated, 3 Exposed ground). The width of each segment indicates the proportion of all species (N =
 704 9576) in each behavioural syndrome. Segment heights indicate the % of species that are threatened in each
 705 syndrome. Colours indicate threat level (Critically endangered [CR], Endangered [EN], Vulnerable [VU] and
 706 Near Threatened [NT]).



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Figure 4. Variation in the prevalence of threat across behavioural syndromes. Top row: bars indicate the observed proportion of threatened species for different foraging modes, mating behavioural and migratory strategies. Brackets indicate the expected proportion (95% CI) of species threatened based on all other predictor variables. Numbers indicate the number of species in each category. Bottom row: the estimated effect size of each behavioral category (mean and 95% CI). Significant contrasts are indicated at the $p = 0.05$ (*), $p = 0.01$ (**) and $p = 0.001$ (***) level. Effect sizes and significance was assessed with a generalized linear mixed effects model including all predictor variables and family as a random effect.