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Behavioural plasticity is associated with reduced extinction risk in birds

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Behavioural plasticity is believed to reduce species vulnerability to extinction, yet global evidence supporting this hypothesis is lacking. We address this gap by quantifying the extent to which birds are observed behaving in novel ways to obtain food in the wild; based on a unique dataset of >3,800 novel behaviours, we show that species with a higher propensity to innovate are at a lower risk of global extinction and are more likely to have increasing or stable populations than less innovative birds. These results mainly reflect a higher tolerance of innovative species to habitat destruction, the main threat for birds.

Global species diversity is diminishing rapidly with the expansion of anthropogenic encroachments that alter natural habitats and expose organisms to overexploitation and invasive species[1]. Recent International Union for the Conservation of Nature (IUCN) estimations indicate that 27% of the assessed species are globally threatened, including 13% of all bird species[2]. However, it is increasingly appreciated that most species are threatened not only because they are exposed to new stresses, but also because their biology makes them particularly vulnerable. Among biological predictors of extinction, body size, life history and ecological specialization have emerged as particularly important in vertebrates[3,4]. Behavioural plasticity has also long been considered a potentially important mediator of extinction risk[4–7], yet its general importance remains controversial[8,9].

Behavioural plasticity determines the ability of animals to formulate behavioural responses to cope with new or unusual challenges such as food shortages or extreme climatological events[6]. Behavioural plasticity thus has the potential to enhance population fitness following environmental changes[7,10,11], a mechanism known as the cognitive buffer[12–15]. Growing empirical evidence shows that species who accommodate their behaviour to new contexts are better able to cope with environmental alterations (Fig. 1a). However, to what degree behavioural plasticity buffers species against global extinction risk remains unknown. Given that the mechanisms that put species at risk of extinction are diverse[16], it is not obvious that behavioural plasticity should always increase resilience to extinction. In fact, the observation that some of the most behaviourally plastic animals are highly endangered, including many parrots, primates and cetaceans[2], might suggest that behavioural plasticity is not as important as generally assumed.

A major obstacle to estimating the importance of behavioural plasticity in global extinction risks is the challenge of quantifying the degree of plasticity for a wide array of species. As a result, researchers have shifted their attention to indirect metrics, notably brain size, which has provided contradictory results[17,18]. A more direct measure of behavioural plasticity consists of quantifying the extent to which species are observed behaving in novel ways in the wild (hereafter, innovation propensity). For well-studied animals, such as birds and primates, the exhaustive recording of published field observations documenting novel behaviours has allowed researchers to confirm that the capacity to plastically modify behaviours is one of the main adaptive mechanisms through which animals can solve ecological problems[19,20] and cope with novel environmental pressures[21,22].

We extended this framework to ask whether the propensity of birds to innovate can predict their global risk of extinction. To this purpose, we built a unique database of >3,800 published field observations covering most regions of the world documenting the incorporation of new foods in the diet or the use of novel feeding techniques. We combined this dataset with the IUCN extinction risk classifications[2] to investigate whether innovation propensity predicts global extinction risk, employing Bayesian phylogenetic generalized linear mixed models to control for regional differences in exposure to extinction drivers and species non-independence due to their sharing of common ancestors. As measures of behavioural plasticity, we used two metrics of innovation propensity: innovativeness—a binary variable separating species according to whether or not they have been reported innovating; and innovation rate—the total number of innovations reported per species, excluding species with zero innovation. Our analyses revealed a negative association between innovativeness and the risk of extinction ($n = 8,641$ species; Figs. 1 and 2; Supplementary Tables 1 and 2, models 1.1–1.2). Among species with at least one innovation ($n = 1,248$ species), extinction risk also decreased with innovation rate (Figs. 1 and 2; Supplementary Tables 1 and 2, models 1.3–1.4). These results thus yield support for the hypothesis that behavioural plasticity reduces extinction risk.

Observing a bird using a novel food or a new foraging technique in the wild depends not only on its innovative ability, but also on how likely the behaviour is to be observed and reported. However, we found no evidence that the association between innovativeness and extinction risk was caused by some species being easier to observe or more frequently studied than others (Supplementary Table 2, models 1.1–1.16). The effect of innovativeness on extinction risk was also additive to, and not confounded by, the effects of other correlates of extinction risk such as body size, life history, habitat breadth, diet breadth, migratory behaviour and insularity. Although some species are considered at risk of extinction exclusively because of their small range, excluding these species did not alter the conclusion that behaviourally innovative species are less likely to be at risk of extinction (Supplementary Table 2, models 1.9–1.16).

The IUCN categories evaluate current extinction risk but are less informative about population trends. A species that occurs in many

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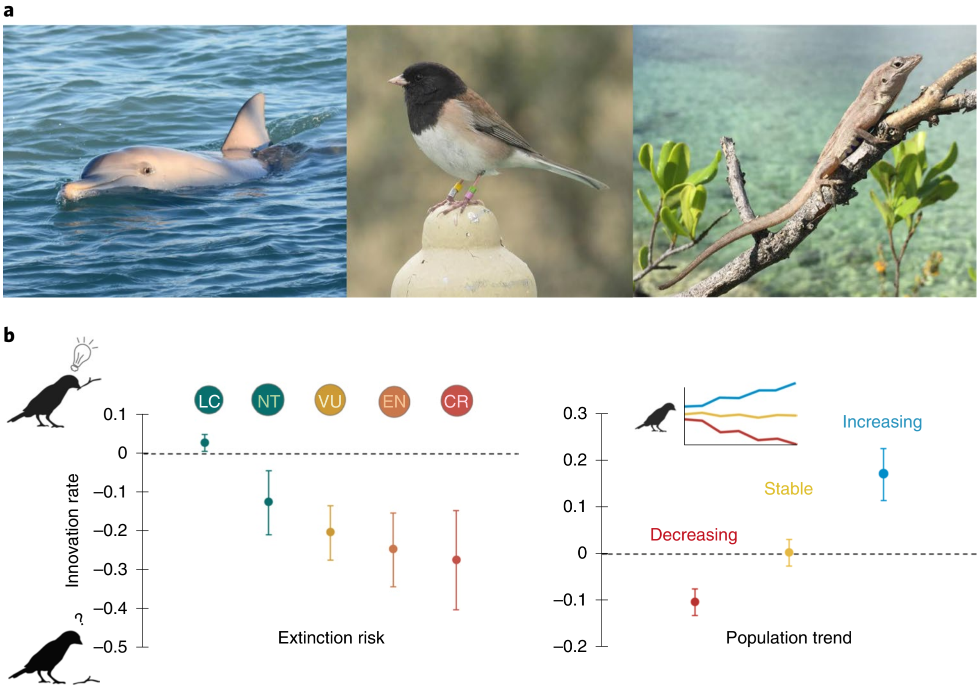

Fig. 1 | Behavioural plasticity is associated with extinction risk. There are several examples of how behavioural plasticity allows coping with environmental changes. **a**, In Shark Bay, Western Australia, bottlenose dolphins (*Tursiops aduncus*) that use sponges as foraging tools were more likely to survive after a heatwave than those that did not use tools[64]. Dark-eyed juncos (*Junco hyemalis*) established in San Diego (California) shifted to off-ground nesting, favouring the persistence of the population in an urban environment[65]. *Anolis sagrei* lizards experimentally translocated to Bahaman islands with predators reduced ground exploration time compared with those from islands without predators, a less risky behaviour that increased fitness and population persistence[66]. Photography credits from left to right: Simon Ducatez, Samuel Bressler, Oriol Lapiedra. **b**, In birds, there are differences in innovation rate (corrected by research effort) between species from the different extinction risk categories (left panel) and population trend categories (right panel). The points show the mean innovation rate of each category and the bars the corresponding 95% confidence interval. LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.

regions or has a large population can be classified as 'Least Concern' even if it is declining globally. Conversely, a species distributed in a small geographic area, or with a small population size, can be classified as 'Endangered' even if its abundance is increasing. To obtain a more complete picture of the effect of behavioural innovation on species decline, we examined the association between innovation propensity and global population trends. This analysis confirmed that innovative species are more likely to exhibit a stable or increasing population trend than non-innovative ones ($n = 8{,}012$ species; Figs. 1 and 2; Supplementary Tables 1 and 2, models 1.17–1.18, 1.21–1.22). Likewise, among species with at least one recorded innovation, increasing population trends were more likely to be found in those with higher innovation rates ($n = 1{,}160$ species; Figs. 1 and 2; Supplementary Tables 1 and 2, models 19–20, 23–24). The results thus confirm that a higher innovation propensity is associated with a lower probability of species decline.

So far, we have assumed that all behavioural innovations in our dataset were functionally equivalent. However, this is unlikely to be true. Some foraging innovations in our dataset described small changes to existing behaviours, such as the incorporation of new foods in a species' diet ('consumer' innovations, hereafter). Other innovations instead involved devising novel searching and handling techniques ('technical' innovations, hereafter), such as the use of tools to open mussels in the white-winged chough (*Corcorax melanorhamphus*)[23]. A priori, a species that is only capable of slight behavioural adjustments may have more trouble coping with drivers of extinction than a species able to devise substantial behavioural changes. However, substantial behavioural changes are cognitively demanding[24] and may incur higher costs (increased searching and handling times, new predators), counterbalancing potential benefits. Testing how consumer and technical innovations affect extinction risk, we did not find substantial differences. Species with at least one innovation—either consumer or technical—had a lower risk of extinction than non-innovative species and were more likely to have increasing or stable populations (Supplementary Tables 1 and 2, models 1.25–1.72; Extended Data Fig. 1). Among innovative species, we could not detect any association between extinction risk and the number of either consumer or technical innovations, but we found clear evidence that populations were less likely to decline as the number of innovations increased, regardless of innovation type (Supplementary Tables 1 and 2, models 1.25–1.72). Both types of innovation therefore have similar, positive effects on species performance, suggesting that the ability to make both minor and more substantial behavioural changes can reduce the risk of extinction.

Different threats drive species towards extinction and behavioural innovation is likely to help species to respond to some but not all of them. The ability to formulate behavioural responses may, for example, help to cope with habitat alterations, but not to respond to direct threats such as overexploitation by humans. We therefore tested the association between innovation propensity and extinction risk as a function of the main drivers of extinction risk[25]. Our analyses indicated that innovation propensity (both innovativeness and innovation rate) decreased the effects of habitat destruction on extinction risk but did not affect sensitivity to invasive species or overexploitation (Supplementary Table 3 and Extended Data Fig. 2). Since our measure of behavioural plasticity is restricted to foraging innovations, this finding could reflect the fact that the adoption of novel foods or foraging techniques affords important benefits

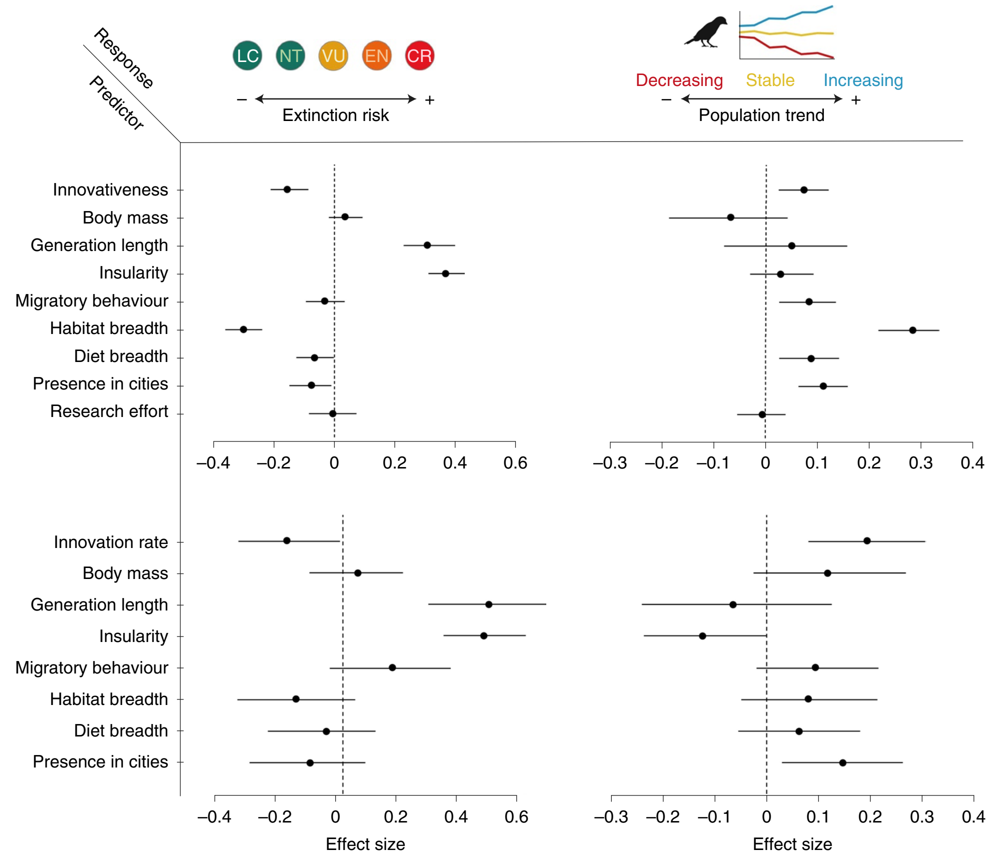

Fig. 2 | Coefficient estimates of models predicting extinction risk and population trends. Coefficient estimates of models considering innovativeness (top panels) or innovation rate (bottom panels) as predictors, while controlling for phylogenetic effects and other potential predictors of extinction risk (for details see Supplementary Table 2). For extinction risk, a negative effect means that the predictor (for example, innovativeness) reduces the risk of extinction, while for population trend, a negative effect means that the predictor increases the probability that the species is declining.

when habitat alteration affects food availability. Instead, foraging innovations can do little to guard against threats like overexploitation. Highly innovative animals typically have slow life histories and should be particularly sensitive to increases in adult mortality[21]. Thus, overexploitation, while not a major cause of extinction for most birds, may disproportionately affect animals that prioritize future over present reproduction even when they exhibit high behavioural plasticity[26–28], such as parrots, primates and cetaceans. Altogether, our results highlight the importance of partitioning overall extinction risk according to different threats[16], contributing to explain past difficulties in empirically linking behavioural plasticity to extinction risk[29].

Our results position behavioural plasticity at the forefront of the arsenal of strategies organisms use to increase their resilience to environmental changes, together with ecological generalism and life history. While we have found that innovativeness is associated with a lower risk of extinction in species exposed to habitat destruction—in line with the cognitive buffer theory[12–14]—it is less clear whether it may also help in other contexts. These findings highlight the need to broaden current theory to better integrate the diverse mechanisms through which organisms may avoid extinction.

Methods

Extinction risk and population trend. The most comprehensive listing of species extinction risk comes from the IUCN, which attributes a category of extinction risk to all 10,965 extant (that is, not extinct or extinct in the wild) bird species, except for 56 data deficient species[2]. The IUCN Red List classification is based on a robust system to evaluate the risk of global species extinction[30,31], and has allowed researchers to identify a range of traits that influence vulnerability[3,16,32–36]. We used the IUCN Red List status[2] as our measure of species extinction risk, excluding extinct, extinct in the wild and data deficient species. We converted the risk categories to an ordinal index ranging from Least Concern (1) to Critically Endangered (5). Because the IUCN classifies some species as threatened based exclusively on their small geographic range, we tested for result consistency by performing analyses on both all species and the subset of species not listed under the small-range criterion (that is, excluding species considered as at risk of extinction under the criterion B). We also considered the population trend as given by the IUCN, converting it into an ordinal index from decreasing to increasing trends (1, decreasing; 2, stable; 3, increasing; excluding species for which the trend was unknown). In addition to the IUCN red list status, which integrates population size, range size and population trend to estimate extinction risk[31], a focus on population trend allowed us to test the effects of specific traits on species decline, independently of population and range sizes.

Innovation data. Our behavioural data were drawn from an expanded and updated version of the innovation database provided in Overington et al.[24,37]. This database was compiled by systematically searching for reports of new behaviours in the short notes of 204 ornithology journals published between 1960 and 2018. The journals include academic serials (for example, *British Birds, Emu, Ibis, The Auk, Wilson Journal of Ornithology*) as well as publications that are edited by local birding organizations (for example, *Florida Field Naturalist, Nebraska Bird Review*) and they cover most areas of the globe except the Philippines, Polynesia, Micronesia and Melanesia. A feeding behaviour was considered an innovation and hence was included in the database, if it was described in the report with key words such as ‘novel’, ‘opportunistic’, ‘first description’, ‘not noted before’, ‘unusual’, and so on[19]. The validity and reliability of this innovation measure has been addressed in previous studies[10,19,38–40]. Examples of innovations included a great egret (*Egretta alba*) predating a common sparrow (*Passer domesticus*) in Brazil[41], a carrion crow (*Corvus corone*) specializing in kleptoparasiting common starlings (*Sturnus vulgaris*) feeding in a dump in Spain[42], a Himalayan griffon (*Gyps himalayensis*), usually a carrion-eater, feeding on pine needles in India[43], yellow-rumped warblers (*Setophaga coronata*) feeding on dormant flies inside a heated milking parlour at a dairy farm during an unseasonably cold weather spell in Saskatchewan[44], or great cormorants (*Phalacrocorax carbo*) timing their fishing strategy with the movement of commercial ferries at a wharf in New Zealand, using the strong currents generated by the propellers to catch confused fish[45]. The 10,391 species occurring in the area covered by the database were then classified into 'innovative' (species for which at least one innovation was recorded) and 'non-innovative' (species with no recorded innovation), a binary variable hereafter called innovativeness. In addition, for species with at least one recorded innovation, the total number of innovations reported was extracted; this discrete variable is referred to as the innovation rate.

Following Overington et al.[24] (see also refs. [21,46–48]), we further distinguished 'consumer' innovations (that is, new behaviours involving slight changes, such as the incorporation of new foods in a species diet) and 'technical' innovations (that is, new behaviours involving substantial changes, such as devising novel searching and handling behaviours). Technical innovations refer to reports where the author describes the searching and handling technique itself as novel, regardless of whether the food type was novel or not (see ref. [24] for details on the classification of innovations).

The number of consumer or technical innovations recorded per species depends not only on the innovative ability of the species, but also on how its environment promotes innovations and how likely these behaviours are to be observed and published[10,38,49,50]. Although the number of innovations reported for a species across different regions was repeatable (intraclass coefficient = 0.36), we used five different approaches to account for these potentially confounding effects. First, we ran some of our analyses only on species that had been observed innovating at least once, thus excluding non-innovative species; this also excludes species that may be considered as non-innovative because their innovations are unlikely to be observed (for example, secretive species)[21,24]. Second, we included geographic region (nine different regions and one category for species occupying two or more regions) as a random effect in all models, as a way to account for geographic differences in the probability of observing or reporting innovations. Third, since species occurring in urban areas are more often observed by ornithologists, and since urban environments may elicit innovative behaviours, we included in all of our models a binary variable that accounts for whether or not a given species occurs in urban areas. Species presence in cities was extracted from the IUCN habitat scheme, attributing a score of 0 (absent in cities) or 1 (present in cities) to each species.

We further controlled for potentially confounding effects by including a measure of research effort in all of our analyses, using the number of papers published on each species between 1978 and 2008 according to the online version of the Zoological Record[51]. Research effort and innovation frequency (either the total number or the number of technical or consumer innovations) were correlated, so we avoided including them as covariables in the same model. Instead, we calculated the residuals of the log–log regressions of the number of innovations (either total, technical or consumer innovations) versus research effort as metrics of innovation rate, technical innovation rate and consumer innovation rate. For models considering innovativeness (either global, technical or consumer innovativeness, binary variables with 0 for species with no recorded innovation and 1 for species with at least one recorded innovation), we included both innovativeness and research effort as covariables. Finally, we ran the analyses again to show that most models yielded consistent results when excluding little studied species (≤ 10 references in Zoological Records).

Covariables. To further investigate the relationship between innovativeness and extinction risk, we also considered a set of ecological and life-history traits that have been found to affect extinction risk, including body mass, generation time, insularity, migratory behaviour, habitat breadth and diet breadth. Previous studies demonstrated the association between innovation propensity and migratory behaviour[52], niche breadth[37,46] and life history[21], underlining the importance of considering these traits in our models. Body mass data were obtained from[53–55]; generation time data were extracted from Birdlife's digital resources on the birds of the world[53]. Species insularity was coded as 0 for mainland species and 1 for insular species, using data from the IUCN[2]. As an index of migratory behaviour, we used data from Birdlife's website[53] and built an ordinal variable, with 1 representing sedentary or nomadic, 2 representing altitudinal migrant and 3 representing long distance migrant. As an index of habitat breadth, we used a recently developed index based on patterns of species co-occurrence within each of the 101 habitat categories recognized by the IUCN[56]. Briefly, a species was allocated a quantitative score based on the diversity of other taxa with which it co-occurs, such that a generalist species is one that occurs in a range of habitat categories that vary considerably in species composition, whereas a specialist species is found only in habitats that contain a consistent suite of other species[56]. This index has been shown to reliably reflect habitat breadth compared with previously used indices based on subjective numbers of habitat classes[46,56]. To estimate diet breadth, we defined food types using six categories of the classification scheme from[57], as in[37,46]: vertebrate carrion, vertebrate prey, invertebrate prey, nectar or pollen, fruit or seeds and leaves or stems. We measured dietary generalism by counting the number of food categories consumed by adults of each species as noted in ref. [58].

Threats. The IUCN identifies a number of threats to which species can be exposed[59]. We reclassified the threats into three most relevant categories for birds: habitat destruction, overexploitation and invasive species (see Supplementary Table 4). This reclassification allowed us to identify groups of species exposed or not exposed to each of these three main threat categories, and to run models independently on each of these groups. Determining whether a given species is exposed or not to a given threat can be challenging, and the use of binary variables is a simplistic solution that shows some limitations. These variables can, however, be informative, especially for intraclass species comparisons[25], and have the advantage of being available for the entire class Aves.

Phylogeny. To take into account phylogenetic uncertainty in our analyses, we built two maximum clade credibility trees, each based on 10,000 phylogenetic trees from one of the two backbones of the complete phylogeny of birds[60] available at www.birdtree.org. These backbones are those of Ericson and colleagues[61] and Hackett and colleagues[62]. A major difference between these two backbone trees is that they either ignore (Ericson et al.[61]) or include (Hackett et al.[62]) information from the β-fibrinogen. The impact of this β-fibrinogen on higher-level avian relationships is still poorly understood, and studies that include it find that the Neoaves can be split into the Metaves and the Coronaves, whereas the Metaves are not a monophyletic group in studies that exclude it (see supplementary material in ref. [60]). Thus, Jetz et al.[60] used two backbones that considered topological constraints, which either include (Hackett et al.[62]) or exclude (Ericson et al.[61]) β-fibrinogen. For each backbone they then assigned each species to one of 158 clades, and for each clade they generated relaxed-clock trees. They then partially constrained species without genetic information within their clade based on a combination of consensus trees (from the relaxed-clock trees) and taxonomic information. The placement of these species was then consistent with the partial constraints and a pure birth model of diversification. Based on these clade trees, final trees were built by combining clade trees with the time-calibrated relaxed molecular clock backbone trees (see refs. [60–62] for more information on trees construction).

Analyses. For all bird species for which we had information (see sample sizes in Supplementary Table 1), we tested whether extinction risk and population trend were affected by innovativeness or innovation rate by means of phylogenetic generalized linear mixed models with ordinal error structures, using a Bayesian approximation as implemented in the R package MCMCglmm[63]. This approach has proved efficient to model ordinal variables with unbalanced numbers of observations, and also allows the inclusion of the phylogeny in a random Gaussian process to deal with the non-independence of species due to common ancestry[63]. Because threats and innovation rates may vary across regions, but since we were not interested in estimating the effect of each region on the response variables, we modelled geographic region as a random effect to avoid over-parametrization of the models. Body mass, generation time, insularity, migratory behaviour, habitat breadth, diet breadth and presence in cities were included as fixed effects, together with either innovativeness and research effort, or residual innovation rate (correlations between fixed effects were always <0.7). Phylogeny was included as a random effect, and each model was run twice, once per tree. For each model, the Monte Carlo Markov chains were run for 550,001 iterations with a burn-in interval of 50,000 to ensure satisfactory convergence. A total of 1,000 iterations were sampled to estimate parameters for each model. We checked that autocorrelation levels among samples were lower than 0.1. Following Hadfield[63], we fixed the covariance structure and used inverse Wishart priors ($V = 1$, $\nu = 0.002$) for the variances. Explanatory variables were standardized to a mean of 0 and a variance of 1 to obtain comparable coefficients.

We built a total of 72 different models, resulting from first crossing each of the six behavioural innovation metrics (innovativeness, innovation rate, technical innovativeness, technical innovation rate, consumer innovativeness, consumer innovation rate) as predictors with our three measures of endangerment (extinction risk, extinction risk excluding species in which risk is exclusively determined by their small range size and population trend) as response variables. Then, we re-ran all the models excluding species with a research effort of ten or fewer articles. Finally, the 36 resulting models were run considering either the maximum clade credibility tree based on the Ericson backbone or that based on the Hackett backbone. A summary of the innovation metrics effect is presented in Supplementary Table 1, and the entire model outputs are presented in Supplementary Table 2.

To determine whether innovation propensity buffered birds against extinction risk due to some, but not other, threats, we then ran similar models on different subsets of species. Out of the 2,593 bird species exposed to at least one of the three threat categories considered (habitat destruction, overexploitation and invasive species), 1,406 were exposed to two or three threats. Isolating the effect of innovation propensity on the risk of extinction in response to a specific threat was thus not possible directly. Instead, we compared the effect of innovation propensity on extinction risk in species exposed versus in species not exposed to each threat category. We built four models per species subset (two innovation propensity metrics—innovativeness and innovation rate—by two phylogenetic backbones), considering six different subsets (species exposed or not exposed to each of the three threat categories). We used the same covariables and model specifications as detailed above. If innovation propensity mostly limits the effects of a specific threat on extinction risk (for example, habitat destruction), we expected innovation propensity to decrease extinction risk in species exposed to the threat, but not in species that are not exposed to it. In contrast, the effect of innovation propensity on extinction risk should not differ between species exposed versus non-exposed to a threat that is not buffered by innovation propensity.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The dataset used in this study is available from Dryad (https://doi.org/10.5061/dryad.sf7m0cg2k).

Code availability

The R code used in this study is available from Dryad (https://doi.org/10.5061/dryad.sf7m0cg2k).

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Author contributions

S.D. and L.L. initiated the project. L.L. compiled the innovation dataset. S.D., D.S. and F.S. compiled the remaining data. S.D. designed the analyses with the help of D.S. and F.S., and ran the analyses. S.D. wrote a first draft of the manuscript. All authors edited and approved the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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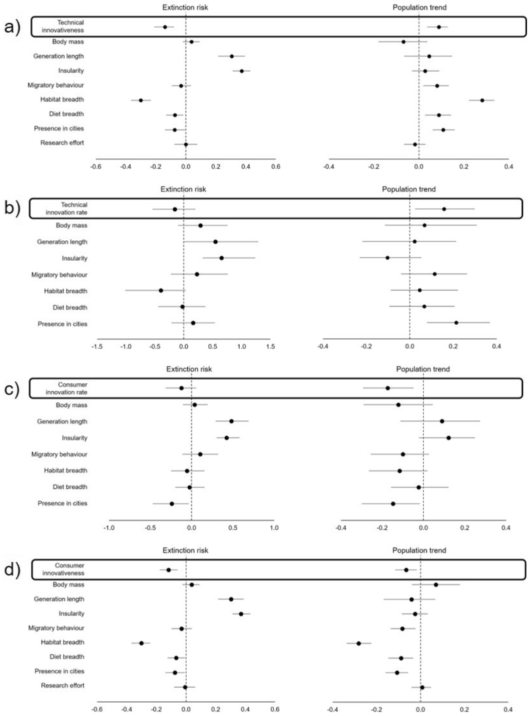
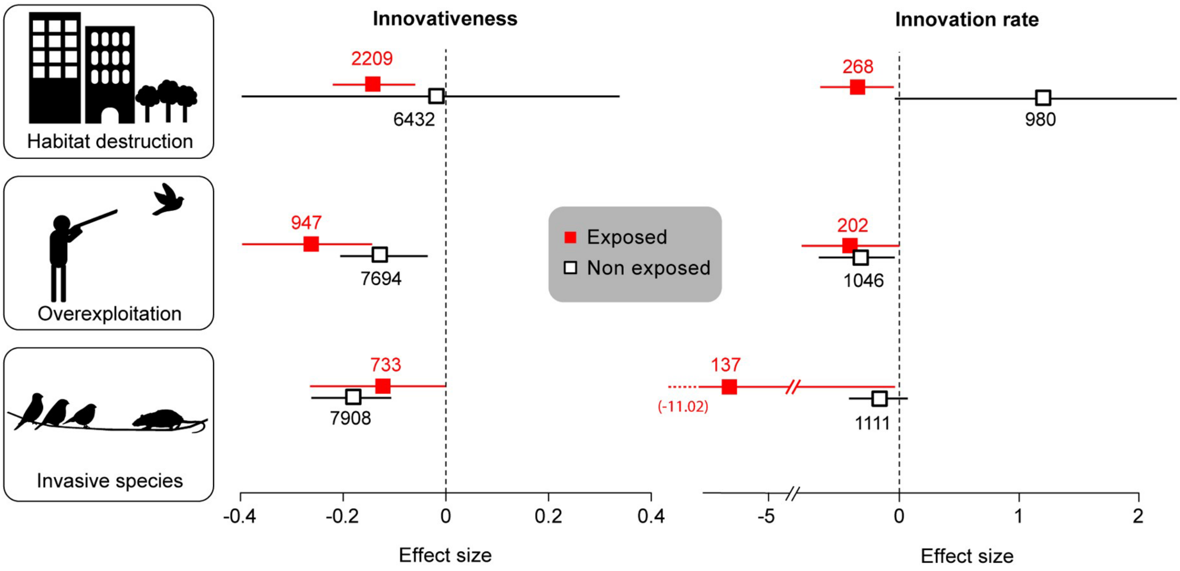


Extended Data Fig. 1 | Effect size of the regression coefficients of technical innovativeness (a), technical innovation rate (b), consumer innovativeness (c) or consumer innovation rate (d) and covariables on bird extinction risk and population trend estimated with Bayesian phylogenetic mixed models. The effect is considered significant when its credibility interval (CI) does not overlap zero. Extinction risk (ordinal, from 1 = LC to 5 = CR) was modelled so that a negative effect of, for example, innovativeness, means that innovative species have a lower risk of extinction, and population trend (ordinal, from 1 = decreasing to 3 = increasing) was modelled so that a positive effect of, for example, innovativeness, means that innovative species are more likely to have increasing populations. All parameters are in the same model which also includes phylogeny and geographic region as random factors. Error bars are the 95% CIs estimated by MCMCglmm.



Extended Data Fig. 2 | Coefficient estimates of models predicting extinction risk as a function of innovativeness (left panel) or innovation rate (right panel) according to the type of threat. Most endangered birds are exposed to more than one threat, making isolating species responses to a specific threat difficult. We therefore compared the effect of innovation propensity on extinction risk in subsets of species exposed vs. not exposed to each threat. If innovation propensity limits the effects of a specific threat on extinction risk, it should decrease extinction risk in species exposed to the threat, but not in species that are not exposed. If innovation propensity does not buffer the effect of a certain threat, its effect on extinction risk should not differ between exposed and non-exposed species. Posterior effect size means, credibility intervals and species numbers are shown.

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Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection
Data analysis	Our code is available from Dryad (https://doi.org/10.5061/dryad.sf7m0cg2k). We used the following software and packages: R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. R package MCMCglmm: Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22 (2010). R package ape: Paradis E. & Schliep K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526-528.

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Ecological, evolutionary & environmental sciences study design

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Study description	We tested whether extinction risk and population trend differed between innovative and non-innovative species, and between innovative species with varying innovation rates, by means of Phylogenetic Generalized Linear Mixed Models (PGLMMs), with a Bayesian approximation as implemented in the R package MCMCglmm. As the response variables were ordinal (IUCN status or population trend), we used models with an ordinal distribution of errors. Body mass, generation time, insularity, migratory behaviour, habitat breadth, diet breadth and presence in cities were included as fixed effects, together with either innovativeness and research effort, or residual innovation rate. Geographic region was included as a random effect. To take into account phylogenetic uncertainty in our analyses, we built two maximum clade credibility (MCC) trees, each based on 10,000 phylogenetic trees from one of the two backbones of the complete phylogeny of birds available at www.birdtree.org. Phylogeny was included as a random effect, and each model was run twice, once per tree. Details on the different datasets on which these models were run are provided in the methods, as well as all details for the specificity of each model (a total of 96 different models were built).
Research sample	The sample covers the entire class Aves, except for species for which data on life history, ecology, extinction risk or population trend were not available. Our maximum sample included 8641 species, though we also conducted analyses on smaller samples depending on the aims of the models (details on the sample size, and the rational behind species selection, are provided below and in the methods and main text).
Sampling strategy	The sample sizes were always determined by the maximum number of species with available data for each model. Details on the exact sample size for each model are provided in the Extended Data Tables.
Data collection	Our data were collected in the HBW alive (del Hoyo et al 2019), the IUCN red list website and a few other references listed in the text (e.g., Dunning 2007, Ducatez & Lefebvre 2014). Details on how the innovation dataset was built are provided in the methods: "Our behavioural data were drawn from an expanded and updated version of the innovation database provided in published papers. This database was compiled by systematically searching for reports of new behaviours in the short notes of 204 ornithology journals published between 1960 and 2018. The journals include academic serials (e.g., British Birds, Emu, Ibis, The Auk, Wilson Journal of Ornithology) as well as publications that are edited by local birding organizations (e.g., Florida Field Naturalist, Nebraska Bird Review), and they cover most areas of the globe except the Philippines, Polynesia, Micronesia and Melanesia. A feeding behaviour was considered an innovation, and hence was included in the database, if it was described in the report with key words such as “novel”, “opportunistic”, “first description”, “not noted before”, “unusual” etc. "
Timing and spatial scale	All data were collected from the literature. Most information were collected between 2017 and 2019, though the innovation dataset has been gathered and implemented continuously since 1995, based exclusively on a literature review. It covers the entire globe except the Philippines, Polynesia, Micronesia and Melanesia.
Data exclusions	Different analyses were focused on different groups of species, based either on data availability (e.g., whether their population trend is known or not), or on criteria of species selection for analyses on subsets of data (e.g., analyses focused on species with a research effort of more than 10 papers, or analyses excluding species considered as at risk of extinction because of their small geographic range size). The rationale behind species selection for each analysis is always explained, and directly responds to the aim of each analysis.
Reproducibility	To test for results consistency (rather than reproducibility as we ran comparative analyses, but did not conduct an experiment), we repeated our analyses on different datasets (e.g., by excluding or not rarely studied species, or by excluding or not species considered as at risk of extinction because of their small range size), and considering different measures of endangerment (extinction risk or population trend). We also considered different metrics of innovation propensity (binary variable segregating innovative and non-innovative species, number of innovations, number of technical or food type innovations etc.).
Randomization	Our analyses take into account phylogenetic non-independence, by always including phylogeny as a random factor.
Blinding	Our study is a comparative analysis based on data from the IUCN and data collected in the literature. Blinding was thus not directly relevant, though we tackled potential non-randomness in reports of behavioural innovations using different ways explained in details in the methods, e.g. by including a measure of research effort in the analyses, or by re-running the analyses after removing species with a low research effort.

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