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Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies

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Seasonal variation in food resources and predation risk imposes major constraints on herbivores, which must adjust their behaviour to maximize their energy intake and survival. In seasonally driven landscapes, it is not yet clear what the primary drivers are that shape seasonal variation in vigilance and feeding rates. These rates have been shown to vary in relation to various environmental, social and individual factors, but many of these factors also vary through the year, due to variation in food supply. We studied wild female eastern grey kangaroos, *Macropus giganteus*, under low predation risk over a year to investigate whether vigilance and feeding rates varied seasonally and whether this variation was mainly driven by food quantity or quality, group size or individuals' reproductive states. Both vigilance and feeding rates varied seasonally, as did food quantity and quality and group size. Vigilance, including antipredator (head orientation away from the group) and exclusive (i.e. vigilance without chewing) vigilance, decreased and feeding rate increased with increasing group size. However, because group size increased with food quality and quantity, food resources emerged as the primary driver of variation in behavioural strategies. These results suggest that the observed effects of group size on the trade-off between food acquisition and safety are in fact corollaries of the seasonal variation in food supply in our study system, in which the risk of predation on adults is low, and hence are by-products of the foraging choices made by kangaroos in response to the dynamics of the quantity and quality of food.
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Most animals live in seasonally changing environments (Bronson, 1985) and must adjust their behaviour accordingly (Nelson, 1990). Both food availability and predation risk can change seasonally, and thus the trade-offs that many animals need to make between getting enough to eat and staying safe from predators are expected to change as well. Seasonal behavioural adjustments are particularly pronounced for herbivores when their food resources vary greatly in quality and quantity through the year due to fluctuations in temperature and rainfall (Owen-Smith, 2008). The productivity of grasslands is closely related to rainfall, so that not long after rain the food of grazers is generally abundant and nutritious (February, Higgins, Bond, & Swemmer, 2013), allowing individuals to select the best quality food items. However, following dry periods, vegetation usually becomes depleted and reduced in quality, forcing individuals to ingest lower quality food to maintain their energy intake (Owen-Smith, 2008). Studies on the feeding preferences of short-grass grazers including eastern grey kangaroos, *Macropus giganteus*, red kangaroos, *Macropus rufus*, sheep, *Ovis aries*, and Thomson's gazelles, *Gazella thomsoni*, have shown that increasing grass biomass generally decreased digestibility (Fryxell, 1991), making the relationship between food intake, the greenness and biomass of food (and thus its seasonal variation) complex to understand. Indeed, these species tend to preferentially exploit green patches of low to intermediate biomass for which forage digestibility is high (Wilmshurst, Fryxell, & Colucci, 1999).

In response to such seasonal variation in food resources, herbivores adjust their feeding patterns in diverse ways. For example, female bison, *Bison bison*, selected pasture with the most profitable food items, using social information more in winter than in summer to find the best pastures (Courant & Fortin, 2012). Once in such high-quality patches, they took shorter steps than they did in lower quality patches. At a larger scale, many large herbivores migrate in response to changes in food availability (reviewed by Fryxell & Sinclair, 1988). While the foraging strategies of herbivores have received much attention, both theoretical (e.g. Owen-Smith,

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Fryxell, & Merrill, 2010; Spalinger & Hobbs, 1992) and empirical (Wilmshurst et al., 1999), the effects of seasonal changes in forage characteristics on the trade-off between foraging and predator detection are far from clear.

Most herbivores must also dedicate time to watching for predators (Fortin, Boyce, Merrill, & Fryxell, 2004), and predation risk can vary seasonally for many reasons (Valeix et al., 2009). For example, predators may change their movements seasonally, visibility and thus the ability of prey to detect predators can change with vegetation height, and the presence of young can attract predators. Vigilance in grazers involves an animal lifting its head up and looking around and can thus be quantified relatively accurately. This is an important antipredator behaviour (Elgar, 1987; Périquet et al., 2012), but is time consuming and consequently imposes a cost on individuals by reducing their foraging time, or time spent in maintenance activities such as resting. Although herbivores can reduce the foraging costs of vigilance somewhat by being vigilant while chewing vegetation (Favreau et al., 2015; Fortin et al., 2004), vigilance nevertheless affects their energetic gains, creating a trade-off between vigilance and foraging (Baker, Stillman, Smart, Bullock, & Norris, 2011; Brown & Kotler, 2004; Favreau et al., 2014; Lima, 1998; Ruckstuhl, Festa-Bianchet, & Jorgenson, 2003). This trade-off is likely to be important to individuals' fitness in landscapes in which seasonal changes in resource availability constrain animals' access to high-quality food at some times of the year. However, the mechanisms underlying the seasonal changes in herbivores' vigilance–foraging trade-offs are often difficult to understand as vigilance and feeding rates (i.e. the two components of the trade-off) have both been shown to be affected by numerous environmental, social and individual factors.

Group sizes of grazers can vary spatially and temporally for a number of reasons and can affect vigilance patterns. Group size is often correlated with the availability, quality and distribution of food resources, with social foragers forming bigger groups in areas or periods with better food conditions, when intraspecific competition is likely to be reduced (e.g. Bergström & Skarpe, 1999; Jarman, 1974). For a number of reasons, animals feeding in areas with high quantity or quality of food may spend less time in vigilance (Pays et al., 2012). This may occur because individuals in larger groups are safer from predation (Jarman, 1974), aggression between conspecifics for access to food is rare when they forage on large, good patches (Johnson, Grant, & Giraldeau, 2004), lower aggression levels reduce social vigilance (time spent monitoring conspecifics) and higher feeding rates on good patches reduce the time available for vigilance (Beauchamp, 2009). Grazers foraging in open grasslands may be particularly likely to reduce their vigilance on good pasture (Fortin et al., 2009; Jarman, 1974; Pays, Fortin, Gassani, & Duchesne, 2012), both because grass tends to be more abundant in open areas and because predator detection and visual contact between group members are improved (Borkowski & Furubayashi, 1998).

Given the complexity of all the patterns described above, it can be very difficult to untangle the factors that directly or indirectly affect vigilance/feeding trade-offs. We tested two nonexclusive possibilities. The first is that variation in food quantity and quality directly affects feeding rates (and is thus the primary driver of the vigilance/feeding trade-off). The second is that food availability directly affects group size, which in turn affects vigilance and/or feeding rates, so that feeding rate is indirectly affected by food availability. Our test of this second hypothesis is the novel aspect of this paper. If predation risk is low, food availability is expected to be the primary driver determining the vigilance/feeding trade-off, particularly for herbivores, which eat low-energy food and therefore must spend much of their day feeding. However, even if food availability is the primary driver, it is not clear whether it affects feeding rates directly, or indirectly by affecting group sizes.

To test these two possibilities, we investigated seasonal variation in vigilance and feeding rates in female eastern grey kangaroos monthly over a 1-year period while they foraged on grassland at Sundown National Park (Australia), where environmental conditions vary seasonally, albeit somewhat unpredictably. To consider both the type and intensity of vigilance in our study, we recorded antipredator vigilance when a female oriented her head away from her group (compared with social vigilance) and exclusive vigilance when she raised her head without chewing (compared to vigilance while chewing). While we can never be sure what an animal is paying attention to, research at our study site showed that what we considered antipredator and social vigilance each varied with group size as predicted (antipredator vigilance decreased while social vigilance increased with increasing group size; Favreau, Goldizen, & Pays, 2010), suggesting that we correctly identified the vigilance type most of the time. We assumed that predation risk for our focal adult females was negligible (Best, Seddon, Dwyer, & Goldizen, 2013) as there was no evidence of dingoes, *Canis lupus dingo*, or any other large predators that could threaten animals of their body size (20–36 kg, Yom-Tov & Nix, 1986) within the study area during the year of this study or the previous one (E. C. Best, personal communication). However, predators of young kangaroos were regularly observed, including red foxes, *Vulpes vulpes*, and wedge-tailed eagles, *Aquila audax* (Favreau et al., 2015). Despite the lack of predators of adult kangaroos, antipredator vigilance was expected because of the presence of foxes, which were regularly seen hunting juvenile kangaroos, and because antipredator vigilance is presumably a behaviour that would have been selected for over many generations. Adult kangaroos were observed both running from foxes and running towards ones that were chasing juveniles (P. Corvalan, personal communication).

Previous studies have reported variation in both vigilance and feeding rates between winter and summer in this species, suggesting that food quality and energy requirements might have a major influence on the vigilance/foraging trade-off (Clarke, Jones, & Jarman, 1989, Clarke, Jones, & Jarman, 1995). To achieve our aim of testing whether variation in food quality and quantity directly or indirectly affected the vigilance/feeding trade-off, we investigated how seasonal changes shaped food quality, group size and reproductive state, and how in turn these factors related to the behavioural strategies of kangaroos. We took the following approach. First, we investigated whether food quality, group size, reproductive state, vigilance and feeding rates varied significantly over time across a year. Then, controlling for the effects of time in the data set (e.g. seasonal effects, daily data collection), we tested how food quality, group size, distance to cover and reproductive state all related to vigilance and feeding rates. Finally, we investigated whether food quality shaped group size.

We predicted that food availability would be the primary driver of the vigilance/feeding rate trade-off of females. As previous studies have shown that herbivores adjusted their feeding rates to food resources (Bradbury, Vehrencamp, Clifton, & Clifton, 1996; Edouard, Duncan, Dumont, Baumont, & Fleurance, 2010), and vigilance and feeding rates were negatively related in this species (Favreau et al., 2014), food quality and quantity should also indirectly affect vigilance (e.g. Pays et al., 2012). Vegetation varies seasonally, albeit somewhat unpredictably, in most ecosystems in eastern Australia (Mott, Williams, Andrew, & Gillison, 1985), and thus food availability varies over time, and should cause seasonal variation in feeding rates as well as vigilance. At our study site, grass quality and quantity increase about 1 month after good rain (Menz, Goldizen, Blomberg, Freeman, & Best, 2017). We predicted

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