Experimental evidence for adaptive personalities in a wild passerine bird

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Individuals of the same species differ consistently in risky actions. Such 'animal personality' variation is intriguing because behavioural flexibility is often assumed to be the norm. Recent theory predicts that between-individual differences in propensity to take risks should evolve if individuals differ in future fitness expectations: individuals with high long-term fitness expectations (i.e. that have much to lose) should behave consistently more cautious than individuals with lower expectations. Consequently, any manipulation of future fitness expectations should result in within-individual changes in risky behaviour in the direction predicted by this adaptive theory. We tested this prediction and confirmed experimentally that individuals indeed adjust their 'exploration behaviour', a proxy for risk-taking behaviour, to their future fitness expectations. We show for wild great tits (*Parus major*) that individuals with experimentally decreased survival probability become faster explorers (i.e. increase risk-taking behaviour) compared to individuals with increased survival probability. We also show, using quantitative genetics approaches, that non-genetic effects (i.e. permanent environment effects) underpin adaptive personality variation in this species. This study thereby confirms a key prediction of adaptive personality theory based on life-history trade-offs, and implies that selection may indeed favour the evolution of personalities in situations where individuals differ in future fitness expectations.

Keywords: asset protection; life-history trade-offs; *Parus major*; animal personality; reproductive value; risk-taking behaviour

1. INTRODUCTION

Individual animals differ consistently in suites of behaviours comparable to how humans vary in personality [1–3]. Certain individuals are, for example, consistently more aggressive, bold, and explorative, than other individuals from their population [2,4]. Such personality variation has been reported for a wide range of taxa and may therefore represent a ubiquitous feature of animal populations. Yet, the persistence of divergent personality types in populations is not predicted by classic evolutionary theory [5,6]. Theoreticians have therefore recently developed adaptive explanations for the existence of personalities (reviewed in [5,7–9]), but predictions of their models await empirical testing.

Evidence for animal personalities comes primarily from research documenting individual variation in 'risky' actions that increase immediate fitness gains at the cost of later fitness losses [7]. Theoreticians have therefore largely focused on explaining variation in more 'risky' versus more 'cautious' personalities [10,11]. Historically, many studies have proposed adaptive explanations for between-individual differences in behaviour based on the idea that variation in individual 'state' underpins this variation [12,13]. Importantly, such 'classic' (*sensu* [14]) evolutionary models typically assume that individuals simply have a fixed behavioural type (e.g. genetically determined) and therefore do not provide an explanation for why behavioural differences are in fact repeatable [14]. More recent theory, in contrast, explicitly investigates conditions that would favour the evolution of repeatable individual differences in behaviour. Such modelling exercises show that individuals should differ consistently in their behaviour in situations where optimal behaviour is state-dependent and state is relatively stable [10,15,16]. In this study, we focus on a recent state-dependent personality model by Wolf *et al.* [11] who used game theoretical modelling and simulations to explain personality variation based on the asset protection principle. Asset protection theory essentially predicts that

animals should take more risks when they do not have much to lose [17]: individuals with high assets, i.e. high future fitness expectations, should aim to live long enough to harvest these assets and therefore behave consistently risk-averse. Individuals with low assets should instead behave more risk-prone. In their model, Wolf *et al.* [11] demonstrate that asset protection can explain both the evolutionary emergence of repeatable variation in risky behaviour as well as the emergence of syndromes of risk-related behaviours, such as the commonly documented aggressiveness–boldness syndrome [18]. The idea that individual variation in future fitness expectations would lead to the evolutionary emergence of personality through asset protection has, however, also been criticized because long-term individual differentiation should only emerge in situations where assets and risky behaviour mutually reinforce each other by means of positive feedback mechanisms [19]. Descriptive studies have provided examples of correlations between future assets and risk-taking behaviour that are consistent with predictions of Wolf *et al.*'s model [20,21] but these patterns warrant experimental validation. In the current study, we therefore describe manipulations that are known to affect future fitness expectations and explicitly investigate long-term rather than direct (e.g. short-term) effects on risky behaviour.

To test the prediction that individuals adjust risk-taking behaviour to changes in assets [11], we experimentally altered the breeding environment known to affect future fitness expectations of wild great tits (*Parus major*), and measured exploration behaviour of a large number of birds before and after the manipulation. Future fitness expectations were manipulated by altering both parental brood size and competitive regimes via fledgling sex ratio manipulations in 12 study plots of a spatially structured population of great tits. We have previously shown that the interaction between the brood size and the sex ratio manipulations induced significant variation in annual adult survival probability among treatment groups [22]: survival probability significantly declined with increasing brood size and with an increasing proportion of males in the local environment (range of survival probabilities among treatment groups = 0.25–0.47; in male-biased plots, adding three nestlings reduced survival probability by about 44%; see the electronic supplementary material S1 for further details). Our previous work suggests that these experimental effects on survival originated from the interaction between competitive ability of the parents (owing to the brood size manipulation) and the strength of intra-specific competition for local resources (due to the fledgling sex ratio manipulation; [22]). In the current study, we make use of this experimental variation in survival probability to test a key prediction of adaptive personality theory by evaluating whether individuals within treatment groups with reduced future survival probability increased their risk-taking behaviour more than those in treatment groups with increased future survival probability. We used within-individual changes in the speed of exploration in a novel environment before versus after the manipulation as proxies for changes in risk-taking behaviour. We did so because previous work has shown that in two different populations, speed of exploration correlates positively (both phenotypically and genetically) with aggressiveness

and risk-taking behaviour [23,24]. Moreover, given that great tit populations show relatively little genetic structuring even among large spatial scales [25], we assumed that correlations between risky behaviours and exploration also exist in our study population. Because 'fast' explorers explore their environment faster but more superficially compared with 'slow' explorers [23,24], we expected an increase in risk-taking behaviour to translate into an increase in the speed of exploration for birds experiencing decreases in future fitness expectations. The speed of exploration is both repeatable [26] and heritable [27–29] in natural populations.

Provided that individuals can adjust their behaviour to their state, the explanation by Wolf *et al.* [11] for between-individual differences in behaviours [11] comes with an explicit prediction about how individuals should *change* their behaviour in response to changes in state [7]. For a naive reader, this prediction might seem counterintuitive because personality exists when individuals are relatively stable in their behavioural expression. Nevertheless, phenotypic plasticity and consistency both support adaptive personality theory when they are tuned, respectively, to changes in state and to temporarily repeatable difference between individuals in state (i.e. future fitness expectations). Our experimental approach towards testing adaptive personality theory thus explicitly assumes that adaptive phenotypic plasticity underpins personality variation: by affecting the breeding environment known to affect the survival probability of parents, we induced long-lasting individual differences in 'state' (i.e. future fitness expectation) that are expected to lead to consistent individual differences in risk-taking behaviour post-manipulation. To validate this assumption, we used quantitative genetic approaches to partition the observed between-individual variation in exploration behaviour into its underlying permanent environment (V_{PE}) and additive genetic effects (V_A). Permanent environmental effects refer to environmental variation causing consistent individual differences over the time span within which the repeated measures were taken, i.e. they do not necessarily imply environmental effects that permanently affect the phenotype [30]. The existence of significant permanent environmental effects (i.e. $V_{PE} > 0$) would thus imply that non-genetic between-individual differences indeed characterize our population of great tits, and that variation 'state' should therefore be regarded as a possible explanation for personality variation in this system.

2. MATERIAL AND METHODS
(a) *Data collection*
The study was carried out in a nest-box population of great tits in the Lauwersmeer area in the north-eastern part of the Netherlands (53°23′ N, 6°14′ E), which was established in 1993 [22]. From 2005 onwards, the study site consisted of 12 woodlots (plots) that were partly separated by open grasslands, and fitted with 50 nest boxes each. Breeding was monitored using standard techniques detailed in [31].

A previous study, where brood sizes and nestling sex ratios were manipulated for 3 consecutive years (2005, 2006 and 2007), showed that these treatments affected annual survival probability of parents exposed to these manipulations ([22]; electronic supplementary material, S1; $n = 1012$ individuals).
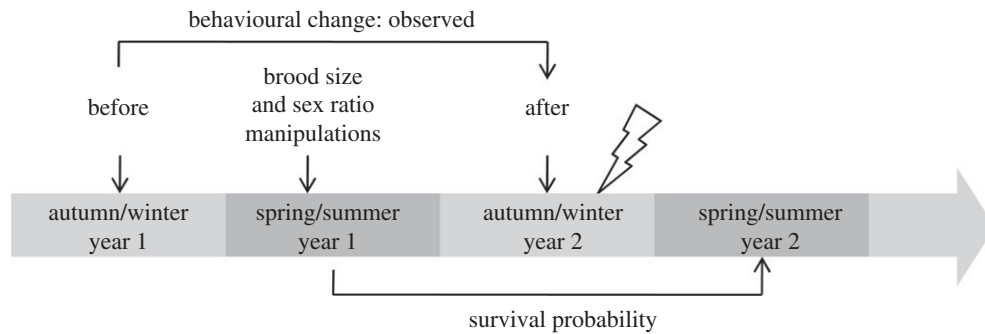
Figure 1. Experimental design. We previously showed that our manipulation of brood size and sex ratio induced variation in survival probability of manipulated parents [22]. In this study, we investigate whether this manipulation caused changes in exploration behaviour for 146 individuals that were assayed both before and after the manipulation. The second measurement was taken before most of the treatment-specific mortality occurred (as depicted by the lightening sign; see main text), approximately 5–8 months after the manipulation was applied.

In the current study, we make use of 2 years of this experiment, 2006 and 2007 ($n = 688$ individuals), because behavioural data were not available for the year 2005, and ask whether treatment groups with reduced future survival probability increased their risk-taking behaviour more than treatment groups with increased future survival probability (figure 1). Here, we provide only a brief summary of the experimental protocol that has been detailed extensively elsewhere [31]. In short, nestlings were blood sampled when they were 2 days old and sexed molecularly. They were then exchanged between same-age nests when they were 6 days old to facilitate brood size and sex ratio manipulations. Brood manipulations were carried out such that broods were categorized as either 'female', 'control' or 'male' biased (approx. 25, 50 and 75% male nestlings) and as 'small', 'intermediate' or 'large'. We defined 'intermediate' broods as those equal to the average brood size of the population in a given year (e.g. 8); 'small' and 'large' broods differed, respectively, by −3 or +3 nestlings from the 'intermediate' brood size category (e.g. 5 or 11). Brood sizes were manipulated within plots, and sex ratios were manipulated between plots (for reasons outlined elsewhere; [31–33]). To achieve the plot level sex ratio treatments, all the broods of the same plot were sex-biased towards the desired treatment. These treatments were randomly assigned to plots in the first year of study (2005) and systematically randomized in the following year (to ensure that a plot would be given a different treatment the second year). The manipulation resulted in nine treatment groups within each of the 2 years (see the electronic supplementary material, S1).

Manipulated parents were caught with spring traps in the nest box of breeding, and fitted with an aluminium ring (if unringed at capture), when their offspring were 7 days old. Cross-year adult re-capture rates are close to one for this population (mean ± s.e.: 0.90 ± 0.05) [34], and breeding adults not re-captured from one year to the next were therefore considered dead. We previously showed that our manipulations affected annual survival probability of manipulated parents ($n = 688$ individuals, [22]): brood size enlargement decreased annual survival probability but only in male-biased plots (see the electronic supplementary material, S1). These treatment effects affected survival largely in the second half of winter [22], i.e. when most of the behavioural tests (detailed below) had already been repeated. This implies that all treatment groups had equal probability to be re-tested for risky behaviour. Survival probability was

thus estimated based on recaptures in the following spring rather than in early winter because the latter would lead to considerable upward bias in our estimate of survival.

Outside the breeding season, individuals were caught using mist nets at feeding stations or captured when roosting in nest boxes during winter. Exploration behaviour was assayed in a 'novel environment room' in winter (November–February) following standard procedures established for this species [27]. Details regarding housing and testing conditions are given in [26,27]. Exploration scores were calculated as the total number of flights and hops within the first 2 min after arrival in the room as detailed in [26,27] and subsequently used as a proxy for risk-taking behaviour. For individuals sampled more than once per winter, we only use their first test score in the statistical analyses. We restricted subsequent analyses only to individuals that were tested both in the winters before and in the winter after the manipulation (figure 1; $n = 146$ retained out of 688 individuals). To do so, we used behavioural scores collected in winter seasons of 2005 and 2006 (November–February) for individuals manipulated in spring 2006, and behavioural scores collected in winters 2006 and 2007 (November–February) for individuals manipulated in spring 2007.

(b) Statistical analyses

We used a general linear mixed-effects model (GLMM) to quantify whether within-individual changes in exploration score (after minus before manipulation) varied with the expected future survival probability of its treatment group (fitted as a continuous fixed effect). Expected future survival, centred on the control group's mean of a given year, was estimated for each combination of treatment and year (18 groups) using each group's estimated survival value based on the survival analysis described in [22]. This survival analysis modelled individual survival probability as a function of an individual's experimental brood size, experimental local sex ratio, interaction between the treatments and years. Random intercepts were included for plot, year and nest box (for details see [22]). Subsequently, we modelled within-individual changes in exploration score as a function of those expected future survival estimates. To account for substantial uncertainty around the survival estimates, we derived a posterior distribution of probable estimates for the 18 year-specific treatment groups using 1000 simulations of our survival analysis described above. We then modelled the within-individual changes of exploration score using

one of 1000 group-specific survival estimates for each run. We estimated the fixed effect coefficients and their 95% CIs using the coefficient distribution derived from these 1000 models [35]. Year-specific treatment group (9 treatment-groups × 2 years = 18 levels; 'cohort') was included as a random effect, such that the significance of treatment-specific survival probability could be estimated without bias due to pseudo-replication. Inter-test interval (days) and pre-manipulation exploration scores were also included as continuous fixed effects to control for previously documented effects of time of year [26,27] and statistical ceiling effects [36], respectively. Analyses of exploration behaviour in great tits typically also control for seasonal effects within years [26]. However, date was not be included in this case because inter-test interval and Julian date (the days from 1st July) effects are not statistically distinct in datasets such as these where each individual was represented only twice. Exploration score was normalized prior to analysis using square-root transformation and all fixed effects were centred on the population mean. We used the R package 'arm' in the R v. 2.14.1 for all statistical analyzes [37]. All GLMMs were performed using the function 'lmer' and the 1000 simulations were run using the function 'sim' [38]. We considered effects to be statistically significant if the 95% CI did not include zero. Total sample size was 146 individuals.

Preliminary analyses showed that neither sex (female/male) or year (2006/2007), nor their interaction with expected future survival significantly affected the response variable (estimates (95%CI): sex = −0.05 (−0.319, 0.080); year = 0.151 (−0.276, 0.303); sex × expected future survival = 0.053 (−0.375, 0.933); year × expected future survival = 0.467 (−0.082, 1.107)), and these terms were therefore not included in the model that we present in §3.

Alternative ways to analyse the data where post-manipulation risky behaviour (as opposed to changes in behaviour) was used as the response variable (detailed in electronic supplementary material, S2*a*) yielded the same general conclusions as presented in §3. Pre-manipulation exploration scores did not differ among our experimental groups (see the electronic supplementary material, S2*b*), implying that the application of treatments was not biased towards birds with certain behavioural types [39].

We used an 'animal model' [40,41] based on 1790 assays of 1243 individuals to partition the phenotypic variance in exploration score into its underlying between-individual (V_I) and within-individual (V_R) variance components, with a fixed effect structure detailed in electronic supplementary material, S3. We did not restrict our dataset to individuals that had been manipulated because (i) quantitative genetic analyses were used to verify whether, overall, environmentally induced differences between individuals underpin repeatable variation in exploration behaviour in the studied population (see §1) and (ii) the resulting small sample size would have greatly reduced the accuracy of the estimated variance components. As a second step, the between-individual variance was decomposed into its permanent environment (V_{PE}) and additive genetic (V_A) variance components. Repeatability (*r*) was calculated as $V_I/(V_I + V_R)$, i.e. the proportion of variance not explained by fixed effects (i.e. 'REML' variance) attributable to between-individual variation (so-called 'adjusted' repeatability; [42]; narrow-sense heritability (h^2) was calculated as $V_A/(V_A + V_{PE} + V_R)$, i.e. the proportion of REML variance attributable to additive genetic variation. The proportion of between-individual variance attributable

to environmental (as opposed to additive genetic) effects was calculated as $V_{PE}/(V_A + V_{PE})$. Permanent environment effects occur when individuals differ consistently from each other for other reasons than additive genetic effects [35], for example because of variation in previous experience with certain stimuli, 'condition' (e.g. energy reserves) or maternal effects [43]. Quantitative genetics parameters were fitted in ASR_EML_ v. 3.0 [44] following procedures advocated in [30,45] and detailed in electronic supplementary material, S3.

3. RESULTS

(a) *Future fitness expectations and risky behaviour*

All treatment groups increased their speed of exploration after the manipulation (implied by the parameter estimate; for the intercept value of the GLMM presented in table 1; intercept (95%CI) = 1.299 (1.056, 1.471); figure 2*a*, visually illustrated by the positive slopes of the reaction norm plots presented in figure 2*b*). This behavioural change was more pronounced with larger inter-test intervals and for individuals with low exploration scores in the previous year (table 1). Such temporal changes with repeated exposure have been documented for all West-European great tit populations where this trait has been quantified [26]. Importantly, even though all the birds increased their speed of exploration between the two tests, the extent of the increase in exploratory scores was inversely related to their survival probability as predicted (estimate (95%CI) = −1.938 (−3.288, −1.070); table 1). Within-individual changes in speed of exploration behaviour were negatively associated with the future survival probability of their treatment group: birds with enhanced survival prospects remained relatively slow in exploration, i.e. presumably more cautious, compared with other manipulation categories (table 1, figure 2*a,b*; panel 3 versus panels 1–2).

(b) *Decomposition of between-individual variation*

Quantitative genetics analyses (see the electronic supplementary material, S3) showed that exploration score was repeatable ($r \pm$ s.e. = 0.46 ± 0.03; χ^2_1 = 77.11, $p < 0.001$). Decomposition of the between-individual variance ($V_I \pm$ s.e. = 0.61 ± 0.05) into permanent environment and additive genetic variance components revealed both significant permanent environment ($V_{PE} \pm$ s.e. = 0.47 ± 0.07; LRT: χ^2_1 = 116.34, $p < 0.001$) and additive genetic (i.e. heritable) variation ($V_A \pm$ s.e. = 0.14 ± 0.06; LRT: χ^2_1 = 116.34, $p < 0.001$; $h^2 \pm$ s.e. = 0.10 ± 0.05).

Table 1. Sources of variation in within-individual changes in exploration behaviour of great tits. For each fixed effect, we give the estimates of modes of the posterior distributions and their 95% CI. Positive estimates imply that exploratory tendency (i.e. a proxy for risky behaviour) increases with increasing value of the fixed effect covariate.

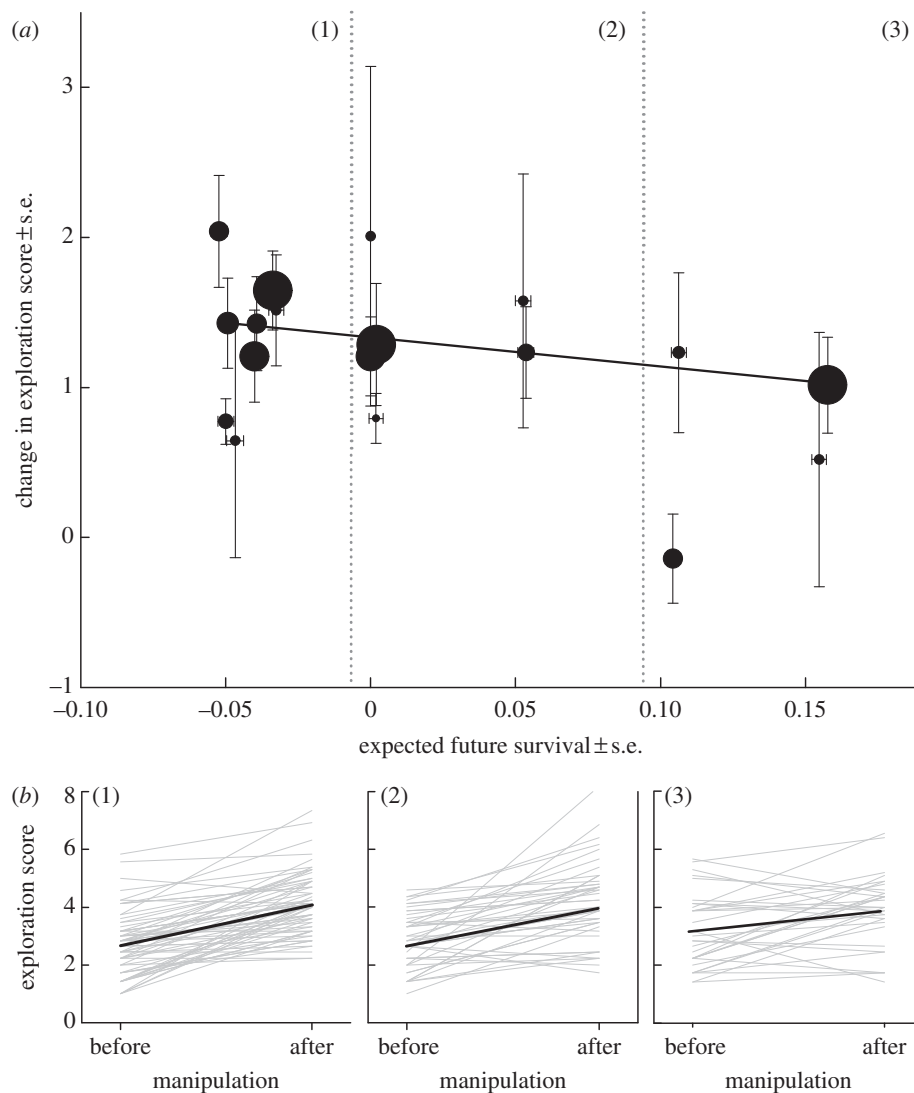| fixed effect	estimate	95% CI
intercept	1.299	(1.056, 1.471)
expected future survival	−1.938	(−3.288, −1.070)
pre-manipulation score	−0.466	(−0.478, −0.445)
inter-test interval	0.504	(0.482, 0.542)

Figure 2. Effects of experimentally induced variation in future survival prospects on exploratory behaviour within-individual great tits. (*a*) Within-individual change in exploration score (square root transformed) as a function of treatment-specific survival probability (we give here the raw data; nine categories per year, see the electronic supplementary material, S1), where the parameter estimate of expected future survival is the fitted line (*n* = 146 individuals). Dot size reflects sample size (range: 3–16 individuals). (*b*) Individual reaction norms of exploration score across time (raw data). For illustrational purposes only, we present here separate plots for treatment categories falling within the (1) 0–33, (2) 33–66 and (3) 66–100 percentile of 'expected future survival' range within each year (dotted lines in panel *a*).

The majority (77.54 $\pm$ 0.10%) of the between-individual variance was thus attributable to permanent environment effects.

4. DISCUSSION

In this study, we investigated whether individual great tits adjust exploration behaviour, a proxy for risk-taking behaviour in two other great tit populations, according to their future fitness expectations as predicted by adaptive personality theory based on life-history trade-offs [10]. In agreement with model predictions, we found that individuals whose survival prospects were most enhanced remained relatively more cautious compared with birds whose survival prospects were most decreased. This study thereby confirms a key prediction of adaptive personality theory, and implies that animal personality variation may indeed result from adaptive state-dependent decisions in populations where animals differ in future fitness expectations.

We explicitly assumed that adaptive phenotypic plasticity underlies personality variation in this system. Quantitative genetic analyses revealed that over 75 per cent of the between-individual variation in exploration behaviour was explained by non-genetic effects (i.e. permanent environmental variance). Given the substantial amount of non-heritable repeatable variation, our experimental approach thus represented a valid paradigm for this study species. Variation between individuals in exploration behaviour was, to a lesser extent, also caused by additive effects of genes. Additive genetic variance in exploration behaviour has previously been documented for various other West-European populations of this species (Belgium: P. Korsten, T. van Overveld, F. Adriaensen & E. Matthysen 2012, personal communication; the Netherlands: Dingemanse *et al.* [26]; United Kingdom: Quinn *et al.* [29]), and does thus appear to generally characterize great tit populations. We therefore propose that future research estimates genetic correlations between personality and life-history decisions

to reveal whether asset protection may also explain the maintenance of heritable variation in risky actions [46]. Moreover, behavioural ecologists would benefit tremendously from the development of adaptive theory that would predict the ecological conditions under which personality variation should be environmentally rather than genetically determined [6].

We used exploration behaviour as a proxy for risk-taking behaviour, assuming that more explorative individuals have a higher propensity to take risks. We are well aware that this behaviour represents a surrogate measure for risk-taking, and that confirmation of our findings based on risk-taking behaviour *per se* (e.g. anti-predator boldness) is now needed. We are taking up this challenge in our current research. Nevertheless, given the *a priori* nature of our hypothesis, we interpret our findings as experimental confirmation of predictions of the asset protection principle.

We have shown that individuals adjust exploration in a direction predicted by adaptive personality theory. One next important step will be to identify the proximate mechanisms and pathways underlying the changes in risk-taking behaviour as described in this study. We did not focus on this topic because Wolf *et al.*'s [10] model does not hinge upon specific mechanisms but rather provides the general predictions that state and behaviour become 'somehow' linked (for a full discussion see [6]). Insight into possible proximate pathways that facilitate the reported state-dependent changes in behaviour would nevertheless greatly facilitate our further understanding of how such patterns come about. For example, in our study, the increased investment into current reproduction in high competitive environments may have carried some physiological costs (e.g. reduced body reserves [47], reduced immune system [48] or delayed moult [49]) which may have led to stable differences in states and thus in state-dependent risky behaviour many months after the manipulation.

Future research may also address interactions (i.e. feedbacks) between assets and risky behaviour. In principle, three types of interactions are conceivable. First, when risky actions give rise to increased future assets (e.g. when risky behaviour is associated with monopolizing food resources [50], defending high-quality territories [51] or by dispersing into productive habitats [52–54]), differences in assets will decrease over time. Depending on the strength of this *negative* feedback and on the initial differences in assets, asset protection may then explain only short-term behavioural consistency [11]. Second, risk-prone individuals might invest acquired resources immediately (e.g. into current reproduction), which would not result in asset accumulation and thus preserve initial differences in assets and thus behaviour [55]. Third, assets and behaviour might be coupled by a *positive* feedback interaction: when more cautious behaviour is associated with increased future assets, any initial differences in assets will be reinforced and will lead to long-term behavioural consistency [11,55]. For example, by behaving cautiously, individuals with high future fitness expectations might reduce mortality risks (e.g. predation risk or agonistic interactions with conspecifics) which in return would reinforce their future assets. We have not addressed the interactions between assets and behaviour explicitly. Nevertheless, our manipulation of assets affected exploration, a proxy for risky behaviour, up to 8 months post-manipulation (the

mean ± s.e. interval between the manipulation and the post-manipulation exploration assay was 7.6 ± 0.07 months, $n = 146$ individuals), implying that any negative feedback that might have existed was not sufficient to erode variation in either assets or behaviour, and that asset protection therefore appears to provide an adaptive explanation for relatively long-term differences in avian personality.

In conclusion, this study demonstrated experimentally that between-individual variation in state in combination with asset protection provides a viable explanation for why between-individual variation in risky actions exists in natural bird populations. Our research has focused on a model organism for life-history evolution and personality research, where fitness components can be quantified under natural conditions [27,56]. The behavioural literature holds various examples of correlations between future assets and risk-taking behaviour that are in line with predictions and found in other species/taxa than great tits (e.g. mammals: [20], birds: [57], fish: [21]). Although such studies do not ultimately allow for confirmation of theoretical predictions because of their non-experimental nature, they do imply that the proposed evolutionary mechanisms revealed in great tits (i.e. asset protection) might generally apply to a diverse array of taxa, and that more experimental verification is now warranted.

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