**LETTER**

**Disentangling the roles of frequency-vs. state-dependence in generating individual differences in behavioural plasticity**

Kimberley J. Mathot,1* Piet J. van den Hout,2 Theunis Piersma,2,3 Bart Kempenaers,1 Denis Réale4 and Niels J. Dingemanse1

Abstract

Theoretical work suggests that both negative frequency-dependent payoffs and state-dependent payoffs can lead to individual variation in behavioural plasticity. We investigated the roles of both frequency- and state-dependence on the occurrence of individual variation in behavioural plasticity in a series of experiments where we manipulated perceived predation danger for red knots (*Calidris canutus islandica*). We found individual variation in plasticity in a trait with negative frequency-dependent payoffs (vigilance), but not in a trait with positive frequency-dependent payoffs (escape flights). Furthermore, there was no correlation between the average level of vigilance under low predation danger and the magnitude of response to increased predation danger, as would be expected under state-dependence. Thus, our results provide support for the hypothesis that negative-frequency dependence favours individual variation in plasticity. However, negative-frequency dependence alone cannot explain why plasticity would be consistent within individuals, and future studies should address the factors that might favour individual consistency.

Keywords

Anti-predation behaviour, behavioural plasticity, *Calidris canutus*, frequency-dependent, red knot, state-dependent.


**INTRODUCTION**

Although behaviour is often considered highly plastic, there is growing awareness that individuals not only show limited behavioural plasticity, but that individuals from the same population can also differ in their degree of behavioural plasticity (Dingemanse et al. 2010; Réale & Dingemanse 2010). For example, female great tits (*Parus major*) differ in how much they increase their provisioning effort in response to a chick's demand (Kölliker et al. 2000), and juvenile convict cichlids (*Amatitlania nigrofasciata*) differ in how rapidly they respond to the presence of a predator (Jones & Godin 2010). Given the potential selective advantage to individuals of being able to adjust their behaviour to current conditions, it is a challenge to understand why plasticity should be limited at all, and further, why it should differ between individuals (Wolf et al. 2008).

Recent theoretical work has shown that negative frequency-dependent payoffs can favour individual variation in behavioural plasticity (Eliassen et al. 2006; Wolf et al. 2008; Dubois et al. 2010). When the payoffs for a trait are negatively frequency-dependent, then plasticity exhibited by a single group member can benefit all group members. This would reduce the benefit to other group members to exhibit plasticity themselves. For example, in an ideal free distribution game, if patch A is being overexploited compared to patch B, a single individual exhibiting behavioural plasticity and shifting to patch B will reduce the benefit for any subsequent individual to also shift its behaviour. Under negative-frequency dependence, external factors (i.e. the behaviour of others) affect the payoffs experienced by an individual for a given behavioural choice. An alternative (non-exclusive) explanation for individual variation in behavioural plasticity is that individuals differ intrinsically in the benefits they derive from plasticity (i.e. state-dependent behavioural plasticity) (Wolf & Weissing 2010). For example, individuals may differ in their energetic state, which in turn affects the net benefit of continuing to exploit the current patch vs. moving to the next patch (Van Gils 2010). All else being equal, possessing greater energy reserves tends to favour a higher rate of transitions between patches (Van Gils 2010).

Although several studies have now documented individual differences in behavioural plasticity (Dingemanse et al. 2010; Morand-Ferron et al. 2011), we are not aware of studies which have attempted to disentangle the roles of frequency- vs. state-dependence in generating individual differences in behavioural plasticity. However, the extent to which each of these alternative mechanisms contributes to individual differences in behavioural plasticity has important implications. Under negative frequency-dependence, variation in behavioural plasticity should not be associated with inter-individual variation in fitness (Maynard Smith 1982). In contrast, under state-dependence, the payoffs experienced by individuals of differing states will not be equal (Houston & McNamara 1999).

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1Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard Gwinner Straße 7, 82319 Seewiesen, Germany

2Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

3Animal Ecology Group, Centre for Ecology and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

4Groupe de Recherche en Écologie Comportementale et Animale, Département des Sciences Biologiques, Université du Québec à Montréal, Case postale 8888, Succursale Centre-ville, Montréal, Québec, H3C 3P8, Canada

*Correspondence: E-mail: kmathot@orn.mpg.de

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In this study, we investigate the roles of both frequency- and state-dependence on the occurrence of individual variation in behavioural plasticity in red knots (Calidris canutus) by testing individual variation in plasticity in the same individuals for two behaviours that differ in the nature of their frequency-dependent payoffs: escape flight duration (positively frequency-dependent) and anti-predator vigilance (negatively frequency-dependent). In a series of controlled indoor experiments, red knots were exposed to three levels of predation danger and we recorded the duration of anti-predation escape flights and the proportion of time spent vigilant. Many aerial predators have a higher success rate capturing prey on the ground (Cresswell 1993; Dekker 1998), and birds can use escape flights to evade such predators. In this case, one individual in a group choosing to respond to a predator with an escape flight does not reduce the value of escape flights for other members of the group. In fact, the decision of one individual to engage in an escape flight will likely increase the value of escape flights for the remaining group members because dilution of predation risk will be reduced (Rudebeck 1950, 1951; Lima 1993). Even small deviations in the timing of escape flight initiation (i.e. fractions of seconds) can have important consequences for an individual’s probability of being depredated (Hilton et al., 1999), and variation in the timing of landing should similarly affect an individual’s probability of being depredated, resulting in positive frequency-dependent payoffs for overall escape flight duration. In contrast, anti-predation vigilance is negatively frequency-dependent, because all members of a group can benefit from the vigilance of a single group member (Pulliam 1973). Consequently, as soon as one individual increases its anti-predation vigilance in response to an increase in predation danger, the benefit for other members of doing so is diminished.

Given the contrasting patterns of frequency-dependent payoffs associated with plasticity in escape flights vs. anti-predation vigilance, if negative-frequency dependence favours the maintenance of individual variation in plasticity, we predict individual variation in plasticity for vigilance behaviour but not escape flights (Fig. 1a). Alternatively, if state-dependent variation in the benefit to plasticity underlies individual variation in plasticity, then we would expect to find (for both escape flight duration and vigilance) a significant correlation between the average level of the behaviour during the lower predation danger period, and the magnitude of the response to increased perceived predation danger. Asset protection models predict that individuals with the highest assets, such as energy reserves, should generally invest more in anti-predation behaviour and also show the strongest response to increasing predation danger (Clark 1994; Luttbeg & Sih 2010). State-dependent safety models predict the opposite effect of state, with high asset individuals investing less in anti-predator behaviour and also changing their behaviour less across a gradient of predation danger (Luttbeg & Sih 2010). These contrasting effects of state under asset protection vs. state-dependent safety models both predict a positive correlation between elevation and slope of a given anti-predation behaviour (Fig. 1b). However, state-dependent anti-predation behaviour may also generate a negative correlation between elevation and slope if the levels of anti-predation behaviours are constrained within a finite range of values. In this case, individuals with intrinsically greater vulnerability to predation may generally invest more in anti-predation behaviour, but also have little scope to further increase their investment with increasing predation danger, which would generate a negative correlation between elevation and slope (Fig. 1c). Importantly, state-dependent variation in anti-predation behaviour should always generate non-zero associations between elevation and slope. However, negative frequency-dependence and state-dependence are not mutually exclusive. If both mechanisms contribute to individual differences in behavioural plasticity, then the precise patterns of individual variation in plasticity and correlations between average behaviour and degree of plasticity will depend on the relative contribution of each in generating individual differences in plasticity.

MATERIALS AND METHODS

Study subjects

Fifty knots of the islandica subspecies were captured using mistnets on the mudflats of Richel 53°16’57” N, 05°23’82” E. and Simonsand 53°29’28” N 06°24’19” E, in the Wadden Sea, The Netherlands, on 8 August and 3 September 2005. Birds were housed in avaiaries (3.85 m by 1.85 m and 2.40 m high) at the Royal Netherlands Institute for Sea Research (NIOZ) prior to experiments in four flocks of 12 to 13 birds. The aviary floors were kept wet with a constant stream of seawater. A tray of running freshwater for drinking and bathing was always present, and food (the mudsnail Hydrobia ulvae) was provided ad libitum. Each individual was given a unique combination of 1 to 4 colour flags prior to experiments. All birds were in good condition following the experiments, with an average mass of 127.7 g [range 101.1–147.3 g which is within the normal range for this species (Piersma & Davidson 1992; Piersma 2007)]. After the experiments, between September and December 2005, birds were released into the wild during low tide at a mudflat near the experimental facility. The experiments complied with Dutch law regarding animal experiments (Dutch animal ethics committee licence NIOZ 04.04).

Experimental setup

The experiments took place from 21 August through 28 November 2005 at the indoor mudflat facility of the NIOZ (7 by 3 m and 3.5 m high). A schematic layout of the experimental mudflat is presented elsewhere (Mathot et al. 2009). During the experiments, a constant photoperiod was implemented (lights on from 0600 h to 2100 h), with ‘moonlight’ mimicking illumination being provided during the dark phase. A total of 48 birds were used in the experiments, with 6 individuals in each of 8 flocks. Individuals were assigned to flocks randomly, and flocks were tested in random order in the experimental mudflat facility (see below for details). Each trial consisted of a 2 day habituation period, followed by a 5 day control and a 5 day experimental period. The order of experimental and control periods was determined at random for each flock, with four flocks receiving the experimental period first, and four flocks receiving the control period first. During the experimental period of the trials, two event types were used to elevate predation danger. The first involved presenting a model of a perched sparrowhawk supplied with a built-in electromotor which allowed head movement (intermediate predation danger). The perched sparrowhawk model was hidden behind a black curtain except during ‘perching’ events, when the curtain was lifted and the perched model was rolled into the mudflat arena for 1 min, approximatly 0.5 m above the mudflat surface. The perching sparrowhawk faced directly away from the plane of the wall from which it emerged, and the side-to-side head movements encompassed ~ 90° angle. Consequently, the
perching sparrowhawk scanned the entire artificial mudflat. The second event type consisted of a gliding sparrowhawk model accompanied by digital recordings of red knot alarm calls (high predation danger). The stuffed model glided across one end of the mudflat, passing over the food tray. During the experimental period, perching and gliding events were carried out once each day at randomly assigned times between 0930 h and 1700 h with the constraint that the two event types not occur within 90 min of each other to allow sufficient time for focal observations between events. Because the order of perching and gliding events was randomised for each of the five experimental days for each flock, there were no systematic differences between flocks in the order that treatments were experienced, and therefore order effects cannot account for flock-level differences in response, nor could they account for differences in mean response to intermediate vs. high predation danger treatments.

During all phases of the trials (i.e. habituation, control and experimental), the mudflat was flooded briefly with sea water (for between 10 and 30 min) at 1800 h to clean it. During this time, the birds could rest on an elevated roosting platform. Food was also replaced at this time. Trays of *Hydrobia* were provided in sufficient quantity to allow *ad libitum* feeding for the following 24 h.

**Behavioural observations**

Extensive behavioural observations were carried out to assess the general responses of red knots to gradients in predation danger, and these results are presented elsewhere (Mathot et al. 2009). To evaluate individual differences in plasticity, we compared vigilance and escape flight behaviour across three levels of predation danger. Behavioural observations were carried out on each flock member immediately after each predator event type, as well as observations matched for the same time of day as the perching sparrowhawk event made during the control period (i.e. no predator present). This yielded a total of five observations for each of 48 individuals for each level of predation danger (no predator present = low danger, perching sparrowhawk = intermediate danger, gliding sparrowhawk = high danger), generating a total of 720 observations for vigilance, and 480 observations for escape flights. The duration of each focal observation was 5 min. Escape flights never occurred when no predator was present, and therefore no observations were generated for this behaviour during the control period. The order of observation of individuals was randomised for each observation period. Focal observations were made from behind a 1-way mirror, dictated into a recorder, and later transcribed using the Observer 3.0 Event Recorder software (Noldus Information Technology, Wageningen, The Netherlands). All observations were carried out by KJM. Vigilance behaviour, defined as the bill being parallel to the horizon or higher with accompanying side-to-side movement of the head, was scored to allow us to calculate the proportion of time spent vigilant for each individual across different levels of predation danger treatments.

**Statistical analyses**

We followed Nussey et al.’s (2007) hierarchical approach for testing individual variation in reaction norm components. Because the experiment consisted of categorical levels of predation danger, analyses for changes in anti-predation behaviour were carried out in two steps: between low and intermediate predation danger (for vigilance only), and between intermediate and high predation danger
(for both vigilance and escape flights). This approach, with only two levels of the environmental factor in each reaction norm analysis was possible because we had five repeated measures per individual for each category of the environmental variable. This approach also allowed the anti-predation behaviour of individuals to be modelled as a continuous function of predation danger within each analysis, and made it possible to investigate non-linear effects of predation danger on anti-predation behaviours by comparing effect sizes across the gradient from low to intermediate predation danger vs. intermediate to high, where unequal effect sizes would indicate non-linear effects. Spurious significant individual variation in reaction norms (I × E) can appear because of uncontrolled between-flock differences in reaction norms. Random slopes for flocks were significant in all cases (all \( P < 0.001 \), see Supplementary Table S1), and therefore we included random slopes for flocks in the basic models (models 1.1, 2.1 and 3.1 in Table 1). Starting from the described basic model, random intercepts for individuals (I) were added followed by random slopes for individuals (I × E). The significance of added random effects was tested using a likelihood ratio test (LRT) over two degrees of freedom because two extra random parameters were estimated: variance in slopes and the covariance between elevations and slopes (Pinheiro & Bates 2000).

Models were constructed using R v.2.10.1 (‘lmer’ function of the ‘lme4’ package of the R statistical computing environment, The R Foundation for Statistical Computing, Vienna, Austria (R Development Core Team 2008)). Models for escape flight behaviour were analysed using a Poisson error distribution. Models for the proportion of time spent vigilant were analysed by specifying a binomial error distribution (family = binomial), where the response variable was a two-column matrix representing the count of ‘successes’ (i.e. seconds spent vigilant) and ‘failures’ (i.e. seconds spent on behaviours other than vigilance). We included ‘day’ (1 through 5) as a covariate in all models to control for any potential habituation over the course of the experiments. For each final model we estimated the repeatability of anti-predation behaviour (escape flights or vigilance) following Nakagawa & Schielzeth’s (2010) methods for non-Gaussian data. Conventional methods for calculating repeatability do not take into account the possibility of individual variation in slope, which will result in an underestimate of behavioural consistency when I × E is present if a single repeatability is estimated across all levels of the environmental gradient (E) (Hayes & Jenkins 1997; Martin et al. 2011). Consequently, when final models included significant random slopes for individuals, environment specific repeatabilities were calculated following Martin et al. (2011). In other words, one repeatability value was estimated for each predation danger category (low, intermediate and high).

Where significant individual variation in reaction norms was found, we tested for the significance of the elevation-slope covariance by comparing a model where it was estimated with one where it was constrained to be zero using a LRT over one degree of freedom. It is generally recommended to centre fixed effects on the median value (Pinheiro & Bates 2000). However, our predictions regarding correlations between elevation and slope are explicitly formulated with reference to the level of the behaviour during the lower predation danger context. Consequently, in one analysis, low predation danger was coded as 0 and intermediate predation danger as +1, and in the subsequent analysis intermediate predation danger was coded as 0 and high predation danger as +1. Thus, a positive covariance would indicate the hypothetical patterns shown in Fig. 1b. For all tests, significance was set at \( P < 0.05 \).

### RESULTS

Red knots responded immediately to predator events with escape flights. Although the duration of escape flights tended to be longer following high danger predator events compared with intermediate danger events (estimated effect size 0.92 ± 0.77 s, mean ± SE), the overall effect of danger was not significant (Table 1, model 1.2, \( z = 1.204, P = 0.23 \)). There was a small (estimated effect size 0.059 ± 0.006) but significant effect of day (\( z = 10.20, P < 0.001 \)). However, there were significant differences between flocks in how they responded to changes in predation danger (Fig. 2). There were significant individual differences in intercept (I), but no individual differences in reaction norms (I × E) for escape flights within flocks (Table 1, comparison of model 1.2 vs. model 1.3). The individual repeatability of escape flight behaviour was 0.15%.

Red knots showed threat sensitive adjustment in vigilance behaviour. Overall, the proportion of time spent vigilant increased with increasing predation danger (low to intermediate: estimated effect size 1.34 ± 0.35, \( z = 3.83, P < 0.001 \); intermediate to high: estimated effect size 1.08 ± 0.29, \( z = 3.64, P < 0.001 \)). There were also small but significant effects of day (low to intermediate: estimated effect size 0.013 ± 0.004, \( z = 2.99, P = 0.003 \); intermediate to high: estimated effect size -0.038 ± 0.005, \( z = -7.51, P < 0.001 \)). Again, there were both flock and individual differences in patterns of anti-predation vigilance (Fig. 3). There were significant individual differences in both Tables 1 Hierarchical models describing anti-predator behaviour (either escape flight duration or proportion of time spent vigilant) of 48 red knots as a function of experimentally manipulated predation danger (E)

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>Flock</th>
<th>Flock × E</th>
<th>I</th>
<th>I × E</th>
<th>log L</th>
<th>Test</th>
<th>LRT</th>
<th>d.f.</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Escape flight duration (int – high)</td>
<td>Model 1.1</td>
<td>5.64</td>
<td>4.62</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Model 1.2</td>
<td>5.63</td>
<td>4.62</td>
<td>0.0049</td>
<td>—</td>
<td>—</td>
<td>2.828</td>
<td>1.1 vs. 1.2</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Model 1.3</td>
<td>5.63</td>
<td>4.62</td>
<td>0.0063</td>
<td>3.18e-4</td>
<td>—</td>
<td>2.8225</td>
<td>1.2 vs. 1.3</td>
<td>0.75</td>
<td>2</td>
</tr>
<tr>
<td>Proportion of time vigilant (low – int)</td>
<td>Model 2.1</td>
<td>0.71</td>
<td>0.94</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Model 2.2</td>
<td>0.71</td>
<td>0.98</td>
<td>0.35</td>
<td>—</td>
<td>—</td>
<td>2.6191</td>
<td>2.1 vs. 2.2</td>
<td>7445.9</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Model 2.3</td>
<td>0.72</td>
<td>0.88</td>
<td>0.25</td>
<td>0.65</td>
<td>—</td>
<td>2.4823</td>
<td>2.2 vs. 2.3</td>
<td>2736.5</td>
<td>2</td>
</tr>
<tr>
<td>Proportion of time vigilant (int – high)</td>
<td>Model 3.1</td>
<td>0.21</td>
<td>0.36</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Model 3.2</td>
<td>0.13</td>
<td>0.42</td>
<td>0.63</td>
<td>—</td>
<td>—</td>
<td>-23987</td>
<td>3.1 vs. 3.2</td>
<td>9126.5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Model 3.3</td>
<td>0.17</td>
<td>0.32</td>
<td>0.94</td>
<td>1.95</td>
<td>—</td>
<td>-21667</td>
<td>3.2 vs. 3.3</td>
<td>4640.0</td>
<td>2</td>
</tr>
</tbody>
</table>

The estimated variance is given for terms included in the models. “—” indicates terms that were not included in the models. Models are nested with increasingly higher order terms, where the significance of each higher – order term is based on the increase in the log likelihood (log L). Escape flight duration was expressed in seconds, and was modelled with a Poisson error distribution. Vigilance was modelled with a binomial error distribution. For each dependent variable, the best model is indicated in bold.

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intercept (I) and in the reaction norm (I × E) for vigilance behaviour across the gradient from low to intermediate predation danger, as well as the gradient from intermediate to high predation danger (Table 1). The repeatability of vigilance behaviour was 7.18% at low predation danger, 22.37% at intermediate predation danger and 34.23% at high predation danger. There was no evidence of a significant correlation between intercept and slope across the gradient from low to intermediate predation danger ($\chi^2 = 2.62, \text{d.f.} = 1, P = 0.11, r = 0.06$). However, there was a significant negative correlation between the intercept and slope across the gradient from intermediate to high predation danger ($\chi^2 = 9.80, \text{d.f.} = 1, P = 0.0017, r = -0.45$); individuals that spent the lowest proportion of time vigilant under intermediate predation danger showed the greatest response to the increase in predation danger. An individual’s behavioural plasticity in the proportion of time spent vigilant was negatively correlated across the two contexts (i.e. from low to intermediate danger and from intermediate to high danger) ($r^2 = 0.21, F_{1,46} = 12.27, P = 0.001$, Fig. 4). Overall, our results are consistent with negative frequency-dependent payoffs for plasticity favouring individual variation in plasticity (I × E) (Fig. 1a).

**DISCUSSION**

We investigated individual variation in behavioural plasticity in red knots in two anti-predation behaviours with contrasting patterns of frequency-dependence: escape flights (positive frequency-dependent payoffs) and vigilance (negative frequency-dependent payoffs). Although flocks differed in their escape flight behaviour in relation with the level of predation danger, within flocks individuals were highly cohesive, and there was virtually no between-individual
variation in escape flight duration. In contrast, individuals differed in their degree of plasticity for the proportion of time spent vigilant across a gradient of predation danger. We did not find any evidence that the proportion of time spent vigilant under low predation danger was correlated with the degree of behavioural plasticity, as predicted if plasticity were state-dependent. However, we did find a negative correlation between the proportion of time spent vigilant under intermediate predation danger and the increase in vigilance under high predation danger. Our results provide support for the prediction that negative-frequency dependence favours individual variation in plasticity (Wolf et al. 2008; Dubois et al. 2010), while positive-frequency dependence favours cohesiveness among group members. However, the mechanism generating consistent individual differences in plasticity remains to be revealed.

On average, knots responded to the gliding sparrowhawk model with longer escape flights compared with the perching sparrowhawk (Mathot et al. 2009). However, within flocks, there was no individual variation in behavioural plasticity for the duration of escape flights following presentation of a model predator. We are confident that this result is not due to lack of statistical power, because it is based on 480 observations (10 observations for each of 48 individuals), which is well above the recommended sample size of 200 for random regression analyses (Martin et al. 2011). Furthermore, visual inspection of the data suggests no trend towards individual variation in escape flight duration within flocks (Fig. 2). We interpret the lack of individual variation in plasticity for escape flight durations as evidence that positive-frequency-dependent payoffs constrain the expression of individual variation in plasticity. This interpretation hinges on the underlying assumption that escape flight durations exhibit positively frequency-dependent payoffs. This assumption is widely supported in the literature, particularly for Charadriiformes, where coordination of escape flight behaviour among flock-mates increases their

Figure 3 Proportion of time spent vigilant as a function of experimentally manipulated predation danger: no sparrowhawk = low predation danger, perching sparrowhawk = intermediate predation danger, gliding sparrowhawk = high predation danger. Lines connect the mean proportion of time spent vigilant (±1 s.e.) for individuals across the three levels of predation danger, and individuals are offset from one another for clarity.
Individual differences in behavioural plasticity were observed for the proportion of time spent vigilant. The general trend was for a higher proportion of time to be spent vigilant with increasing predation danger (Mathot et al. 2009). However, the pattern differed markedly between individuals (Fig. 3). This result is consistent with the prediction that negative frequency-dependent payoffs allow for individual variation in plasticity. The assumption of negative frequency-dependent payoffs for plasticity in vigilance behaviour is based on the premise that an increase in the vigilance behaviour of some group members can benefit all group members (also known as the ‘many eyes hypothesis’) (Pulliam 1973; Lima 1990, 1995). This idea has been supported by many studies, including several studies of vigilance behaviour in non-foraging contexts (Redpath 1988; Burger 1992; Roberts 1996, 2003), where increased competition for food could be discounted as an alternative explanation for the decrease in vigilance with increasing group size. If individuals can benefit from the collective vigilance of their congeners, then the payoffs for plasticity in vigilance behaviour should be negatively frequency-dependent because under changing levels of predation danger, plasticity exhibited by a single group member can benefit all group members, reducing the incentive for those group members to exhibit plasticity themselves. Although we observed strong individual variation in plasticity for vigilance behaviour, it is interesting to note that the patterns of behavioural plasticity among individuals in flock 1 differed dramatically from the other flocks, and appear more consistent with patterns expected under positive frequency-dependence. Given that the experiments were carried out under standardised conditions, and that individuals were randomly assigned to flocks, the reason as to why the patterns of behavioural variation in this flock differed from the other flocks is unclear.

Although negative frequency-dependence can explain how individual variation in plasticity could occur, it is not sufficient to explain why individuals should differ consistently in their degree of behavioural plasticity. Yet we did find that the individual differences in plasticity observed in this study were consistent across repeated observations of the same individuals. Several state variables have been identified that influence investment in anti-predation behaviours, including age, sex and dominance rank (Caro 2005), and state-dependent behavioural plasticity is one mechanism through which consistent individual differences in plasticity could persist. Under state-dependence, we would predict correlations between the average level of vigilance during the lower predation danger period, and the magnitude of the response to increased perceived predation danger. We did not observe any correlations between intercept and slope across the gradient from low to intermediate danger, suggesting that individual differences in plasticity across this gradient in predation danger cannot be explained by state-dependent payoffs for plasticity. However, we did observe a negative correlation between intercept and slope across the gradient from intermediate to high predation danger, which is likely due to the fact that the proportion of time spent vigilant is constrained to values between 0 and 1 (i.e. numerical constraint: Fig. 1c). Any individuals that increased their vigilance markedly between low and intermediate danger necessarily had less scope to further increase their vigilance between intermediate and high danger. This interpretation is supported by the observation that individual plasticity across the first gradient of predation danger was negatively correlated with plasticity across the second gradient (Fig. 4). Thus, taken together, our results do not provide strong evidence in support of state-dependent plasticity. However, birds in this study had ad libitum access to food throughout the experiments which may have reduced individual differences in state. It would be interesting to test whether or not patterns of elevation-slope covariance differ when animals are tested under conditions where they are forced to compete for limited resources.

If individual differences in plasticity observed in this study do not reflect state-dependent benefits to plasticity, why do individuals differ consistently in their behavioural plasticity across the gradient from low to intermediate predation danger? Earlier theoretical work has suggested that consistent differences in plasticity may come about via positive feedbacks, whereby the cost of being plastic is reduced for individuals that have previously been plastic (Wolf et al. 2008). However, these types of positive feedbacks are expected to generate cross-context correlations in plasticity (Wolf et al. 2008), which was not the case in our study (see Fig. 4). An alternative explanation for consistent individual differences in behavioural plasticity is learning (Sih et al. 2004; Morand-Ferron & Giraldeau 2010; Morand-Ferron et al. 2011). In a game-context, where an individual’s optimal investment in a behaviour depends both on extrinsic factors and the behaviour of congeners, developing consistent behavioural responses to particular conditions may allow groups to reach equilibrium levels of behaviour more rapidly (Morand-Ferron & Giraldeau 2010), if the same group encounters the same conditions repeatedly. Learning as a mechanism generating repeatable individual differences in behavioural plasticity is consistent with the findings from at least two other studies. In one study, Morand-Ferron et al. (2011) found that individual nutmeg mannikins (Lonchura punctulata)
showed consistent individual differences in plasticity in two behav-
ioral games (patch choice and producer-scrounger foraging), but that
individual plasticity was not consistent across games (where both
context and group composition were changed). In another study,
Rieucau et al. (2010) found no evidence of individual variation in
plasticity for vigilance behaviour in nutmeg mannikins as a function of
increasing group size. Although statistical power may have been an
issue in the latter study (Martin et al. 2011) (only six individuals were
observed eight times each), the lack of individual differences in
plasticity is also consistent with learning as a mechanism underlying
consistent individual differences in plasticity. In their study, each focal
individual was observed in a new group composition across each
repeated observation within the same context (i.e. group size)
(Rieucau et al. 2010), which would preclude any advantage to learning.
Although our findings support the notion that negative frequency-
dependent payoffs for plasticity can favour individual variation in
behavioural plasticity, future studies should investigate the role of
learning in the development of consistent individual differences in
plasticity (Morand-Ferron et al. 2011).

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AUTHORSHIP

KJM, PvdH, and TP designed the study. KJM and PvdH collected the data.
KJM, DR and NJD performed the statistical analysis. KJM wrote
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REFERENCES

Burger, J. (1992). Drinking, vigilance, and group-size in white-tipped doves and
Press, Chicago.
reaction norms: animal personality meets individual plasticity. Trends Ecol. Evol.,
25, 81–89.
strategy choice by some keeps learning from evolving in others. Proc. R.

1324.
Fernández-Juricic, E., Gall, M.D., Dolan, T., O’Rourke, C., Thomas, S. & Lynch,
prey species: white-crowned sparrows and California towhees. Anim. Behav., 81,
705–713.
274–279.
speed of escape-flight response on attack by an avian predator. Behav. Ecol., 10,
391–395.
632.
quantitative genetic basis of offspring solicitation and parental response in a
Interpretation and Explanation in the Study of Animal Behaviour (eds Bekoff, M. &
Luttbeg, B. & Shi, A. (2010). Risk, resources and state-dependent adaptive
predator detection: insightful contrasts between a plow and a sandpiper. Proc. R.
differences in reaction norms in field and experimental studies: a power analysis
knots, Calidris canutus, to perching and flying sparrowhawk, Accipiter nisus, models.
individual phenotypic plasticity in wild populations. J. Evol. Biol., 20, 831–
844.
Piersma, T. (2007). Using the power of comparison to explain habitat use and
422.
R Development Core Team (2008). R: a language and environment for statistical
project.org Vienna, Austria.
Réale, D. & Dingemans, N.J. (2010). Personality and individual social specialisa-


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Table S1** Hierarchical models testing for flock-level differences in plasticity for antipredator behaviour (either escape flight duration or proportion of time spent vigilant) of 48 red knots as a function of experimentally manipulated predation danger (E).

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