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Behavioural responses are often the first reaction of an organism to human-induced rapid environmental change (HIREC), yet current empirical evidence provides no consensus about the main environmental features that animals respond to behaviourally or which behaviours are responsive to HIREC. To understand how changes in behaviour can be predicted by different forms of HIREC, we conducted a meta-analysis of the existing empirical literature focusing on behavioural responses to five axes of environmental change (climate change, changes in CO_2, direct human impact, changes in nutrients and biotic exchanges) in five behavioural domains (aggression, exploration, activity, boldness and sociability) across a range of taxa but with a focus on fish and bird species. Our meta-analysis revealed a general absence of directional behavioural responses to HIREC. However, the absolute magnitude of the effect sizes was large. This means that animals have strong behavioural responses to HIREC, but the responses are not clearly in any particular direction. Moreover, the absolute magnitude of the effect sizes differed between different behaviours and different forms of HIREC: Exploration responded more strongly than activity, and climate change induced the strongest behavioural responses. Model heterogeneities identified that effect sizes varied primarily because of study design, and the specific sample of individuals used in a study; phylogeny also explains significant variation in our bird model. Based on these results, we make four recommendations to further our understanding: 1) a more balanced representation of laboratory and field studies, 2) consideration of context dependency, 3) standardisation of the methods and definitions used to quantify and study behaviours and 4) consideration of the role for individual differences in behaviour.

Keywords: Bayesian, behaviour, climate change, field, laboratory

Introduction

Currently, human-induced rapid environmental change (HIREC) is exposing organisms to novel selection pressures that are vastly different from those experienced previously (Lowry et al. 2013). Whilst evolutionary responses to environmental change can

occur quickly and buffer the ability of species to persist in a changing environment (Hoffmann and Sgró 2011), behavioural responses are often the initial response of organisms to change (Wong and Candolin 2014). Moreover, behavioural change can mediate genetic adaptation by allowing time for genetic changes to occur (Tuomainen and Candolin 2011) or impeding change by shielding organisms from selection pressures (Muñoz and Losos 2018). Thus, understanding how behaviours are modified by changes in the environment is a crucial step in revealing how human-induced environmental changes affect animals.

In response to environmental change, organisms can adapt, relocate and/or acclimatise (Wong and Candolin 2014). First, populations can respond to changing environments at a genetic level, through evolutionary adaptation resulting from selection (Hoffmann and Sgró 2011). Secondly, organisms can relocate via dispersal into habitats in different geographic spaces in response to environmental factors such as temperature and resource availability (Tesson and Edelaar 2013). Finally, organisms can acclimate through phenotypic plasticity, which may be physiological, morphological or behavioural (Noble et al. 2018). Behavioural plasticity allows organisms to respond to a changing environment rapidly by modifying their behaviour to better suit new environmental conditions (Komers 1997).

Environmental change induces behavioural responses through various pathways, for example, by changing the availability of resources (Berumen and Pratchett 2006), or through changes in information transmission in the sensory environment (Sih et al. 2011). If an individual has an evolutionary history that has resulted in traits suitable for changing conditions, then short-term behavioural plasticity will be possible (Sih et al. 2011). Where evolutionary history has produced traits allowing for fast evolutionary responses, such as traits with high genetic variation, behavioural adaptations to HIREC could evolve (Hendry et al. 2011). Behavioural responses can occur initially through behavioural plasticity (Wong and Candolin 2014) that can then be transmitted socially, before evolving over subsequent generations (Tuomainen and Candolin 2011). Over time, behavioural modifications can therefore promote adaptation; an important process for predicting persistence in a changing environment (Wong and Candolin 2014).

There are five behavioural domains that have become central in modern behavioural ecology research: aggression, exploration, activity, boldness and sociability (Reale et al. 2007). These behavioural domains are important since they are related to resource acquisition, dispersal and many other ecologically important processes, as well as being linked with life history and physiology (Réale et al. 2010, Dammhahn et al. 2018). A focus on these domains has allowed for a broad scale comparability of behavioural expression across different species, contexts and time (Koski 2014). It has also been shown that behaviour scales up to influence population and community-level processes (Dall et al. 2004, Wilson et al. 2020).

Animal behaviour has been studied in relation to various forms of HIREC, with responses varying within and across taxa. Changes in land use, such as an increase in urbanisation,

are associated with increased boldness and exploration in birds (Donaldson et al. 2007, Evans et al. 2010), but led to greater caution in lizards (Lapiedra et al. 2017). In terms of climate change, evidence suggests that increasing air temperatures can alter the phenology of bird species, increasing interspecific competition and associated aggression during breeding seasons (Samplonius and Both 2019). In fishes, increases in aggression have been associated with warming water (Kvarnemo 1998) and decreasing water levels associated with drought (Flood and Wong 2017), but decreases in aggression have been suggested following warming-induced mass coral mortality (Keith et al. 2018). Despite variability in behavioural responses towards changing environments, the same mechanisms have been used to explain both increases and decreases in different behaviours in response to HIREC, such as energetic expenditure (Enzor et al. 2017), resource availability (Grémillet et al. 2012) and fitness consequences (Dingemanse and Reale 2005). There are, therefore, numerous explanations for behavioural responses to HIREC across different studies, but no consensus.

It is unclear whether inconsistencies in behavioural responses to HIREC reflect different mechanisms operating in different taxa or systems or variation in methodologies across studies. For example, there are multiple methods that can be used to measure a single behaviour, such as boldness, and there are also multiple behaviours (e.g. boldness, exploration and activity) that can be measured using one test, such as latency tests (Carter et al. 2013). Furthermore, the differences between laboratory and field methods, and the effects of these differences in behavioural expression, are unresolved. Field-based methods allow for observation and/or manipulation under naturally varying conditions (Cuthill 1991) but are subject to noise from uncontrolled factors (Calisi and Bentley 2009). Laboratory experiments allow numerous environmental factors to be controlled for, making it easier to establish cause and effect yet lose realism (Cuthill 1991). Laboratory environments can induce expression of behavioural variation that has not been tested by natural selection (Niemelä and Dingemanse 2014), potentially causing a mismatch between laboratory and field studies.

Here, we explore and quantify the direction and absolute magnitude of behavioural responses to HIREC using meta-analytic tools. Specifically, we focus on the five key behavioural domains (Reale et al. 2007) to determine the extent to which changes in those behaviours can be predicted by different types of HIREC. Moreover, we aim to identify the contributions of different factors influencing behavioural responses, specifically differences between animal taxa and between different methods used to study and quantify behaviour, to provide a deeper understanding of responses to HIREC.

Material and methods

Literature search and inclusion criteria

We used the standardised 'Preferred Reporting Items for Systematic Reviews and Meta-analysis' (PRISMA) method for selection of studies to include in the analysis (Moher et al.

2009, Supporting information). We searched the Web of Science core collection database on 5 November 2018 using the following search term: (Animal (Personality OR behav* OR "behav* syndrome") AND ("Environmental change" OR "Climate Change" OR "Global warming" OR "Habitat degradation")). We included terms 'Personality' and 'behav* syndrome', in addition to general 'behav*', in our search since research in the field of animal personality has forcefully focused on estimating behavioural responses across different environments (Sih 2013). Moreover, animal personality research also focuses on the key five behavioural domains used in our work (Reale et al. 2007). The Web of Science search identified 974 records, and we collated a further 49 records by searching the reference lists of relevant review papers (Supporting information). Following the removal of duplicates, we had a total of 1023 papers to screen. Titles and abstracts for these 1023 records were assessed for relevance, and we eliminated a further 658 papers that did not include reference to both 'behaviour' and 'environmental change'.

The remaining 365 papers were then read in full and data were extracted for analysis. During this screening, 59 review papers, 52 theoretical modelling papers, 3 method papers, 4 response papers and 21 theoretical papers were excluded as they contained no experimental data. We excluded an additional 64 papers as they did not contain appropriate behavioural data, for example they referred to natural seasonal variations in behaviour, or thermoregulatory behaviour. Similarly, 53 papers were removed as they contained behavioural data, but not in relation to environmental change. Five studies that used a repeated measures design were eliminated to avoid issues with calculating sampling error variance. Two papers that had been retracted or were, to our knowledge, being investigated since the initial search were also eliminated. Twelve relevant papers from which we were unable to extract suitable data for quantitative analyses were retained for qualitative analyses. In total, we included 418 data points from 102 studies in qualitative analyses and 381 data points from 90 studies in quantitative analyses (Supporting information).

Data extraction

Qualitative data
For each paper included in the analysis, we extracted the following information: study taxa (bird, fish, crustacea, mammal, other), study species, study habitat (Supporting information), axis of environmental change, behavioural domain, method of measuring/quantifying behaviour, laboratory or field based and wild or captive population. For study taxa, 'other' grouped poorly represented taxa including amphibians, echinoderms, elasmobranchs, insects, molluscs and reptiles, which were each included in fewer than 10 papers.

We modified the five axes of HIREC from Sala et al. (2000) to broaden their applicability beyond terrestrial systems and assigned all papers to one axis. Direct Human impact ('Changes in land use', Sala 2000) encompassed a wider spectrum of anthropogenic effects including urbanisation, human disturbance, fishing pressures and anthropogenic

noise. Changes in CO_2 concentration ('Atmospheric CO_2 concentration', Sala 2000), encompassed both changes in atmospheric CO_2 and ocean acidification. Changes in nutrients ('nitrogen deposition and acid rain', Sala 2000) concerned changes in water column turbidity and eutrophication. Climate change (Sala 2000) encompassed changes in both water and air temperature and subsequent changes in habitat. Biotic exchanges refer to the impact of invasive species on native populations. In all cases, changes in CO_2 and temperature are unidirectional and refer to increases only.

The five behavioural domains we considered were aggression, exploration, activity, boldness and sociability (following Reale et al. 2007). There is often a discrepancy in how behaviours are defined (Carter et al. 2013) so for consistency, we used the definitions of Reale et al. (2007) to assign behaviours to one of the five domains: aggression is defined as a social contest involving agonistic behaviours; boldness as response to a risky situation (that is not novel); exploration as response to novel situations (which can also be risky); activity as general activity in non-risky and non-novel situations and sociability as a non-agonistic response to a conspecific. Where focal studies in our data had themselves used Reale et al. (2007) as a guideline for defining behaviours, we used the authors' definition of behaviour.

We collected multiple effect sizes from the same studies, some of which were on the same sets of animals introducing a source of non-independence that we dealt with in our analysis. We also noted whether studies were laboratory or field-based and whether study methods were observational or experimental. We then assigned each study to one of the following three study designs: Studies that had taken a single wild population and then used an independent design to measure behaviour across different environmental conditions, such as increased temperature of CO_2 levels, were categorised as 'experimental manipulations of environmental conditions'. Where behaviour had been measured across two or more populations that exist in different environmental conditions, studies were labelled as 'cross-sectional'. Finally, studies that considered populations on a temporal scale were marked as 'longitudinal'. We also noted the precise way in which behaviour was quantified, to account for non-independence in methodologies between different studies. This random effect included a total of 19 methods (Supporting information).

Quantitative data
Because dependent variables measured across the studies were highly variable due to a lack of consistency in measuring and defining behaviours, we selected Hedge's g as an effect size statistic that standardises the dependent variable (Lipsey and Wilson 2001). We calculated Hedge's g with a bias correction and the associated variance based on the standard error, to account for studies with small sample sizes (Supporting information). Hedges g values were calculated from the control and experimental mean values, sample sizes and standard deviations for each study (Supporting information).

For studies that considered a relationship between two continuous variables, we calculated values for the Pearson's correlation (r) with a Fisher's z transformation to ensure a normal distribution and converted to Hedge's g values (Supporting information). We estimated variance due to sampling error as the standard error of each estimate squared (Hadfield 2010, Supporting information). Latency time is often used to measure exploration, boldness and activity. However, longer periods of time do not always equate to greater levels of boldness/exploration or activity. To ensure our biological interpretations were correct and uniform across estimates, we multiplied effect sizes by −1 for instances where higher values do not equate to greater expressions of behaviour. This was the case for 60 data points across 26 papers. Following this standardisation, all effect sizes had the same directionality: positive effect size indicates an increase in behaviour, and a negative effect size indicates a decrease in behaviour.

To account for phylogenetic non-independence in our models, we obtained the phylogenies for all species using the NCBI common tree, which is based on molecular phylogenies (Supporting information) and was the only available tree with complete species coverage. We produced a single phylogeny for all the species in our dataset. To improve the resolution of this phylogeny, we randomly resolved the polytomies. Our final phylogeny consisted of a tree with 103 tips, and 102 nodes, with a subsequent resolution of 100%. We then computed an inverse phylogenetic matrix that was incorporated into all our models following Moiron et al. (2020). To ensure we had controlled for the two sources of among species variation: a shared evolutionary history (i.e. phylogeny) and a shared ecology, we also included a species random effect in all our models (Kruuk and Hadfield 2007).

Analysis

For all analyses and plots, we used R ver. 3.5.1 (<www.r-project.org>) and Bayesian 'MCMCglmm' package (Hadfield 2010). Phylogenies were produced using the 'ape' package (Paradis and Schliep 2019) and were randomly resolved using the *bifurcatr()* function in the 'PDcalc' package (Nipperness 2016). To evaluate potential publication bias, we produced funnel plots and ran an Egger's regression analysis to visually and statistically test if the distributions of effect sizes were symmetrical (Stuck et al. 1998, Supporting information). We also calculated Orwin's fail-safe N (Orwin 1983), which uses the 'trivial' effect size to determine the number of additional missing studies that would be needed to bring the true effect size under the trivial effect size and render our results non-significant.

Meta-analytic models

We built Bayesian generalised linear mixed-effects models (GLMMs) based on Gaussian distributions. In all models, behaviour and environmental axes were fitted as categorical fixed effects. The Hedge's g sampling variances were also included in all models (Supporting information). Moreover, we included study identity (i.e. paper reference), the phylogeny, method of measuring behaviour (19 levels, Supporting information) and animal group (avian, crustacean, mammal, teleost, other) as random effects in all models. All studies included in our analyses utilised an independent design, such that animals were split and placed in either a control or treatment group. However, for some studies, we extracted multiple effect sizes from the same sample of animals. For example, where studies measured two behaviours, we extracted effect size estimates for each behaviour separately. However, these two estimates would be non-independent since they came from data collected from the same sample of animals. To account for this non-independence, each data point was assigned with an 'animal sample identity'. In total, our 381 quantitative data points were collected by using 217 different animal samples.

All models were based on two chains, 1 550 000 iterations, with the first 50 000 discarded as a burn-in, and a thinning interval of 100 (Supporting information). Due to model complexity and to ensure convergence, a weakly informative parameter-expanded prior was selected, built on the following parameters: variance matrix, $V = 1$, degree of belief parameter, $nu = 0.002$, prior mean, $\alpha mu = 0$, covariance matrix, $\alpha = 1000$ (Hadfield 2010). Histograms of fixed and random effect posterior distributions were produced to visually assess the precision of posterior mean estimations. Model convergence and the presence of autocorrelation were analysed visually from trace and density plots (Supporting information) and we compared simulated data of 100 models against our data to check the fit of all models (Supporting information). We also conducted a Gelman diagnostic analysis (Gelman and Rubin 1992), to calculate a scale reduction factor and assess the convergence of the two Markov chain Monte Carlo (MCMC) chains (Supporting information). A scale reduction factor of 1.1 or less suggests good convergence between MCMC chains.

We calculated unconditional mean effect sizes for each effect size, using the posterior distributions from each of our models. Unconditional mean effect sizes were calculated using weighted average of each level for our fixed effects, across the different combinations of fixed effects in each model (Tarka et al. 2018). For both conditional and unconditional model estimates, we computed 50% and 95% credible intervals. We also calculated the probability of direction (PD) as an index of effect existence (Makowski et al. 2019). The PD is the probability, calculated as a percentage between 50% and 100% that the posterior distribution of a model is positive or negative, and is based on posterior mean values. Whilst the PD can correspond with the frequentist p-value (Makowski et al. 2019), we include the PD purely as a visual aid to show the extent to which an effect is positive or negative. We use credible intervals to assess the significance of effects in our models. Specifically, we consider an effect to be significant if credible intervals do not overlap zero.

We also calculated the absolute magnitude mean effect sizes for three behaviours (boldness, activity and

exploration), three axes of environmental change (climate change, changes in CO_2 and direct human impact), fish data, bird data, field data and laboratory data, using methods based on Noble et al. (2018) and Moiron et al. (2020). We excluded sociability, aggression, biotic exchanges, changes in nutrients and longitudinal study design from this analysis, due to small sample sizes in our dataset. The absolute magnitude of the effect size gives additional information compared to the traditional, directional, effect sizes by indicating whether animals do respond to HIREC but are just inconsistent in the direction of the response. We ran separate intercept models for each of the above parameters, and then obtained the absolute values (i.e. without a positive or negative direction) from the model by folding the posterior distribution of the effect size for each intercept model (Morrissey 2016). As a guide, we considered overall magnitude effect sizes of over 0.8 to indicate a large response to HIREC (Cohen 1992).

Heterogeneity estimates (I^2) were calculated for each random effect in all models (above), whilst controlling for sampling variance. I^2 is a proportion of total variance in the response variable explained by a focal random effect (Huedo-Medina et al. 2006). Under the classification by Higgins and Thompson (2002), total sampling variance over 50% is 'medium' and over 75% is 'high'. Furthermore, Senior et al. (2016) identified that for meta-analyses, total heterogeneity usually falls between 60% and 90%.

In total, we ran eight separate models (Supporting information). Initially, we generated a global meta-analytic model based on the full quantitative dataset of 90 studies and 381 data points. Behavioural domain, environmental axes, study design (experimental manipulations of environmental conditions, cross-sectional or longitudinal) and data background (laboratory/field) were fitted as categorical fixed effects. Reference categories for the fixed effects were set as exploration (for behavioural domain), climate change (for environmental axes), experimental manipulations of environmental conditions (for study design) and laboratory (for data background), the best-represented categories in the dataset. We ran three sub-models for the three individual environmental axes that dominated our dataset: climate change, changes in CO_2 and direct human impact, and four additional models based on subsets of the data included in the global model. Specifically, we ran separate models for laboratory and field studies, and separate models for fish and bird studies, using the same reference categories as our initial model.

Results

Qualitative analyses

In total, 418 data points from 102 studies and 103 species were included in qualitative analyses. 'Climate change' and 'direct human impact' were the best-represented axes of environmental change (135 and 112 incidences respectively). A majority of studies used laboratory-based methods (297

incidences), except for studies on 'direct human impact' (Fig. 1). In terms of behaviour, 'boldness' and 'exploration' were the most studied (131 and 132 incidences respectively; Fig. 1). Most research focussed on fish and birds (202 and 68 incidences respectively). For birds, 83% of studies were field based, whereas 87% of fish studies were conducted under laboratory conditions (Fig. 1).

Quantitative analyses

There were 381 data points from 90 studies included in quantitative analyses. Orwin's fail-safe number showed that an additional 381 non-significant studies would be required to change the overall effect. Egger's regression analyses were also non-significant ($p = 0.14$), further supporting a lack of publication bias (Supporting information). Conditional estimates for all models are presented in the Supporting information.

Global model
All parameter distributions had 95% credible intervals that overlapped zero, indicating that there are no clear directional responses to HIREC across all data. Nonetheless, in terms of environmental axes, increased behavioural expression to direct human impact, was the most consistent parameter, with an effect size (g) of 0.48 (95% credible intervals: −0.46, 1.41) and probability of direction (PD) of 75.27%. In terms of behaviour, exploration showed the most increase, with an effect size of 0.32 (−0.53, 1.18) and a PD of 79.07%. Sociability showed the most decrease in response to HIREC, with an estimate of −0.82 (−2.93, 1.26) and a PD of 78.13%. However, for all these estimates, credible intervals overlap zero, and in general, mean estimates are centred around zero.

Environmental axes sub-models
The environmental axes sub-models showed one clear response where credible intervals did not overlap zero: aggression decreased under increased CO_2 conditions, with an effect size of −4.43 (−7.87, −1.30) and a PD of 98.53% (Fig. 2). However, since this estimate is based on just six data points from a single study, our result should be treated with caution. The direct human impact model showed a tendency for consistent responses. Specifically, although credible intervals overlapped zero, the direct human impact model had effect size estimates of 0.62 (−0.41, 1.67) and 0.40 (−0.73, 1.50), with PD values of 89.21% and 76.65% for boldness and exploration, respectively.

Field and laboratory data models
Models ran separately for laboratory and field studies did not yield any parameters with credible intervals not overlapping zero, but there was a general tendency for behavioural responses to be stronger in the field data compared to laboratory data, such that for field data, credible intervals overlap zero to a lesser extent than for laboratory data (Fig. 3). Specifically, for field data, boldness showed the strongest directional response, with an effect size estimate of 1.46
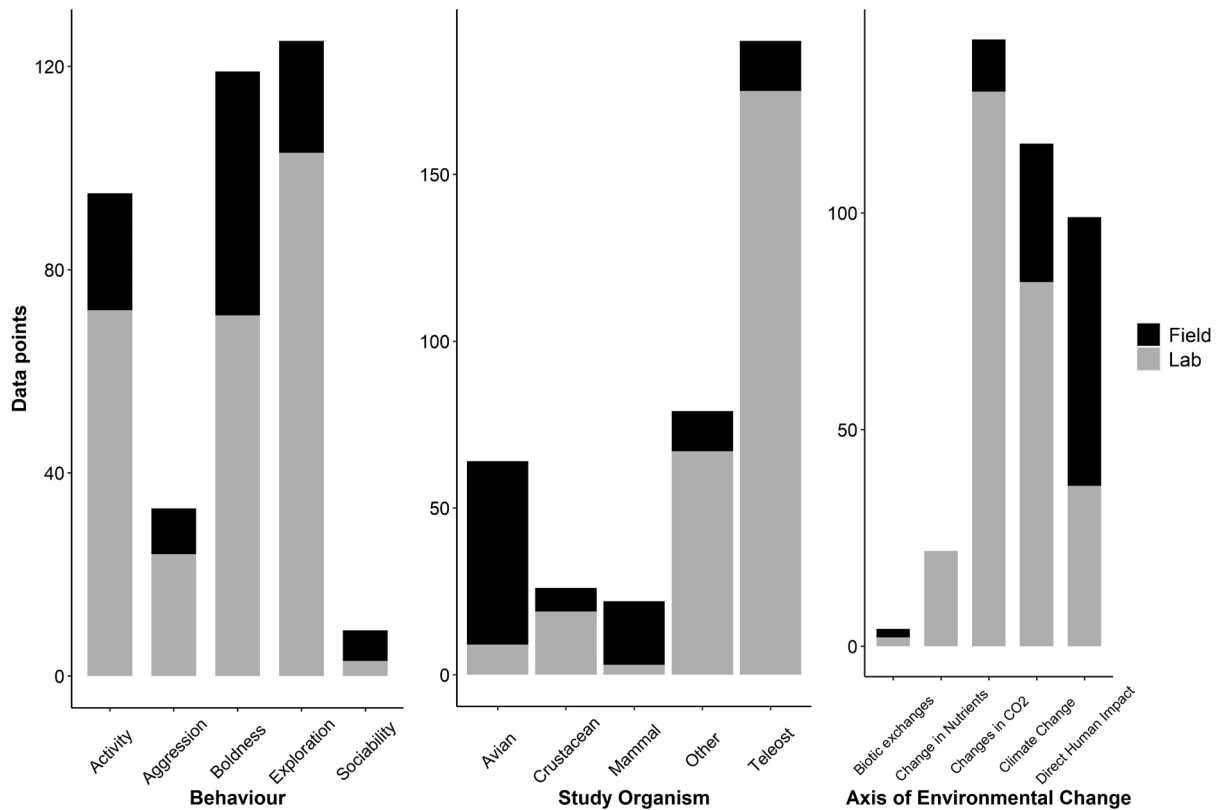
Figure 1. Number of data points compiled from studies addressing the effect of environmental change on animal behaviour in terms of axes of environmental change, behaviours and taxa. Y-axis refers to individual data points. Some studies considered more than one axis of behaviour and/or environment and are included in more than one category.

(−0.02, 2.91) and a PD of 97.44%, compared to an effect size estimate of −0.27 (−1.77, 1.20) and a PD of 65.76% for laboratory data. In terms of axes of environmental change, climate change had the most directional response in field data, with an effect size of 1.01 (−0.26, 2.44) and a PD value of 79.79%, compared to 0.37 (−1.13, 1.81) and 60.30% for laboratory data, although for both, credible intervals did overlap zero. Finally, all three types of study (experimental manipulations of environmental conditions, cross-sectional and longitudinal) showed stronger behavioural responses for field data, with effect sizes and PD estimates of 0.93 (−0.31, 2.22), 1.06 (−0.39, 2.48), 0.91 (−0.70, 2.55) and 93.77, 93.47 and 87.58% respectively. For laboratory data, experimental manipulations of environmental conditions, cross-sectional and longitudinal studies had effect sizes and PD estimates of 0.22 (−1.12, 1.81), −0.37 (−2.11, 1.24), 0.09 (−2.08, 2.54) and 66.14, 67.83 and 52.69%, respectively. Nonetheless, for both models, credible intervals overlapped zero for these parameters.

Taxa specific models
For both the fish and the bird models, there were no effect sizes where credible intervals did not overlap zero, and for most parameters, mean estimates were centred around zero (Fig. 3). Nonetheless, our model showed a tendency for an increase in exploration in fish, with an effect size

of 1.11 (−0.63, 2.90) and a PD of 89.85%, whilst birds showed a tendency for decreased exploration, with an effect size of −0.74 (−3.10, 1.82) and a PD of 75.96%. Furthermore, behavioural responses of birds were generally slightly higher than responses of fish, particularly for boldness and climate change. Specifically, in birds, boldness had mean effect sizes of 1.53 (−0.70, 3.91), and a PD value of 92.79%, compared to −0.42 (−2.02, 1.27) and 70.33% for boldness in fish. Behavioural responses to climate change had a mean effect size of 1.45 (−1.39, 4.19) and a PD value of 87.03% in birds, compared to 0.60 (−1.13, 2.29) and 77.19% in fish.

Absolute magnitude of the effect sizes

Our absolute magnitude effect size estimates were all over 0.8, indicating that when the direction of the effect sizes is ignored, animals show a strong behavioural to HIREC and significant differences between behaviours and axes of environmental change do occur (Fig. 4). Furthermore, credible intervals for all parameters are not close to zero, further indicating significant responses to HIREC. Exploration showed the strongest overall response to HIREC, with an absolute effect size of 3.63 (2.55, 5.23). Boldness also showed a strong response to HIREC, with an effect size
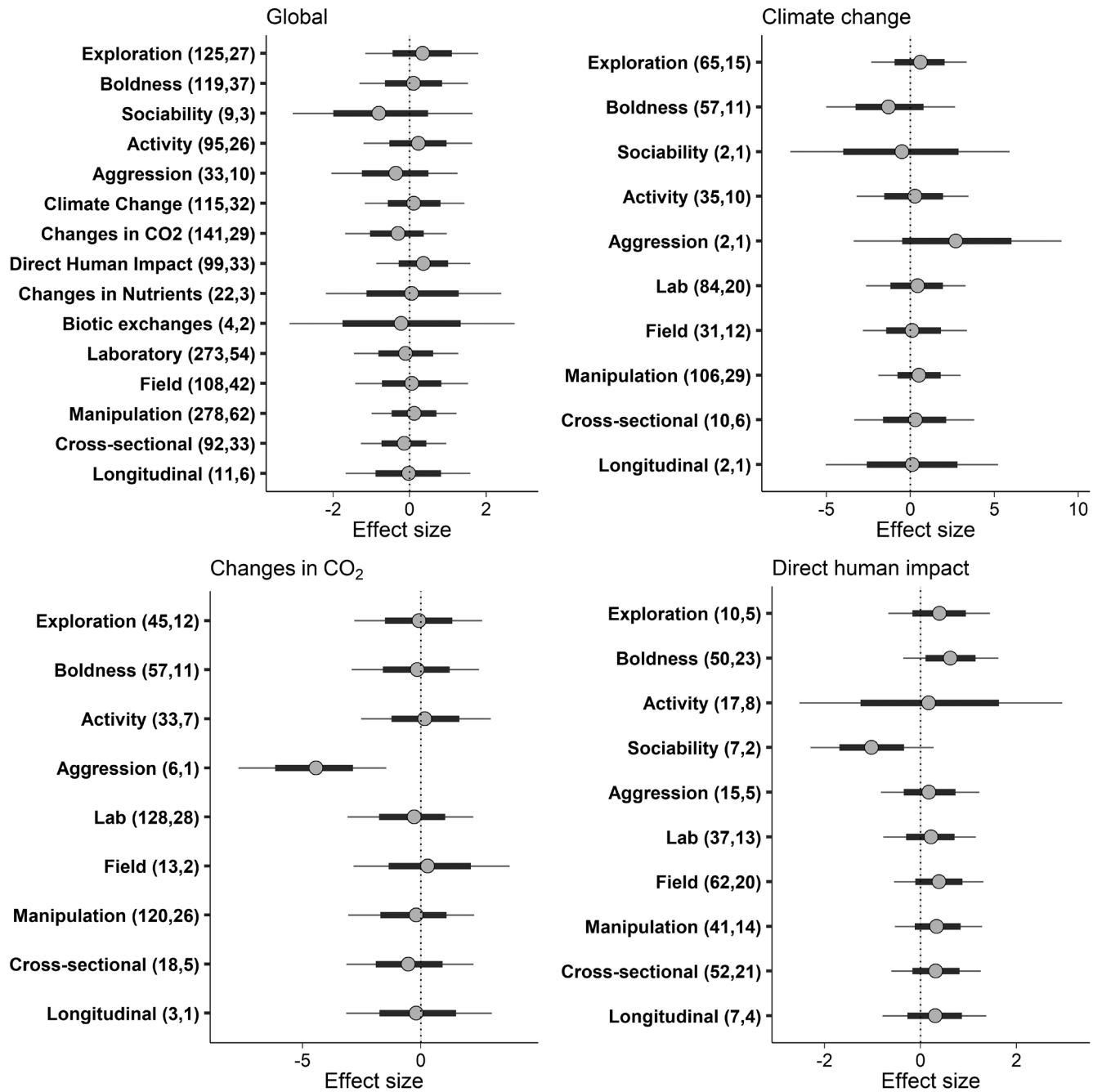
Figure 2. Model parameter estimates from our global model and environmental axes models (see panel titles). Points are unconditional posterior mean values. Thick and thin bars represent 50% and 95% credible intervals, respectively. Numbers next to parameters are the number of data points and the number of studies for each parameter, respectively.

of 2.39 (1.41, 3.60). The responses of both boldness and exploration towards HIREC were significantly higher than that of activity (0.89 (0.45, 1.44)), based on non-overlapping credible intervals for these parameters. Behavioural responses were strongest under climate change (3.70 (2.60, 5.37)), and responses to climate change were significantly greater than responses to direct human impact (1.06 (0.70, 1.50)). For study design, overall responses were significantly greater for experimental manipulations of environmental conditions (2.31 (1.93, 2.74)) than for cross-sectional studies (0.64, 1.58). Finally, the overall responses of behaviour in the laboratory (2.51 (1.97, 3.36)) were higher than in the field (1.50 (0.79, 2.36)) although credible intervals between laboratory and field-effect sizes did slightly overlap.

Field and laboratory

Exploration (22,103)
Boldness (48, 71)
Sociability (6,3)
Activity (23,72)
Aggression (9,24)
Climate Change (31,84)
Changes in CO2 (13,128)
Direct Human Impact (62,37)
Biotic exchanges (2,2)
Manipulation (48,230)
Cross-sectional (55,37)
Longitudinal (5,6)

Effect size

Fish and bird

Exploration (15,55)
Boldness (26,66)
Sociability (6,3)
Activity (10,48)
Aggression (7,18)
Climate Change (17,57)
Direct Human Impact (46,17)
Manipulation (30,163)
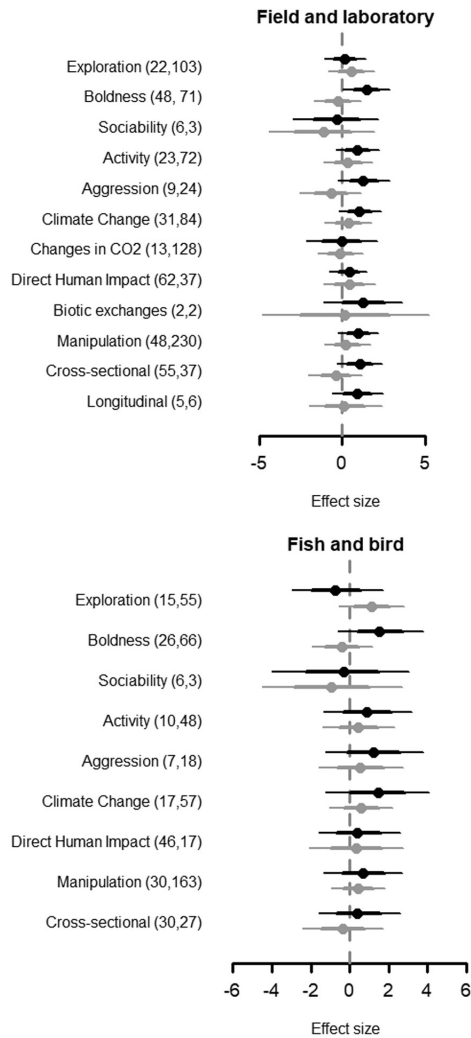Cross-sectional (30,27)

Effect size

Figure 3. Parameter estimates for field (top, black) and laboratory (top, grey) models and for bird (bottom, black) and fish (bottom, grey) models. Points are unconditional posterior mean values with 50% and 95% credible intervals. Numbers next to parameter labels are the number of data points for field and laboratory (top) and fish and bird data (bottom), respectively.

Model heterogeneities

For all models, total heterogeneity was over 90% (Table 1). For the global model, residual heterogeneity was high, at 45%, indicating that effect sizes were variable within each random effect category in our models. Animal samples made up between 26 and 32% of total model heterogeneity across the global, climate change, direct human impact, laboratory and fish models. Effect sizes, therefore, varied more with the specific sample of animals being tested than among individual studies. Phylogenetic heterogeneity was moderate for the field model (11%) and high for the bird model (26%), indicating that there is a substantial phylogenetic signal in behavioural responses to HIREC data collected in the wild and in birds, but not in other data sets. The methods used to measure behaviour made up 48% of model heterogeneity in
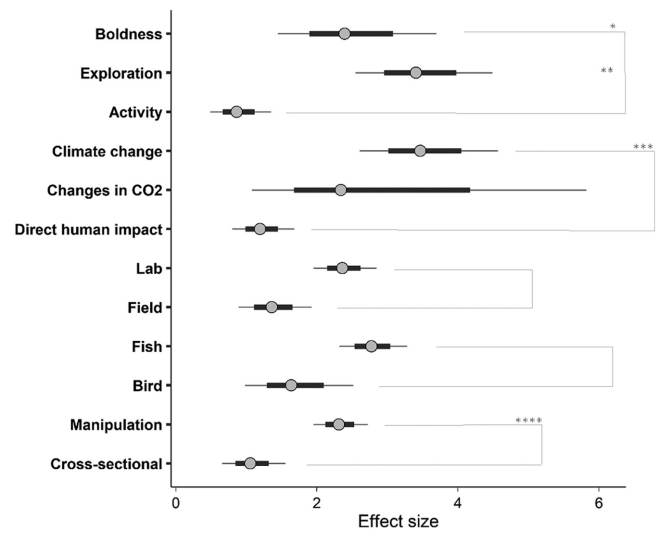

Figure 4. Absolute magnitude effect sizes from folded distributions, calculated from individual intercept models. Thick and thin bars represent 50% and 95% credible intervals, respectively. Grey lines group together the levels of behaviour, environmental change, study form, animal group and study design respectively, and *, **, ***, **** indicate where there are significant differences between two parameters within these groups.

the direct human impact model, 27% of model heterogeneity in the bird model and 32% in the field model. Study design contributed to 20% of heterogeneity in the field and label models. Therefore, effect sizes were variable across different measures of behaviour and study design for the direct human impact model, bird, field and laboratory models.

Discussion

We have provided insight into the patterns and drivers of behavioural responses to environmental change across a range of taxa. Our results show that animals do have strong absolute behavioural responses to HIREC and that the magnitude of response varies across behaviours and different forms of HIREC. Specifically, behavioural responses to climate change were significantly greater than responses to direct human impact. Furthermore, exploration showed a significantly greater response to HIREC than did activity. Animals, therefore, do respond to HIREC behaviourally, but the direction of the responses are variable, such that behaviour may be upregulated and/or downregulated in response to HIREC. Finally, our results show that study design, methods used to measure behaviour, individual animal samples and phylogeny all contribute to variation, that is heterogeneity, in behavioural responses to HIREC.

Global behavioural responses to HIREC

The lack of significant directional responses in our global model could be due to the differences between the types of studies included in the global model. For example,

Table 1. Heterogeneity estimates (I^2) for all Bayesian models. Numbers in brackets are standard deviations.

	Total	Study	Phylogeny	Species	Animal group	Sample	Method	Residual
Global	0.99 (0.001)	0.17 (0.05)	0.01 (0.02)	0.01 (0.02)	0.04 (0.09)	0.26 (0.06)	0.01 (0.02)	0.45 (0.07)
Climate change	0.99 (0.001)	0.13 (0.09)	0.04 (0.05)	0.02 (0.03)	0.13 (0.18)	0.26 (0.12)	0.03 (0.05)	0.37 (0.12)
Changes in CO_2	0.98 (0.01)	0.14 (0.14)	0.05 (0.06)	0.02 (0.03)	0.26 (0.30)	0.04 (0.04)	0.10 (0.11)	0.38 (0.19)
Direct human impact	0.97 (0.01)	0.14 (0.14)	0.06 (0.07)	0.07 (0.07)	0.10 (0.14)	0.18 (0.11)	0.48 (0.16)	0.07 (0.07)
Lab	0.99 (0.002)	0.16 (0.07)	0.02 (0.02)	0.20 (0.14)	0.09 (0.14)	0.30 (0.08)	0.02 (0.03)	0.39 (0.09)
Field	0.98 (0.007)	0.17 (0.14)	0.11 (0.14)	0.20 (0.13)	0.14 (0.18)	0.01 (0.012	0.32 (0.15)	0.02 (0.03)
Fish	0.99 (0.001)	0.22 (0.11)	0.04 (0.05)	0.02 (0.03)		0.32 (0.09)	0.03 (0.04)	0.37 (0.08)
Bird	0.99 (0.006)	0.14 (0.14)	0.26 (0.22)	0.10 (0.08)		0.03 (0.04)	0.27 (0.15)	0.08 (0.07)

manipulation studies measure intra-generational plastic responses to environmental conditions, whilst cross-sectional studies measure differences between two populations, which could reflect intra- or inter-generational plastic changes, or evolutionary responses to divergent selection pressures (Kinnison and Hendry 2001). These differences likely generate a lot of 'noise', making it difficult to infer underlying mechanisms behind behavioural responses. Nonetheless, we did find a non-significant tendency for increased behavioural expression under direct human impact, specifically a non-significant tendency for increased expression of boldness under HIREC in field-collected data. As boldness captures responses to risky situations (Reale et al. 2007), our results suggest that animals may start to take more risks in response to increasing HIREC. To persist under conditions of direct human impact, e.g. urbanised areas, risk-taking is assumed to be beneficial (Lowry et al. 2013). Thus, increasing boldness might be a general adaptive behavioural response to HIREC, but additional tests are required before this hypothesis can be accepted.

All behaviours expressed strong absolute responses to HIREC, while boldness and exploration showed the strongest response. Furthermore, experimental studies manipulating environmental conditions over a short-term (Kvarnemo 1998) seem to induce stronger behavioural responses than cross-sectional studies comparing populations living in different environments (e.g. urban versus rural; Evans et al. 2010). The lack of overall response in the global model, combined with the high absolute responses for experimental manipulations of environmental conditions studies, and in boldness and exploration indicates that both substantial increases and decreases in behaviour are present. Organisms may invest in buffering the consequences of environmental change, which could reflect differences in boldness and risk-taking behaviours (Du Plessis et al. 2012). In terms of exploration, organisms might invest in gathering information to reduce uncertainty or invest more in finding food that may have been lost under HIREC (Donaldson et al. 2007), which will likely result in increased exploration (Mathot et al. 2012). Alternatively, organisms can become less exploratory to conserve energy and maximise its use of the remaining resources (Grémillet et al. 2012). Different species, populations and even conspecifics within a population differ in ecological and environmental characteristics they face, but also on what

aspect of the species ecology (e.g. competition, predation pressure), demography (birth rate, death rate) or phenology (timing of reproduction, timing of migration) HIREC is affecting (Wong and Candolin 2014). For example, a recent review of how organisms respond to HIREC predicts that individuals that have high basal stress levels, display shyness and have high degrees of plasticity, that is have a reactive phenotype, will be more suited to cope with HIREC than individuals with proactive phenotypes (Geffroy et al. 2020). Therefore, individuals, species and populations could have different optimal behavioural responses to cope with and potentially buffer the effects of environmental change, leading to an absence of clear directional behavioural responses, but the presence of strong absolute behavioural responses in our data.

The strong absolute responses to experimental manipulations of environmental conditions identified in our results compared to cross-sectional studies also indicate that length of exposure to HIREC could play a role in determining the optimal responses to HIREC, such that initial, short-term, sometimes extreme behavioural responses may not always be optimal in the longer term (Sih et al. 2011). Furthermore, evolutionary rates have also been shown to decrease with time since the separation of two populations, perhaps because evolution slows as a population reaches a new optimum condition (Kinnison and Hendry 2001). Short term experimental manipulations of environmental conditions may therefore elicit stronger initial responses than cross-sectional studies comparing two different populations that have evolved to their environmental conditions over a long period of time. Here we show that animals respond strongly to HIREC in an absolute sense, but further research is needed to reveal what is causing the variation in direction of those responses.

Behavioural responses to HIREC in the laboratory versus the field

Laboratory and field research provides complementary insights into the behavioural responses of organisms to change. Although our global model indicated no clear difference between field and laboratory collected data, separate models for field and laboratory data generally indicate that the behavioural responses might be stronger in the field-collected data, although this difference is marginal. Research

on animal behaviour is particularly sensitive to the environment in which observations occur (Calisi and Bentley 2009). For example, a meta-analysis on repeatability identified that behaviours measured in the field were more repeatable than behaviours measured in the laboratory. This difference could be because laboratory experiments do not account for contextual information that can enhance behavioural variability within and across individuals, such as the presence of microniches (Bell et al. 2009), seasonal variation across different populations (Both et al. 2010), or the presence and state of heterospecific competitors in the field (Lehtonen et al. 2010).

Whilst there was a tendency for greater directional responses in our field data when compared to laboratory data, the absolute magnitude of behavioural responses was greater in laboratory data. Although the difference in absolute effect sizes between the laboratory and field data was not significant (slight overlap in the 95% credible intervals), our result suggests that behaviours may both increase and decrease to a greater extent in response to HIREC when measured in the laboratory compared with in the field. Furthermore, the absolute magnitude of behavioural responses to climate change was higher than responses to direct human impact. Laboratory studies dominate the climate change dataset, whilst the direct human impact dataset is dominated by field studies. It is plausible that a difference in behavioural responses to HIREC between laboratory and field studies is at least partly a driver of this difference in overall magnitude effect sizes. Whilst there are some studies that have used field data to support responses identified in the laboratory (Osborn and Briffa 2017), our results suggest that there is a need for a balanced combination of field and laboratory studies, across behaviours, forms of HIREC and across different taxa, in order to fully understand the complexity of behavioural responses to HIREC (Campbell et al. 2009).

Taxon-specific behavioural responses to HIREC

Our results identified a tendency for higher behavioural responses in birds compared to fish, with research on birds focussed on in situ tests of boldness between urban and rural environments. In contrast, behavioural responses in fish were mostly centred around zero, with research focusing on the manipulation of temperature and CO_2 in tanks and monitoring behaviour (Nowicki et al. 2012). This result may reflect differences in the extent of temperature change between terrestrial and marine ecosystems. Long- and short-term temperature changes in terrestrial environments are more variable than in marine environments, thus terrestrial organisms may be predicted to have developed responses to cope with short-term changes which could in turn buffer the effects of longer-term temperature variability (Steele 1985). Marine organisms are unlikely to have developed mechanisms to cope with short-term variability, expressing different or weaker responses compared to terrestrial organisms (Steele 1985). This may also explain why behavioural responses were generally less pronounced in fish than in birds. Evolutionary,

or developmental history might define how well taxa are equipped to respond behaviourally to HIREC, both now and in the future.

Heterogeneity in behavioural responses to HIREC

One of the issues in understanding behavioural responses to environmental change, and the rationale for this meta-analysis, is that there is apparent inconsistency in responses within taxa (Flood and Wong 2017), even where the behaviours have been measured across the same axis of environmental change. Our heterogeneity results provide an important insight into the drivers of this inconsistency and variability in behavioural responses to HIREC. In our global model, 45% of model heterogeneity was attributed to residual heterogeneity, such that effect sizes are variable within each model random effect (study, phylogeny, animal group, animal sample, study design and measure of behaviour). This highlights the importance of accounting for context-specific factors that could influence behavioural responses when analysing behavioural responses to HIREC (Beekman and Jordan 2017). Furthermore, for all models except for the changes in CO_2, bird and field models, heterogeneity estimates for the animal sample were high (between 26% and 32%). The specific sample of animals on which behaviour is measured therefore creates variability in effect sizes. This could be due to inherent differences in behaviour, and in differences in behavioural responses to environmental change, across different individuals, driving variation in group-level behavioural expression (Sih 2013).

The method used to measure behaviour, in the case of the direct human impact, field and bird data, were substantial sources of model heterogeneity. There are numerous different methods in which behaviours can be measured or observed (Cuthill 1991). For example, 'boldness' has been used to define different traits across different studies, which can make inter-study comparisons difficult (Beekman and Jordan 2017). Whether an individual expresses 'activity', 'exploration' or 'boldness' depends on the environment, context and the timescale of any environmental change. Exploration refers to movement in a new situation, activity refers to a non-novel, non-risky scenario and boldness refers to response to a risky situation (Reale et al. 2007). However, under HIREC, behaviours measured via movement could instead be recorded solely as exploration if we assume environmental change places organisms in new or risky situations. To accurately identify behavioural responses to HIREC, clear species-specific hypotheses, definitions and predictions are required.

Heterogeneity for phylogeny was generally small, suggesting that responses to HIREC do not reflect a shared evolutionary history. This result is perhaps to be expected, given that HIREC is a recent phenomenon (Wong and Candolin 2014), thus there has been little time for evolutionary divergence to occur. However, the role of phylogeny varied across taxa. While fish data had low heterogeneity estimates for phylogeny, bird data estimates for phylogeny were the highest at 26%. As mentioned above, changes in terrestrial environments are more variable than in marine environments (Steele

1985), so it is possible that birds have had a longer history of exposure to substantial environmental change, resulting in deeper divergence in response, explaining the higher phylogeny heterogeneity estimate. Phylogeny also explain 11% of variation in the field model. However, as fish comprised most of the laboratory data and birds most of the field data, we cannot determine whether there are response differences between taxa or the mode of study.

Future directions

Explaining the behavioural variation observed in our models, and the evolutionary consequences of HIREC, requires greater focus on differences in behaviours at the individual, rather than population level. This shift in focus is because individual variation in behavioural responses expressed within a population can define the strength of selection on behaviours imposed by HIREC. Moreover, focussing on individual variation expressed under HIREC via repeatability and/or heritability (via additive genetic variation) will allow for the strength of responses to selection to be quantified. Generally, repeatability and heritability of behaviours are moderate (Bell et al. 2009, Dochtermann et al. 2020), indicating that behaviours will respond to selection. However, it is unclear whether repeatabilities or heritabilities of behaviours expressed under HIREC differ from those measured under more normal or natural circumstances. Our models are focused on the population mean differences, as it is this level of response that dominates the current literature, so we cannot identify individual differences in responses to HIREC within a population. Understanding differences at an individual level, in terms of both individual differences and the heritability of behaviour (Hansen et al. 2011) would therefore deliver greater insight into the evolutionary ramifications of behavioural responses towards HIREC.

Conclusions

In conclusion, we have provided insight into predictors of behavioural responses to HIREC and offer four recommendations that, if addressed, would forward understanding of the mechanisms and drivers behind behavioural responses to HIREC. First, increasing the representation of field-based research for fish and laboratory-based research for birds is crucial to identify responses to HIREC in a variety of contexts and to pinpoint underlying mechanisms in controlled settings. Secondly, standardisation of methods and study designs used to measure behaviours in both laboratory and field studies. Thirdly, consideration of context-specific factors, such as animal taxa, phylogeny and the specific sample of animals used in studies. Combined, this would greatly assist with identifying generalised responses and aid comparison across contexts. Finally, a greater consideration of individual differences in behaviour would improve understanding of both the evolutionary ramifications and the drivers of

behaviour that cannot be fully understood by considering population-level responses in isolation. A full understanding of the behavioural responses of organisms to HIREC, as well as the drivers behind these responses, can then be used to accurately predict broader scale population and community-level dynamics.

Author contributions

Rachel L. Gunn: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Ian R. Hartley**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Adam C. Algar**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Petri T. Niemelä**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Sally A. Keith**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.hx3ffbgfb> (Gunn et al. 2021).

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