



## Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos



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Behavioural traits can vary between individuals from the same population. These differences can involve consistent variation in the level of a particular behaviour (personality) or differences in the way individuals adjust their behaviour to environmental gradients (plasticity). In prey species, feeding rates and vigilance vary with environmental, social and individual factors and the feeding rate/vigilance relationship reflects the trade-off between food acquisition and safety. While feeding rates and vigilance have been shown to vary between individuals in relation to group size and predation risk, how they relate to other factors has not yet been investigated, nor has between-individual variation in this trade-off. We studied between-individual variation in vigilance, feeding rates and their trade-off in female eastern grey kangaroos, *Macropus giganteus*, to see whether females showed consistent behavioural differences and different plasticity in relation to ecological (food patch richness), social (group sizes) and physiological (reproductive states) conditions. We addressed two contrasting hypotheses: an 'ecological' hypothesis under which individuals facing the same conditions should behave similarly, and a 'behavioural' hypothesis under which they should behave differently because of their own personality or plasticity. Female kangaroos tended to adjust their behaviours similarly in relation to ecological and social conditions, supporting the ecological hypothesis. However, they also showed differences in personality and plasticity in relation to their reproductive states that could not be explained by energetic demand alone; this was suggestive of different maternal strategies, thus supporting the behavioural hypothesis. Altogether these results suggest that consistent differences in animals' personality and behavioural plasticity can be promoted by physiological conditions and are not necessarily repeatable across different ecological contexts.

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Many behavioural traits are considered to be plastic, allowing individuals to adjust their responses to temporal variation in extrinsic and intrinsic factors (Briffa, Rundle, & Fryer, 2008; Hazlett, 1995). For instance, many prey animals have been shown to adjust their time allocated to vigilance and their feeding rate as group sizes vary (e.g. Lima, 1995; Rieucau & Giraldeau, 2009). Because numerous empirical studies have demonstrated that ecological drivers strongly affect behavioural adjustments, animals from the same population have often been assumed to behave similarly and many studies have considered unexpected individual variation in behaviour as 'noise' (reviewed by Lott, 1991). However, more recent

studies have focused on between-individual behavioural variation in a wide range of behaviours and demonstrated that a general pattern observed at the population level can hide a diversity of individuals' strategies (e.g. Carter, Pays, & Goldizen, 2009). Different individuals from a single population can exhibit (1) consistent behavioural differences in their mean levels of a behaviour (personality; Briffa et al., 2008; Dall, Houston, & McNamara, 2004; Dingemanse et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004), but also (2) different behavioural adjustments in response to environmental gradients (plasticity; Dingemanse, Kazem, Réale, & Wright, 2010). Two alternative hypotheses can be proposed to explain patterns of within-population behavioural differences. Under an 'ecological hypothesis', individuals that experience similar ecological or social conditions (e.g. patch quality, predation risk or group size) and have similar traits (e.g. age–sex class, body size or reproductive state) should experience the same ecological

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constraints and behave in the same way. In contrast, under a 'behavioural hypothesis', individuals should exhibit behavioural variation (different personalities) even when experiencing similar conditions and having similar characteristics, and may also show different behavioural adjustments to environmental conditions (different patterns of plasticity).

Between-individual variation has recently received considerable attention and has been shown to have both genetic and nongenetic bases (Nussey, Wilson, & Brommer, 2007), with the latter including individuals' past experiences (Stamps & Groothuis, 2010) or differing ecological and social niche specializations (Montiglio, Ferrari, & Réale, 2013). To investigate the existence of between-individual variation in personality and plasticity, recent studies have adopted a single framework called 'behavioural reaction norms'. This framework can be graphically represented by plotting an individual's behavioural response (y axis) as a function of an environmental gradient (x axis). The individual can be characterized by the intercept and the slope of its response, representing personality and plasticity, respectively (Dingemanse et al., 2010; Nussey et al., 2007). Therefore, under this framework, when individuals' behavioural responses do not differ in their intercepts and slopes, they do not exhibit different personalities or plasticity, when only the intercepts differ they show different personalities but similar plasticity in relation to the environmental gradient, and when both intercepts and slopes differ, they show different personalities and plasticity (Dingemanse et al., 2010).

Although a wide range of behavioural traits have been examined under this framework (reviewed by Mathot, Wright, Kempenaers, & Dingemanse, 2012), between-individual differences in vigilance and foraging activities have received little attention, despite these activities being crucial for the survival and fitness of many species. Indeed, vigilance is often assumed to incur foraging costs by limiting time available for feeding and by decreasing feeding rates, leading ultimately to a potential trade-off between foraging and vigilance activities (Lima & Dill, 1990). Negative relationships between vigilance time and feeding rate have been reported in many taxa (e.g. Cowlshaw et al., 2004; Fritz, Guillemain, & Durant, 2002; Ruckstuhl, Festa-Bianchet, & Jorgenson, 2003) and provide information on both the impact of a high investment in vigilance in terms of feeding rate and the ability of individuals to adjust their feeding rate with vigilance.

Despite vigilance, feeding rates and their trade-off not being considered as personality traits themselves, they have recently been shown to reflect animals' boldness in different species, with bolder individuals spending less time in vigilance and exhibiting higher feeding rates (e.g. Bergvall, Schäpers, Kjellander, & Weiss, 2011; Carter, Goldizen, & Heinsohn, 2012; Edwards, Best, Blomberg, & Goldizen, 2013). In addition, while vigilance and feeding rates are known to be affected by ecological drivers and individual traits such as group size (e.g. Rieucau & Giraldeau, 2009), food patch characteristics (e.g. Beauchamp, 2009; Pays et al., 2012) and reproductive state, including the presence of dependent young (e.g. Childress & Lung, 2003; Ruckstuhl et al., 2003), these behaviours have been shown to vary between individuals. For example, Rieucau, Morand-Ferron, and Giraldeau (2010) studied vigilance levels and feeding rates in nutmeg mannikins, *Lonchura punctulata*, in relation to group size and found that individuals differed in their mean response levels but showed similar adjustments as group size increased. In contrast, Carter, Pays, et al. (2009) found that eastern grey kangaroos, *Macropus giganteus*, exhibited significant differences in their mean levels of vigilance and also differed in their responses to an increase in group size. Finally, Mathot et al. (2011) showed that red knots, *Calidris canutus islandica*, varied in their adjustment of vigilance when predation risk increased. While these studies showed that patterns of vigilance and feeding rates can vary between

individuals in relation to group size and predation risk, it is not known how they vary in relation to other environmental or individual conditions. In addition, it is not known whether between-individual variation exists in the trade-off between feeding rates and vigilance and if this variation varies in different contexts.

We studied wild female eastern grey kangaroos to test whether patterns of individual variation in vigilance, in feeding rate and in the feeding rate/vigilance trade-off fitted the predictions of the ecological or behavioural hypotheses in relation to three environmental, social and physiological conditions. To do this, we used the behavioural reaction norm approach to test (1) whether there were overall adjustments of vigilance and feeding rates to changes in group size, patch richness and reproductive state across the population, (2) whether individuals differed in their responses to these factors, (3) whether group size, patch richness and reproductive state affected the trade-off between feeding rate and vigilance across the population, and (4) whether individuals experiencing similar environmental or social conditions (food patch richness or group size) or reproductive states differed in their trade-off between feeding rate and vigilance. Eastern grey kangaroos exhibit a fission–fusion social system, forming open-membership mixed-sex groups with individuals frequently joining and leaving groups (Clarke, Jones, & Jarman, 1995; Jarman, 1987). We focused on females as they have been shown to be more vigilant than males (Pays & Jarman, 2008), and as males were far less common in our population, collecting enough data for our analyses would have been challenging. Associations between females have been shown to be nonrandom (Best, Seddon, Dwyer, & Goldizen, 2013), with some females having preferred associates (Best, Dwyer, Seddon, & Goldizen, 2014; Carter, MacDonald, Thomson, & Goldizen, 2009), showing that females differ in their patterns of sociability. In addition, between-individual variation in vigilance has been previously described (Carter, Pays, et al., 2009; Dannock, Blomberg, & Goldizen, 2013) and related to boldness in eastern grey kangaroos, tending to support the behavioural hypothesis (Edwards et al., 2013). Ecological drivers and individuals' characteristics such as group size, patch attractiveness and reproductive states have also been reported to shape feeding rates and/or vigilance in this species (e.g. Favreau, Goldizen, & Pays, 2010; Garnick, Elgar, Beveridge, & Coulson, 2010; Gélín, Wilson, Coulson, & Festa-Bianchet, 2013; Pays, Jarman, Loisel, & Gerard, 2007).

## METHODS

### Study Site and Animals

Data collection was conducted in Sundown National Park (Queensland, Australia, 28°9'S, 151°58'E) for 2 weeks per month from January until December 2011. The study site was composed of open pastures surrounded by mixed open forests predominantly containing eucalypts, *Eucalyptus melanophloia*, and pines, *Callitris intratropica*. The study area contained 240 females and approximately 80 males (Best et al., 2013). Predators included red foxes, *Vulpes vulpes*, wedge-tailed eagles, *Aquila audax*, and possibly dingoes, *Canis lupus dingo*. All field work complied with the current laws of Queensland and Australia. This research was conducted with clearance from the University of Queensland's Animal Ethics Committee (AEC Approval Number: SIB/206/09/NF) and a Scientific Purposes Permit from Queensland's Department of Environment and Resource Management.

### Sampling of Individuals

We followed 34 identified adult female kangaroos of similar body size over the year. Identification of focal females was done

using features such as ear shape, dark or pale patches on the fur and facial markings and scars, and allowed the observer to follow specific females and avoid resampling individuals on the same day (Best et al., 2013; Coulson, 1997; Jarman et al., 1989). Since eastern grey kangaroos mainly forage at night, dawn and dusk and rest during the hot part of the day (Clarke, Jones, & Jarman, 1989), the observations were conducted during late afternoons and early mornings when light intensity was sufficient for accurate observations. The observer (F-R.F.) collected behavioural data by filming (video camera: Sony DCR-SR37, 60× optical zoom, Sony Corporation, Tokyo, Japan) the focal adult females for 10 min while they foraged in groups on the pasture. Videos were recorded by an observer on foot, keeping a minimum distance of 30 m between the focal individual and the observer to minimize disturbance. Because of the nearly continuous presence of researchers in the area, the kangaroos' behaviour did not seem to be affected by our presence during the study. The video sequences were used only if the group in which the focal animal was observed remained constant in size and composition during the observation period. To determine which individuals were included in a group, we used Jarman's (1987) 'chain rule', considering individuals that were within 15 m of their nearest neighbour to be part of the group. The observer never sampled a female more than once per observation session, and so individuals were sampled twice a day at the most. However, on some occasions several focal females were sampled consecutively in the same group. We collected between 32 and 38 focal samples per female, resulting in a total of 1135 behavioural observations from 962 groups.

### Quantifying Behaviour

Vigilance bouts were defined as when kangaroos raised their head above horizontal while either crouched or standing upright, and looked fixedly in one direction or scanned their surroundings (Jarman, 1987; Pays, Renaud, et al., 2007). We quantified bites either by direct observation of bites being taken or based on the quick jerky movements of the head characteristic of the biting of vegetation (Watson & Dawson, 1993). From each video sequence, we extracted the time spent in vigilance and the number of bites taken. We then calculated the proportion of time spent by kangaroos in vigilance and their bite rates (number of bites taken per minute) for each 10 min focal sample.

To study individuals in similar conditions, we measured the following variables for each focal sample. We recorded the group sizes and then categorized them into 'small' groups (1–4 individuals) and 'large' groups (5–30 individuals). We chose these categories because the mean  $\pm$  SD group size during our observation was  $4.64 \pm 3.5$ . We also measured characteristics of the patches exploited by focal individuals in terms of the quantity and quality of vegetation available. To do this, the observer estimated the height of the vegetation where the animal had spent most of its time feeding during the observation. Vegetation height was measured with a pasture meter (PM) and converted into biomass of plants. For the conversion, we calibrated the pasture meter for each season (i.e. summer, autumn, winter and spring) by selecting 60 patches of different heights. The relationship between vegetation height and biomass was measured by clipping, drying and weighing the plant biomass below the pasture meter (summer: biomass =  $4.26 + 2.29 \times \text{PM height}$ ,  $P < 0.001$ , adjusted  $R^2 = 0.85$ ,  $N = 60$ ; autumn: biomass =  $4.53 + 2.86 \times \text{PM height}$ ,  $P < 0.001$ , adjusted  $R^2 = 0.87$ ,  $N = 60$ ; winter: biomass =  $12.09 + 2.66 \times \text{PM height}$ ,  $P < 0.001$ , adjusted  $R^2 = 0.87$ ,  $N = 60$ ; spring: biomass =  $8.34 + 3.11 \times \text{PM height}$ ,  $P < 0.001$ , adjusted  $R^2 = 0.86$ ,  $N = 60$ ). To record the quality of the patches, the observer used a quadrat (90 × 90 cm) with 81 grid crossings, and assigned a

greenness index for all plants under each grid crossing. This index comprised two categories, brown (plants with low energetic value) and green (plants with high energetic value) (Bradbury, Vehrencamp, Clifton, & Clifton, 1996), and allowed us to estimate the percentage of plants that were green for each food patch.

These two characteristics of food patches allowed us to attribute a single patch richness index (i.e. poor patch, medium patch, rich patch) to each focal animal's feeding patch. As kangaroos prefer green grass and tend to avoid long dry grass (Bell, 1973; Clarke et al., 1989), the relationship between greenness, biomass and food intake is complex. Studies on the feeding preferences of other short-grass grazers of similar body size to the eastern grey kangaroo, such as sheep, *Ovis aries*, Thomson's gazelles, *Gazella thomsoni*, and red kangaroos, *Macropus rufus*, have shown that increasing grass biomass generally decreased digestibility (Fryxell, 1991). Such herbivores therefore tended to prefer to exploit patches of low to intermediate biomass for which forage digestibility remained high (Bradbury et al., 1996; Short, 1985; Wilmshurst, Fryxell, & Colucci, 1999). Under this framework we established an index of patch richness, in which rich patches were those at or within 30% of the optimum biomass and greenness for herbivores of kangaroo size, medium patches of intermediate richness were those from 31 to 60% from the optimal patch characteristics, and the poor patches were those furthest from the optimum (Table 1).

Following Jaremovic and Croft (1991) and Gélín et al. (2013), we recorded the presence and the size of pouch-young and young-at-foot of females (hereafter termed 'reproductive states'), as these should reflect the females' energetic needs from lactation demand. We differentiated females with no visible pouch-young (NPY), a small pouch-young (SPY), a medium pouch-young (MPY; when the young's head was sometimes visible), a large pouch-young (LPY; when the young left the pouch for short periods of time) or a young-at-foot (YAF; when the young was permanently out of the pouch but still nursing). In cases where a female had both a YAF and a SPY this was classified as YAF since the energetic demands of the SPY would have been much smaller than those of the YAF.

### Statistical Analyses

To test for the effect of time of day on vigilance, feeding rates and their trade-off, we included this variable in our preliminary analyses, but as it was never significant, we excluded it from subsequent analyses. To test for the effects of group size, patch richness and reproductive state on the vigilance and feeding rates of female

**Table 1**

Table of patch richness index for short grass grazers in relation to patch biomass and greenness

Biomass (g/m <sup>2</sup> )	Percentage of green grass						
	0–40	>40–50	>50–60	>60–70	>70–80	>80–90	>90–100
0–5	Poor	Poor	Medium	Medium	Medium	Medium	Medium
>5–10	Poor	Poor	Medium	Rich	Rich	Rich	Rich
>10–15	Poor	Medium	Medium	Rich	Rich	Rich	Rich
>15–20	Poor	Medium	Rich	Rich	Rich	Rich	Rich
>20–25	Poor	Medium	Rich	Rich	Rich	Rich	<b>Rich</b>
>25–30	Poor	Medium	Rich	Rich	Rich	Rich	<b>Rich</b>
>30–35	Poor	Medium	Rich	Rich	Rich	Rich	Rich
>35–40	Poor	Medium	Medium	Rich	Rich	Rich	Rich
>40–45	Poor	Poor	Medium	Rich	Rich	Rich	Rich
>45–50	Poor	Poor	Poor	Medium	Medium	Rich	Rich
>50–55	Poor	Poor	Poor	Medium	Medium	Medium	Medium
>55–60	Poor	Poor	Poor	Medium	Medium	Medium	Medium

'Poor': poor patch richness; 'medium': medium patch richness; 'rich': rich patch richness. Values for expected optimal patches are highlighted in bold.

kangaroos, we used linear mixed-effect models with the proportion of time spent in vigilance and bite rate as the response variables, respectively, and group size category (small and large), patch richness (poor, medium and rich) and reproductive state (NPY, SPY, MPY, LPY and YAF) as fixed effects, including individual identity as a random effect.

To test for between-individual variation in the levels and plasticity of the behavioural responses (vigilance and bite rates) to changes in group size, patch richness and reproductive state, we used linear random regressions following the reaction norm approach (Dingemanse et al., 2010; Nussey et al., 2007). We tested for consistent individual differences (i.e. individual variation in intercepts) in how vigilance and feeding rates were affected by each factor (group size, patch richness and reproductive state) separately. To achieve this we compared simple linear models with vigilance or bite rate as the response variables and the factor as a fixed effect with the same models but also including individual identity as a random effect. Then to test for between-individual differences in the plasticity of individual responses (i.e. individual variation in slopes), we compared each previous mixed-effects model with a model including the interaction between the factor tested and female identity as a random effect.

To test for behavioural differences in the trade-off between vigilance and feeding rates across conditions, we first adapted the reaction norm approach described previously to compare the average responses across all individuals to each particular condition for each factor tested (group size, patch richness, reproductive state). We thus compared for each factor a model containing bite rate as the response variable and the proportion of time spent in vigilance as a fixed effect with the same models but also including the factor tested as a random effect to test for consistent differences between conditions. Then to test for between-condition differences in plasticity, we compared the previous mixed-effects model with a model including the interaction between the proportion of time spent in vigilance and the factor tested as a random effect.

Finally, to test for between-individual variation in the trade-off between vigilance and feeding rates in each particular condition, we adapted the same method by first comparing a model including bite rate as the response variable and the proportion of time spent in vigilance as a fixed effect with the same model but also including individual identity as a random effect. We then compared that last model with a model also including the interaction between the proportion of time spent in vigilance and the individual identity as a random effect.

We compared models by using R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and the lme function from the nlme package in R 3.0.1 (Pinheiro, Bates, DebRoy, Sarkar, 2013), which allowed us to compare models with and without random effects. To satisfy assumptions of normality and to achieve linearity between bite rate and vigilance, the proportion of time spent in vigilance was arcsine square-root transformed in all models. The model comparisons were done with a likelihood ratio test (following Rieucou et al., 2010) investigating the effect of adding one random effect to a model (Pinheiro & Bates, 2000). Based on simulations, Martin, Nussey, Wilson, and Réale (2011) argued that to test for individual variation using random regression models, the minimum sample size should be 200 observations and the ratio between the number of individuals and the number of observations per individual should be at least 0.5. In our study we made 1135 observations on 34 females sampled between 32 and 38 times each, giving a ratio between 0.89 and 1.06. Therefore this sample size should provide enough power to detect potential between-individual variation in personality and plasticity.

## RESULTS

### Factors Influencing Vigilance and Feeding Rate

On average, individuals decreased their vigilance and increased their feeding rates as group size increased (Table 2, Fig. 1a, b). Neither patch richness nor reproductive state significantly affected either vigilance or feeding rates (Table 2, Fig. 1c–f).

### Individual Differences in Vigilance and Feeding Rate

For each of the three factors tested, the addition of individual identity as a random effect in our models of both vigilance and feeding rates significantly improved their fits (Table 3). The addition of the interaction between individual identity and the factor tested only improved the fits of the models for reproductive state for both vigilance and feeding rates (Table 3). This suggests that individuals exhibited consistent behavioural variation but similar plasticity in vigilance and feeding rates as group size and patch richness varied (i.e. different intercepts, equal slopes), and consistent behavioural variation as well as different patterns of plasticity as reproductive state varied (i.e. different intercepts and slopes; Fig. 1a–f).

### Factors Influencing the Feeding Rate/Vigilance Trade-off

The addition of the factors tested as a random effect in the models of the trade-off between feeding rates and vigilance was significant only for reproductive state, as was the addition of the interaction between the proportion of time spent in vigilance and reproductive state as a random effect (Table 4). Therefore, on average individuals adjusted their feeding rate/vigilance trade-off similarly in different group sizes and in patches of different richness, but exhibited different adjustments in relation to their reproductive states (Fig. 2a–c).

### Individual Differences in the Feeding Rate/Vigilance Trade-off

When we fitted models for each specific condition within each factor, the addition of individual identity as a random effect in the models was significant for small groups, rich food patches and all reproductive states. The addition of the interaction between the proportion of time spent in vigilance and individual identity as a random effect was significant only for females with a young-at-foot (Table 5). Therefore, individuals in large groups, as well as in poor

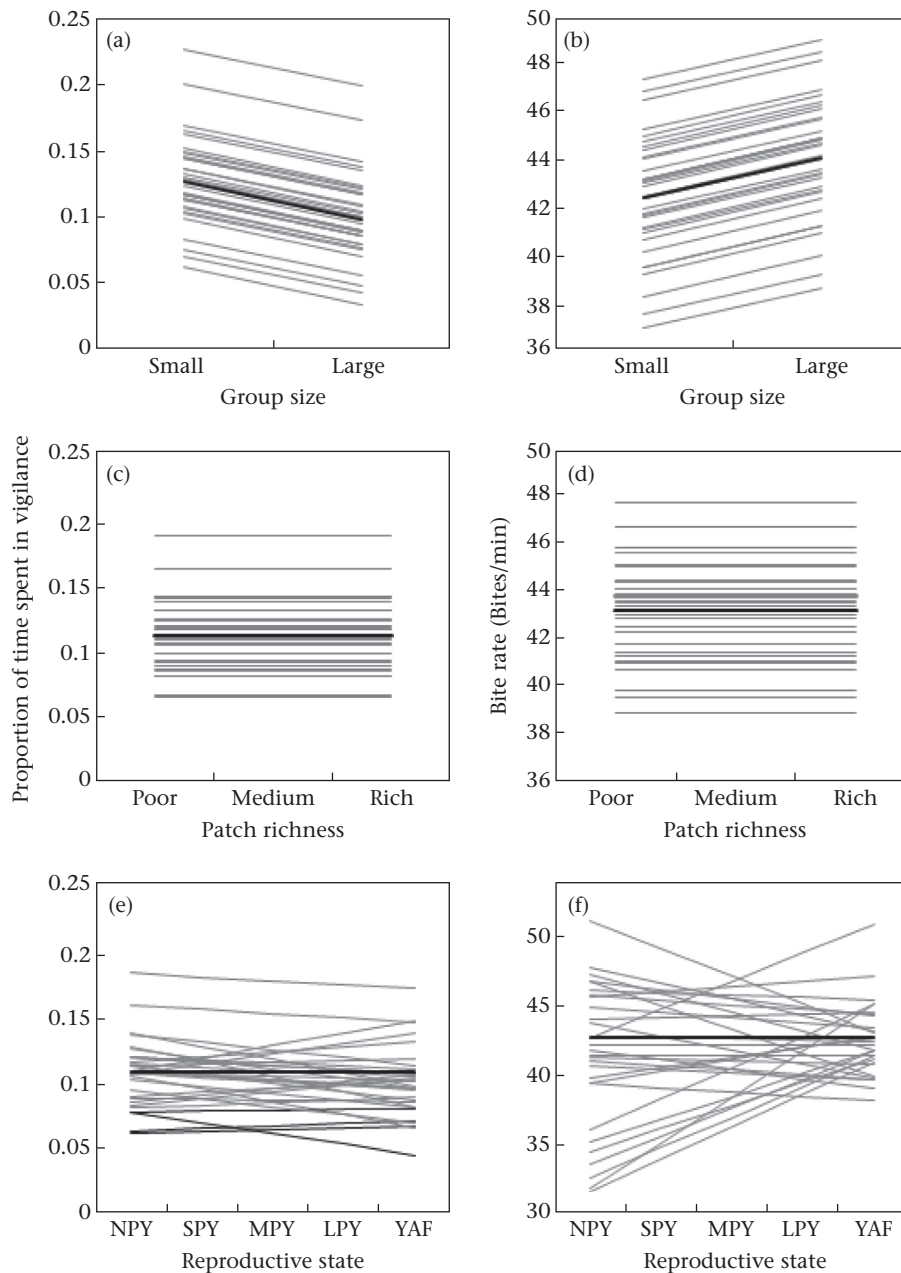
**Table 2**

Effects of group size, patch richness and reproductive state on the proportion of time spent in vigilance (arcsine square-root transformed) and the bite rates of female kangaroos

Factors	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i>	<i>P</i>	Coefficient±SE
<b>Vigilance</b>					
Intercept	1	1094	1900.363	<0.001	0.352±0.017
Group size	1	1094	33.079	<0.001	−0.045±0.007
Patch richness	2	1094	0.850	0.427	
Reproductive state	4	1094	1.545	0.186	
<b>Bite rates</b>					
Intercept	1	1094	16265.240	<0.001	41.436±0.868
Group size	1	1094	15.594	<0.001	1.681±0.419
Patch richness	2	1094	1.472	0.230	
Reproductive state	4	1094	1.293	0.270	

Group size (small, large), patch richness (poor, medium, rich) and reproductive state (NPY, SPY, MPY, LPY, YAF) were categorical (classes used as references are italicized). Individual identity was included as a random factor.





**Figure 1.** Relationships between female eastern grey kangaroos' vigilance and bite rates and (a, b) group size ( $N = 34$ ), (c, d) food patch richness ( $N = 34$ ) and (e, f) reproductive state ( $N = 30$ ). The black line represents the average effect for all observations and each grey line show an individual's relationship.

and medium food patches, did not differ consistently in their levels of the vigilance/feeding trade-off or their patterns of plasticity for this trait (i.e. no differences in intercept or slopes). Individuals in small groups, rich food patches and without an apparent pouch-young, or with a small, medium or large pouch-young, consistently differed in their trade-off between feeding rates and vigilance but showed similar plasticity (i.e. different intercepts but similar slopes) in this trade-off. Individuals with a young-at-foot exhibited both consistent variation in their levels of the trade-off and different patterns of plasticity (i.e. different intercepts and slopes; Fig. 3a–c).

## DISCUSSION

We used the reaction norm approach to investigate whether the mean levels and plasticity of vigilance, feeding rates and the trade-

off between them varied between individuals as a function of group size, food patch richness and reproductive states for female eastern grey kangaroos. Our results highlighted that different patterns occurred for the factors considered. Behavioural adjustments in different group sizes and food patches of different richness seemed to be mainly affected by ecological drivers and thus supported the ecological hypothesis, with some support also for the behavioural hypothesis, whereas adjustments in relation to females' reproductive states seemed to provide strong support for the behavioural hypothesis.

Group size affected vigilance negatively and feeding rates positively at the population level, and although all individuals showed the same patterns of plasticity for these traits, they exhibited consistent variation in their levels of vigilance and feeding rates. It is well known that larger groups are safer and thus

**Table 3**  
Comparison of linear models with different random factors for the effects of group size, patch richness and reproductive state on the proportion of time spent in vigilance (arcsine square-root transformed) and the bite rate of female kangaroos, based on log-likelihood ratio tests (LRT)

Factors	Models	Log-likelihood	df	Models compared	LRT	P
<b>Vigilance</b>						
Group size	M1-1: without ID	653.662	3			
	M1-2: with ID	674.887	4	M1-1 vs M1-2	42.450	<b>&lt;0.001</b>
	M1-3: with ID×Group size	676.259	6	M1-2 vs M1-3	2.745	0.254
Patch richness	M2-1: without ID	636.441	4			
	M2-2: with ID	656.308	5	M2-1 vs M2-2	39.734	<b>&lt;0.001</b>
	M2-3: with ID×Patch richness	658.934	10	M2-2 vs M2-3	5.252	0.386
Reproductive state	M3-1: without ID	633.324	6			
	M3-2: with ID	652.065	7	M3-1 vs M3-2	37.481	<b>&lt;0.001</b>
	M3-3: with ID×Reproductive state	665.702	21	M3-2 vs M3-3	27.275	<b>0.018</b>
<b>Bite rate</b>						
Group size	M4-1: without ID	-3835.287	3			
	M4-2: with ID	-3824.498	4	M4-1 vs M4-2	21.579	<b>&lt;0.001</b>
	M4-3: with ID×Group size	-3823.255	6	M4-2 vs M4-3	2.484	0.289
Patch richness	M5-1: without ID	-3841.080	4			
	M5-2: with ID	-3830.187	5	M5-1 vs M5-2	21.786	<b>&lt;0.001</b>
	M5-3: with ID×Patch richness	-3828.934	10	M5-2 vs M5-3	2.506	0.776
Reproductive state	M6-1: without ID	-3838.758	6			
	M6-2: with ID	-3828.001	7	M6-1 vs M6-2	21.513	<b>&lt;0.001</b>
	M6-3: with ID×Reproductive state	-3805.029	21	M6-2 vs M6-3	45.944	<b>&lt;0.001</b>

For each factor, the first comparison compares models including the identity of the focal female as a random effect with those where ID was excluded (testing for consistent variation among individuals, i.e. differences in intercepts) and the second comparison compares models with an interaction between the factor tested and ID as a random effect with models with only ID as a random effect (testing for interindividual variation in plasticity, i.e. differences in slopes). Significant differences are in bold.

allow individuals to reduce their time spent in vigilance to the benefit of foraging, explaining the higher foraging rates often observed in large groups (Lima, 1995). The decrease in vigilance with group size has been observed in eastern grey kangaroos (e.g. Jarman, 1987; Pays, Jarman, et al., 2007), as was between-individual variation in this pattern (Carter, Pays, et al., 2009). However, while we only observed between-individual variation in vigilance levels, Carter, Pays, et al. (2009) reported variations in both levels and the adjustments to vigilance as group size increased. These differences may have been caused by differences in predation risk or levels of competition between the populations studied. Our results are consistent with the findings of Rieucou et al. (2010), who observed consistent between-individual differences but similar plasticity for vigilance and feeding rates in nutmeg mannikins as group size increased. Overall, female kangaroos did not differ in their feeding rate/vigilance trade-off as group size increased, whereas within the different group sizes, the patterns differed. Female kangaroos showed consistent individual variation in this trade-off in small groups but this was not quite significant in larger groups. Large groups have been shown to induce scramble competition between foragers and several studies have supported the idea that the increase in foraging effort in such groups is mainly due to the increasing competition rather than the decrease in predation risk

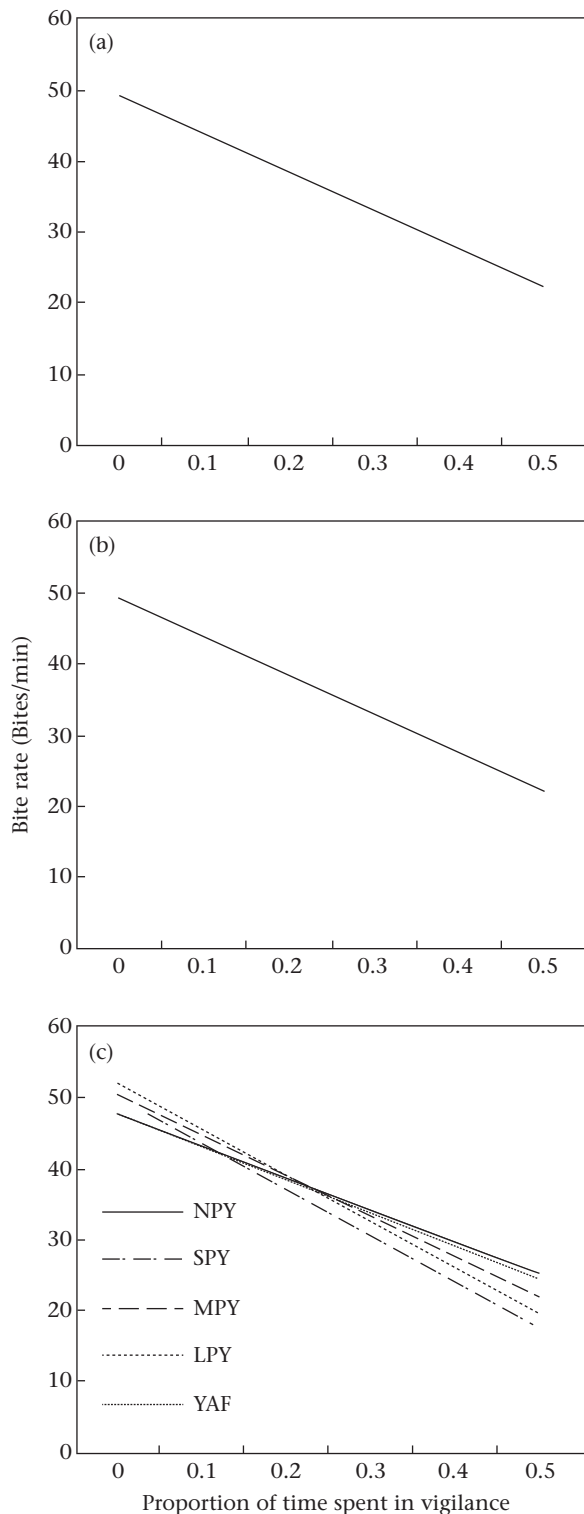
(e.g. Randler, 2005; Rieucou & Giraldeau, 2009). Therefore, increasing competition in large groups could be responsible for the greater standardization of feeding rates as all the individuals would tend to increase their foraging effort to their maximum capacity.

Surprisingly, patch richness did not affect either vigilance or feeding rates, although individuals consistently displayed different levels for both behaviours. We expected patch richness to affect kangaroos' behaviour and especially their feeding rates. Garnick et al. (2010) observed that kangaroos had lower feeding rates in tall swards than in short swards. This pattern is common in herbivores and arises because they usually take larger bites in tall swards, which require longer chewing time, leading to an inverse relationship between bite rate and bite mass (Spalinger & Hobbs, 1992). Clarke et al. (1989) argued that the lower feeding rates and vigilance levels that they observed in winter than in summer occurred because patch quality declined in this season and kangaroos took more time to select food items, which suggests that patch richness should affect vigilance and feeding rates. The absence of an effect of patch richness on individual feeding rates may suggest that, during our study, the range of variation in patch quality in the study area might have been insufficient to force individuals to be more selective at some times than others. Overall, patch richness had no effect on the feeding rate/vigilance trade-off,

**Table 4**  
Comparison of linear models with different random factors for the effects of the proportion of time spent in vigilance (arcsine square-root transformed) on the bite rates of female kangaroos in relation to group size, patch richness and reproductive state based on log-likelihood ratio tests (LRT)

Factors	Models	Log-likelihood	df	Models compared	LRT	P
Group size	M7-1: without Group size	-3504.471	3			
	M7-2: with Group size	-3504.471	4	M7-1 vs M7-2	0.000	0.999
	M7-3: with Group size×vigilance	-3504.45	6	M7-2 vs M7-3	0.043	0.979
Patch richness	M8-1: without Patch richness	-3504.471	3			
	M8-2: with Patch richness	-3504.45	4	M8-1 vs M8-2	0.042	0.838
	M8-3: with Patch richness×vigilance	-3503.086	6	M8-2 vs M8-3	2.726	0.256
Reproductive state	M9-1: without Reproductive state	-3504.471	3			
	M9-2: with Reproductive state	-3498.736	4	M9-1 vs M9-2	11.469	<b>&lt;0.001</b>
	M9-3: with Reproductive state×vigilance	-3489.11	6	M9-2 vs M9-3	19.251	<b>&lt;0.001</b>

For each factor, the first comparison compares models of the relationship between bite rates and the proportion of time spent in vigilance, including the factor considered as a random effect, with those where the factor considered was excluded (testing for consistent variation between factor modalities, i.e. differences in intercepts), and the second comparison compares models with an interaction between the proportion of time spent in vigilance and the factor considered as a random effect with models with only the factor considered as a random effect (testing for variation in plasticity between the factor modalities, i.e. differences in slopes). Significant differences are in bold.



**Figure 2.** Population-level changes in the trade-off between bite rate and the time spent in vigilance in relation to (a) group size, (b) patch richness and (c) reproductive state for female eastern grey kangaroos. In (a) and (b), intercepts were not significantly different under the different conditions; therefore the lines represent the population's change in bite rates in relation to the level of vigilance.

but individuals in rich food patches showed consistent interindividual differences in this trade-off. In poor and medium patches individuals did not differ in their feeding rate/vigilance trade-offs, probably because they were relatively constrained in terms of

food acquisition compared with individuals in rich food patches and needed to maximize their intakes, and maybe also because scramble competition is usually higher when food quality and density are low (Beauchamp, 2009).

Two possible explanations for consistent individual variation in feeding rates, vigilance and their trade-off involve females' ages and personalities. According to Nielsen (1999), consistent differences in feeding rates between individuals under similar conditions may be caused by differences in age, because age is known to cause changes in body size and the capacity of the mouth in terms of bite sizes (Illius & Gordon, 1987; Shipley, Gross, Spalinger, Hobbs, & Wunder, 1994). Old animals are also usually more vulnerable to predation (e.g. Peterson, Woolington, & Bailey, 1984), which should affect their vigilance patterns. We did not know the actual age of each focal female, but we only studied individuals that were adults and of apparently similar body sizes and ages. Thus the effect of potential differences in the ages of adult females was expected to be limited.

We therefore suggest that the consistent individual differences in feeding rates, vigilance and their trade-off may reflect aspects of female kangaroos' personalities. Indeed, personality has been shown to be related to foraging tactics in some taxa, with bolder animals feeding for longer and exhibiting higher feeding rates and intake rates than shy individuals (Bergvall et al., 2011; Carter, Goldizen, & Tromp, 2010; Kurvers et al., 2010). Although the possibility of a relationship between foraging and boldness has not yet been tested in eastern grey kangaroos, recent studies have shown that females exhibit different personalities along a bold–shy continuum and that shyer individuals are more vigilant than bolder ones (Best, 2013; Edwards et al., 2013). In addition, Webster and Ward (2011) developed the idea that increases in conformity (i.e. the tendency of individuals to adopt the behaviour of the majority of their groupmates) and social facilitation (i.e. the changing of behaviours by individuals as a result of the presence of groupmates) in large groups could be responsible for a decrease in the expression of personality types. Our results are consistent with this hypothesis as individual differences in the feeding rate/vigilance trade-off occurred in small groups but not in large ones.

While we suggest that individual variation in vigilance and feeding rates reflects kangaroos' personalities, our results suggest that consistent behavioural differences (or personalities) in the feeding rate/vigilance trade-off may occur only when constraints on foraging are low (i.e. in small groups and rich food patches). When individuals were constrained by food acquisition, they seemed to exhibit similar adjustments, probably to optimize their food intake, mainly supporting the ecological hypothesis. In addition, there were no significant individual differences in patterns of plasticity in feeding rates, vigilance or the trade-off between these behaviours when group sizes and food patches varied, nor for any of the different conditions tested. Therefore, food availability and competition appear to be strong drivers of feeding rate and vigilance, causing animals to exhibit similar patterns of plasticity, in accordance with the ecological hypothesis.

The effects of reproductive state on vigilance, feeding rates and their trade-off were different to those of group size and patch richness. At the population level, the presence of pouch-young of different sizes and of young-at-foot had no effect on either vigilance or feeding rates. The presence of young has been shown to affect mothers' vigilance levels in some species because they have to protect themselves as well as their young from predators (e.g. Burger & Gochfeld, 1994; Childress & Lung, 2003). However, in eastern grey kangaroos, several studies have not observed this relationship; instead of modifying their vigilance time, mothers adapted their time budgets by reducing their time resting, increasing their foraging time and increasing their feeding rates

**Table 5**  
Comparison of linear models with different random factors for the effects of the proportion of time spent in vigilance (arcsine square root transformed) on the bite rates of female kangaroos in different conditions, based on log-likelihood ratio tests (LRT).

Factors	Condition	Models	Log-likelihood	df	Models compared	LRT	P	
Group size	Small	M10-1: without ID	−1968.040	3				
		M10-2: with ID	−1965.624	4	M10-1 vs M10-2	4.832	<b>0.028</b>	
		M10-3: with ID×vigilance	−1963.414	6	M10-2 vs M10-3	4.435	0.109	
	Large	M11-1: without ID	−1533.716	3				
		M11-2: with ID	−1531.935	4	M11-1 vs M11-2	3.561	0.059	
		M11-3: with ID×vigilance	−1531.928	6	M11-2 vs M11-3	0.014	0.993	
Patch richness	Poor	M12-1: without ID	−1207.876	3				
		M12-2: with ID	−1207.876	4	M12-1 vs M12-2	0	1	
		M12-3: with ID×vigilance	−1207.823	6	M12-2 vs M12-3	0.105	0.948	
	Medium	M13-1: without ID	−527.530	3				
		M13-2: with ID	−527.530	4	M13-1 vs M13-2	0	1	
		M13-3: with ID×vigilance	−525.092	6	M13-2 vs M13-3	3.281	0.194	
	Rich	M14-1: without ID	−1759.600	3				
		M14-2: with ID	−1756.676	4	M14-1 vs M14-2	5.846	<b>0.016</b>	
		M14-3: with ID×vigilance	−1754.267	6	M14-2 vs M14-3	2.901	0.236	
	Reproductive states	NPY	M15-1: without ID	−348.895	3			
			M15-2: with ID	−345.290	4	M15-1 vs M15-2	7.211	<b>0.010</b>
			M15-3: with ID×vigilance	−345.290	6	M15-2 vs M15-3	0.010	0.999
SPY		M16-1: without ID	−493.326	3				
		M16-2: with ID	−490.046	4	M16-1 vs M16-2	6.561	<b>0.001</b>	
		M16-3: with ID×vigilance	−488.857	6	M16-2 vs M16-3	2.378	0.305	
MPY		M17-1: without ID	−808.662	3				
		M17-2: with ID	−806.770	4	M17-1 vs M17-2	7.383	<b>0.041</b>	
		M17-3: with ID×vigilance	−805.937	6	M17-2 vs M17-3	1.667	0.434	
LPY		M18-1: without ID	−378.928	3				
		M18-2: with ID	−374.379	4	M18-1 vs M18-2	9.099	<b>0.002</b>	
		M18-3: with ID×vigilance	−374.054	6	M18-2 vs M18-3	0.649	0.723	
YAF		M19-1: without ID	−1428.068	3				
		M19-2: with ID	−1422.063	4	M19-1 vs M19-2	12.009	<b>&lt;0.001</b>	
		M19-3: with ID×vigilance	−1414.209	6	M19-2 vs M19-3	7.787	<b>0.020</b>	

For each factor, the first comparison compares models including the identity of the focal female as a random effect with those where ID was excluded (testing for consistent variation among individuals, i.e. differences in intercepts) and the second comparison compares models with an interaction between the factor tested and ID as a random effect with models with only ID as a random effect (testing for interindividual variation in plasticity, i.e. differences in slopes). Significant differences are in bold.

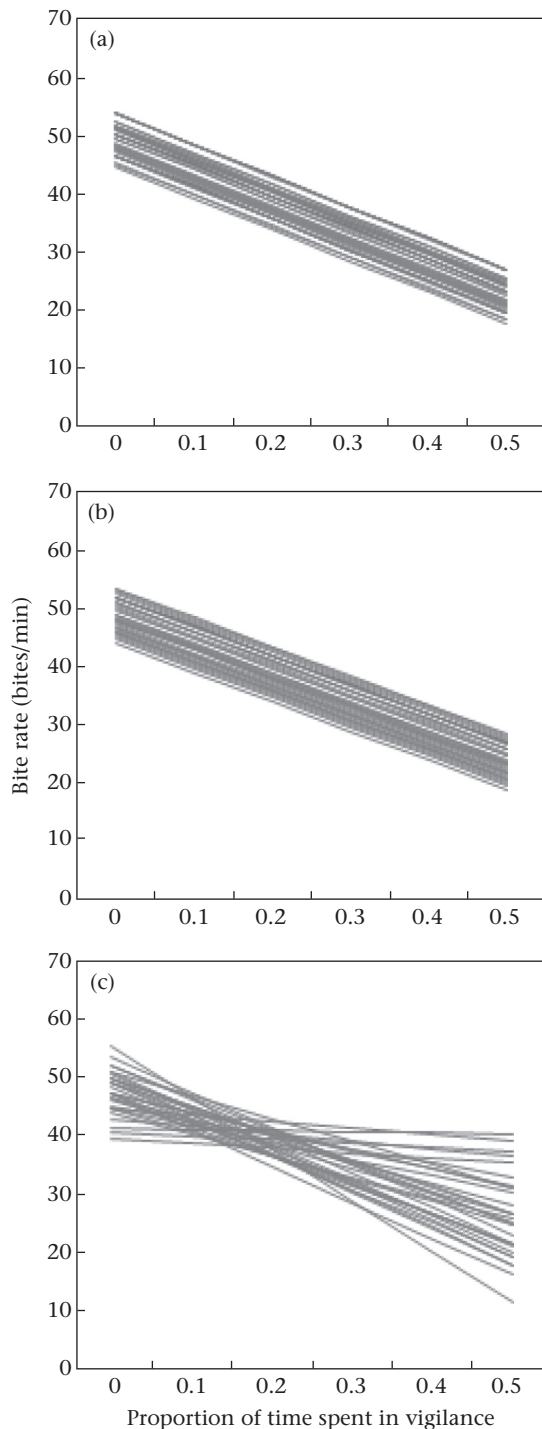
(Cripps, Wilson, Elgar, & Coulson, 2011; Gélin et al., 2013). Reproduction is costly for females because gestation and lactation have high energetic requirements (Robbins, 1983), often leading to higher bite rates for reproducing females compared with other individuals (e.g. Neuhaus & Ruckstuhl, 2002; Ruckstuhl et al., 2003). We did not find any effect of reproductive state on feeding rates at the population level, but at the individual level, females showed consistent differences in how their feeding rates and vigilance adjusted to reproductive state. It appears that the diversity of behavioural strategies displayed by the different individuals masked any general effect at the population level. As we suggest above, differences in vigilance and feeding rates are probably related to individual personalities. In addition, differences in patterns of plasticity between individuals have been shown to be related to genetics, past experiences and interactions between these (Dingemans & Wolf, 2013). In the case of reproductive state, we suggest that females' past breeding experiences (e.g. the number of young previously raised and/or lost) could partly explain differences in their behavioural plasticity.

Overall, the adjustment of feeding rates to vigilance varied among reproductive states. Therefore, the potential cost of vigilance to feeding rates seemed to vary with lactation demand. At low vigilance levels, females exhibited higher feeding rates as reproductive state progressed from females having no pouch-young to females having large pouch-young. However, as vigilance increased, the diminution of feeding rates was more severe when females had pouch-young than when they did not. Surprisingly, females with young-at-foot and females with no pouch-young exhibited similar trade-offs between feeding rates and vigilance, which was not expected as the young-at-foot stage is assumed to be the more 'costly' reproductive state owing to higher lactation

demand (Gélin et al., 2013). Because we observed that the cost of vigilance increased with reproductive state, we would assume that females with young-at-foot would exhibit higher feeding rates at low vigilance levels and incur the severest foraging cost as vigilance increased. Nevertheless, when we investigated females' adjustments within the different reproductive states, we observed consistent differences between individuals in all reproductive states, but different patterns of plasticity only for females with a young-at-foot. We suggest that, as for the variation observed at the individual level for vigilance and feeding rates, described above, the diversity of strategies employed by the different individuals with a young-at-foot may explain this unexpected observation at the population level.

The fact that only females with young-at-foot exhibited different patterns of plasticity in this trade-off could have several explanations. First, although we did not control for the sex of the young-at-foot, part of the plasticity observed in behavioural adjustments may reflect different investment and behavioural strategies of females according to the sex of their offspring. In many species, the cost of reproduction differs in relation to the sex of the offspring produced (Gélin et al., 2013). Sons are usually costlier than daughters to produce because they are larger and tend to suckle more and because they usually impose greater delays on their mother's return to oestrus (e.g. Hogg, Hass, & Jenni, 1992). Second, differences in behavioural adjustments may reflect differences in maternal care displayed by females. Consistent differences in maternal care, termed 'maternal styles' (Hill, Greer, Solangi, & Kuczaj, 1997), have been documented in many primates, including humans, and in other mammals (see Fairbanks, 1996 for a review) such as eastern grey kangaroos (Stuart-Dick, 1987). Maternal care in eastern grey kangaroos involves behaviours such





**Figure 3.** Trade-offs between bite rate and the time spent in vigilance for female eastern grey kangaroos (a) in small groups ( $N = 34$ ), (b) in rich food patches ( $N = 34$ ) and (c) having a young-at-foot ( $N = 30$ ). Each line represents an individual's adjustment of its bite rate in relation to its level of vigilance.

as grooming, protection, playing and lactation (Cripps et al., 2011; Kaufmann, 1975), and could therefore affect vigilance and foraging behaviours. Flexibility in maternal care has been associated with mothers' personalities and could be related to their previous maternal experiences (Bard, 2002; Fleming & Li, 2002). Our results on females in different reproductive states indicate that the ecological hypothesis is not sufficient to explain the variation in females' feeding rates, vigilance and their trade-offs because

individuals showed (1) consistent differences and differing patterns of plasticity in vigilance and feeding rates when their reproductive states varied, (2) consistent differences in their trade-off between these behaviours in all reproductive states and (3) different patterns of plasticity in this trade-off in the most energetically demanding condition. Therefore individuals' characteristics appear to induce more complex and diverse behaviours than external and social factors, which appears to support the behavioural hypothesis.

In summary, herbivorous prey species have to adjust their behaviour to maximize their fitness and survival. Individuals' adjustments of foraging and vigilance would therefore be expected to be comparable when individuals face similar conditions. We found that the effects of factors external to the individuals (group size and patch richness) might reflect certain aspect of individuals' personalities that were more likely to be expressed when foraging constraints were low, and did not induce differences in plasticity. We also observed a high degree of between-individual differences in personalities and plasticity in relation to reproductive state for vigilance and feeding rates as well as in the trade-off between these behaviours when females had a young-at-foot. Therefore individual differences in the levels and plasticity of vigilance and foraging behaviour appear to be specific to different situations and not necessarily repeatable across contexts. More studies are required to examine the effects of these factors on personality and plasticity in the behaviour of wild animals under different conditions.

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