

Does vigilance effort differ between urban and nonurban Little Raven (*Corvus mellori*) populations?

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Vigilance is directed at predators and conspecifics that threaten survival, welfare or resource acquisition. It has commonly been argued that predators of birds may be less abundant in urban than nonurban environments, which should be reflected in a lower vigilance effort by urban prey species. However, the Risk-Disturbance Hypothesis proposes that prey species treat anthropogenic disturbances, which are much more frequent in cities, as analogous to predation risk, which might counteract this trend. This treatment might also be reflected in a greater vigilance effort in areas of the urban environment with higher anthropogenic disturbance levels. The time allocation to vigilance in foraging Little Ravens *Corvus mellori* in south-east Australia was measured to determine whether (a) there was an urban-nonurban difference, and (b) urban individuals were more vigilant in areas with higher ambient pedestrian and vehicular traffic volumes. The mean percentage of a raven's ground-foraging bout allocated to vigilance (36-40%) was similar in urban and nonurban environments. We argue that nonurban ravens' extreme sensitivity to human proximity may dilute the expected influence on their vigilance effort of the much lower frequency of anthropogenic disturbance in rural areas. We also suggest that urban and nonurban relative abundances of Little Ravens' predators need quantification to clarify the role of predator abundance in shaping the similar vigilance effort of ravens in the two environments. Urban ravens' time allocation to vigilance did not vary with pedestrian and vehicular traffic volumes. This finding might reflect a measurement limitation, but alternatively could indicate that many urban individuals are sufficiently habituated to traffic to allow them to inhabit even those areas of cities with very high pedestrian and vehicular traffic volumes.

Keywords: Little Raven; vigilance effort; urban and nonurban environments; Risk-Disturbance Hypothesis; anthropogenic disturbance

INTRODUCTION

Vigilance involves monitoring the environment for potential threats (Beauchamp 2015). It is often incompatible with simultaneously efficiently performing other vital activities e.g. foraging or social interactions (Krause and Godin 1996; Blanchard *et al.* 2017). Consequently, vigilance can be either high cost, detracting from performance of other critical behaviours, or low cost, essentially conducted in an animal's 'spare time' (Blanchard and Fritz 2007). It is directed at predators (antipredator vigilance) (Blank 2018) or at conspecifics constituting a threat to welfare or resource acquisition (social vigilance) (Li *et al.* 2012); distinguishing between the two orientations is sometimes possible (Favreau *et al.* 2010), but often difficult. Numerous factors can influence an animal's antipredator vigilance, including its sex, group size and distance from neighbours and cover, as well as visual obstructions and environmental parameters (e.g. wind velocity and illumination levels) (Beauchamp 2015). In ground-foraging birds, visual vigilance is often measured as the percentage of time spent in a head-up, scanning posture (Fernández-Juricic 2012; McGiffin *et al.* 2013), although it is recognised that this metric may not provide a very complete reflection of the quality of pertinent information obtained through adopting this posture (Jones *et al.* 2007; Fernández-Juricic *et al.* 2011).

Numerous authors have proposed that birds' natural predators are less abundant in cities than in nonurban areas (predation

relaxation or the safe habitat hypothesis) (Tomialojc 1982; Valcarcel and Fernández-Juricic 2009; Schochat *et al.* 2010; Diaz *et al.* 2013; Samia *et al.* 2017; Isaksson 2018). Moreover, conceivably the higher human densities in cities enhance the effect of this alleged lower predator abundance on bird prey species by effectively creating a spatial and temporal refuge or buffer for them from avian predators (Møller 2012; Shannon *et al.* 2014). If both these propositions are correct, avian antipredator vigilance effort would generally be predicted to be lower in urban than in nonurban environments, all else being equal.

However, the Risk-Disturbance Hypothesis (RDH) (Frid and Dill 2002) proposes that anthropogenic disturbances, such as pedestrian and vehicular traffic (Fernández-Juricic and Telleria 2000; Gavin and Komers 2006), are analogous to real predation risk in that, although typically non-lethal, they still substantially divert prey animals' time and energy away from other vital activities. Therefore, prey species should and do respond to them using the same economic trade-off principles exhibited when they respond to real predators (Ciuti *et al.* 2012), and vigilance is an important component of such responsiveness. Cities are a greater source of anthropogenic disturbance than nonurban areas (Lowry *et al.* 2012). The predicted lower prey vigilance effort in urban than nonurban environments resulting from the alleged lower abundance of natural predators could thus be counteracted to some extent by this higher level of anthropogenic disturbance (Valcarcel and Fernández-Juricic 2009).

In accordance with the RDH (Frid and Dill 2002), there is considerable evidence that wildlife commonly respond to heavy vehicular traffic by increasing vigilance and reducing foraging time. Thus, vigilance effort usually tends to be greater and foraging time less near to, than further away from, busy roads (Speziale *et al.* 2008; Ciuti *et al.* 2011; Lian *et al.* 2011). Similarly, wildlife is often more vigilant and forages less when pedestrian traffic volume is relatively high (Riddington *et al.* 1996; Fernández-Juricic and Telleria 2000). However, comparatively few investigations specifically examining the effects of vehicular and pedestrian traffic on vigilance have been conducted in cities, so whether these trends are common in urban environments is unknown. The issue is important, because if these trends in vigilance and foraging are apparent in cities, some wildlife might effectively be excluded from parts of conurbations where vehicular and pedestrian traffic volumes are particularly high (Kitchen *et al.* 2011).

Little Ravens *Corvus mellori* (hereinafter ravens) are restricted to south-east Australia, inhabiting farmland and open forest and woodland from alpine to coastal regions, but in the last 30-50 years they have also successfully colonized many conurbations (Menkhorst *et al.* 2017). They forage predominantly on the ground, capturing mostly invertebrates by gleaning, probing the substrate and 'sweeping', but also consume carrion and human food waste (Lill and Hales 2015). Ravens often forage gregariously, particularly when not breeding, and in the nonurban environment adults and nest contents are preyed upon by large raptors (Rowley 1973).

Adult urban ravens potentially experience a lower predation risk but a higher frequency of human disturbance than nonurban conspecifics. One rationale for the present study was to determine whether these contrasting situations have effectively led to a similar vigilance effort in the two populations. In contrast to some of the findings cited above and apparently in contradiction of the predictions of the RDH, Vines and Lill (2016) found that there was only a limited effect of ambient pedestrian and vehicular traffic volumes on tolerance of human proximity by urban ravens. Consequently, a second rationale for the present investigation was to ascertain whether ambient traffic volume had any effect on the vigilance time allocations of urban ravens. The specific aims of our study were thus to determine for the ground-activity bouts (GAB) of foraging adult ravens whether:

1. urban and nonurban individuals differed in the mean percentage of a bout allocated to vigilance.
2. the percentage of a bout allocated to vigilance by urban individuals was influenced by local ambient pedestrian and vehicular traffic volumes and proximity to roads.

METHODS

Study area and timing

The investigation was conducted in urban and nonurban areas of Victoria, Australia from April to July 2019 in the austral autumn and winter, a period encompassing parts of the raven's non-breeding (April-May) and breeding seasons in this region (Lill and Hales 2015). The urban areas (approximate area in km² and estimated human population in 2019) were four densely built-up and populated conurbations: Melbourne

(10,000 and 5 million), Geelong (1,329 and 198,000), Ballarat (344 and 114,000) and Bendigo (287 and 101,000). However, 72% of urban observations were made in Melbourne. Nonurban areas were in rural environments outside of these cities, mainly agricultural land and woodland, characterised by very low densities of buildings and people. We did not formally measure these urban/nonurban environmental disparities, but they were consistent with operational definitions used in other investigations (e.g. Møller 2012). Observations were made at 143 widely dispersed locations, 73 urban and 70 nonurban (Fig. 1), and spread approximately equally over most times of day in each environment.

Behavioural observations

Ravens were found through systematic vehicular searches. When they were flocking, focal individuals were selected for recording in a consistent, unbiased manner. To reduce pseudoreplication (a) only one GAB was recorded per focal individual, (b) only one individual was sampled in flocks of <5 and no more than two in larger flocks, and (c) sampling sites were at least 500 m apart.

Behaviour recording was restricted to ravens on the ground, which is where most of their foraging occurs and where they are probably most susceptible to predation and disturbance (Lill and Hales 2015). Activity of focal individuals was recorded in real time with a Sony HDR P5430 Camcorder video camera. Video recording of behaviour and measurement of co-variables (see below) was conducted from a vehicle (at a distance which did not disturb the birds) because an observer standing in the open can precipitate fleeing in this species, especially in nonurban areas (Vines and Lill 2016). The activity of a focal individual was recorded for up to 5 minutes, a comparable duration to that used in vigilance studies of American (*Corvus brachyrhynchos*) and Northwestern (*C. caurinus*) Crows (Ward and Low 1997; Robinette and Ha 2001).

Behaviours occurring during a GAB were defined as follows:

1. Vigilance – the long axis of the raven's beak is at or above the horizontal plane and *the beak is not in contact with either food or a substrate* (Fig. 2). This definition accords with that used in many other avian visual vigilance studies (e.g. Fernández-Juricic 2012; McGiffin *et al.* 2013; discussed in Beauchamp 2015). This behaviour category included two postures in which the focal bird was stationary (Vigilance 1 and 2) and two in which it was running or walking (Locomotion 1 and 2) (Fig. 2).
2. Vigilant foraging – any behaviour in which the raven could conceivably be either vigilant, foraging or both. As for (1), *but the beak is in contact with food or the substrate*. Also includes postures in which the head is tilted such that one eye faces above the horizontal plane and the other below it. Vigilance and foraging are not mutually exclusive (Beauchamp 2015); some birds can visually scan for threats while manipulating food in the beak in a head-up posture or even, perhaps less often, in a head-down foraging posture.
3. Searching-foraging – ground foraging in which the long axis of the beak is below the horizontal plane and *the beak is*

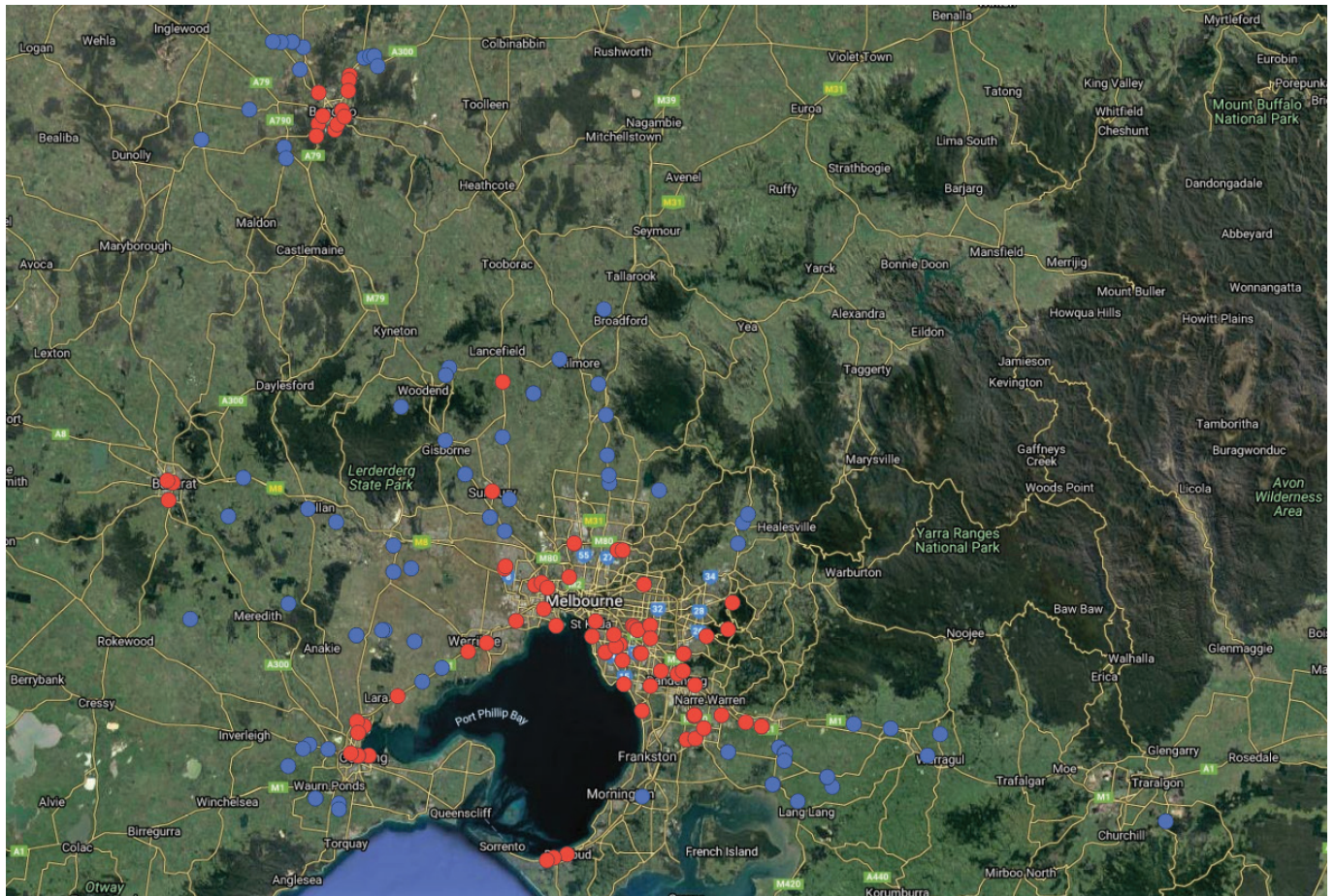


Figure 1. Distribution of sampling locations in Victoria. Urban sites = red filled circles; nonurban sites = blue filled circles. To provide scale, the distance from Melbourne to Geelong is 73.5 km.

- not in contact with food or substrate* (Fig. 2). This category included two postures, one (Searching-foraging 1) in which the focal bird was stationary and one (Locomotion 3) in which it was running or walking (Fig. 2).
4. Contact-foraging – a component of ground foraging in which the beak's long axis is below the horizontal plane and *in contact with food or substrate* (Fig. 2). This behaviour category included two postures in which the focal bird was stationary (Contact-foraging 1 and 2) and one in which it was running or walking (Locomotion 4). Drinking, which was done while stationary, was also included in this category in view of the head-down posture (Drinking 1) and substance consumption (Drinking 2) involved (Fig. 2), but was infrequent and brief.
 5. Other – various other behaviours that can occur during a GAB (e.g. self-maintenance such as auto-preening, aggression etc.).

Measurement of co-variables

The following co-variables were recorded instantaneously for each ground-foraging focal raven in urban and nonurban environments:

1. Number of conspecifics in the foraging group.
 2. Number of people (other than the researcher) within a 30-m radius.
 3. Linear distance (m) to nearest road, measured categorically as 1-5, 6-20, 21-50, 51-100 and 100+.
- Two further co-variables were recorded for each focal ground-foraging *urban* raven only:
- a. Vehicular traffic volume – on the nearest road to the focal bird.
 - b. Pedestrian traffic volume – within a 30-m radius of the focal bird.
- These latter variables were measured on a presence/absence basis at 30 sec intervals for 10 min (as a proxy for volume) at the end of video-recording of behaviour and expressed as percentage presence. Only one measurement of each variable was made per focal flock irrespective of the number of focal birds videotaped. This 'snapshot' method of recording urban traffic volumes has previously been employed by Gravalin *et al.* (2014) and Vines and Lill (2016).

Data analysis

Video-recordings were analysed on a personal computer, generating a complete time-activity budget for each GAB.

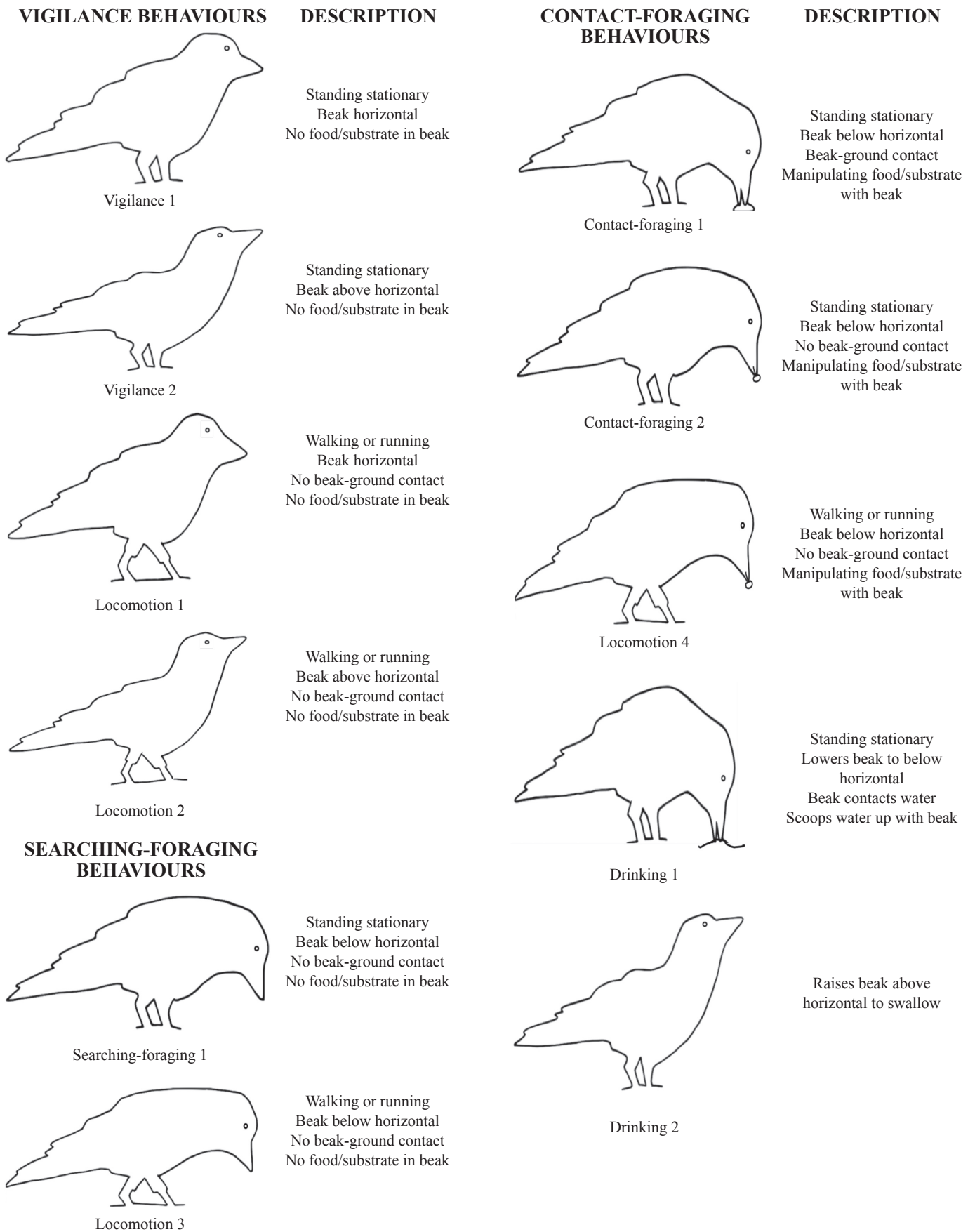


Figure 2. Major vigilance and foraging postures recorded during ground activity bouts of ravens. Vigilant foraging and other behaviours were too variable to illustrate here.

Table 1

Mean (\pm Standard Error) percentage representation of each behaviour in a raven ground-activity bout. Percentages do not exactly sum to 100 due to rounding.

Behaviour	Urban	Nonurban
Vigilance	36.2 (3.9)	40.0 (4.5)
Searching-foraging	32.6 (3.6)	38.9 (4.3)
Contact-foraging	24.7 (4.0)	18.2 (3.8)
Other behaviours	4.7 (2.1)	2.1 (1.7)
Vigilant foraging	2.5 (1.8)	0.7 (1.4)

We recorded 83 urban (total 251 min) and 79 nonurban (total 262 min) GABs. The duration (\pm 0.25 sec) of each distinct behavioural act in a GAB was measured and the percentage representation of each behaviour type in the bout was calculated.

Statistical analysis was conducted mainly in *Rstudio* version 1.1.463. Non-metric multidimensional scaling (NMDS) confirmed that the large complex of behaviours initially identified in GABs could be legitimately and meaningfully collapsed into the five categories outlined above (analysis is not reported here, but available from the authors). All data subjected to parametric statistical analysis were checked for normality and homoscedasticity. Summary data are presented as the mean \pm the standard error (SE).

Linear-mixed-effects models (LMEMs) (Bates and Pinheiro 1998) were used to examine the relationship between the mean proportion of a GAB spent on a behaviour category and several independent variables. Where the assumptions of normality or homoscedasticity were not met, variables were rank normalised using 'rntransformation' (GenABEL) and/or normal quantile-quantile plots were created from their residuals. These procedures indicated that LMEMs then met the assumptions for all five behaviour categories. Separate LMEMs were run for each of the behaviour categories as a response variable. Fixed effects in these models were: number of people nearby (not including the researcher), number of conspecifics in the flock and distance to nearest road (treated as an ordinal categorical variable) (all models), environment (all urban/nonurban comparisons) and traffic volumes (models examining traffic volume effects on urban GAB composition). Nested random effects (season – non-breeding/breeding; time-of-day – am/pm) were also incorporated in all models. Location was not included as a random effect because multiple GABs were recorded at only 12% of locations and 94% of these instances only comprised two GABs. For the entire suite of models run, there was only one significant interaction among the fixed effects and it had no influence on interpretation of the results.

RESULTS

Composition of urban and nonurban ground-foraging bouts

The main GAB constituents were foraging (57%) and vigilance (36-40%). On average, vigilance comprised the same percentage of an urban and a nonurban GAB (Tables 1 and 2). Foraging also comprised a similar percentage of urban and nonurban GABs, but the mean contact-foraging component was significantly greater in the urban than the nonurban

Table 2

Linear-mixed-effects models of percentage representation of each behaviour category in raven ground-activity bouts. SE = standard error. Degrees of freedom = 150 in all models. Significant effects (α = 0.05) in bold font. Environment indicates the urban/nonurban split. Value indicates effect size.

Response variable co-variables	Value	SE	t-value	p-value
VIGILANCE				
Intercept	0.104	0.128	0.817	0.415
Distance to road (m):				
1-5	-0.546	0.219	-2.494	0.014
6-20	0.323	0.194	1.659	0.099
21-50	0.216	0.202	1.068	0.287
51-100	0.046	0.197	0.236	0.814
100+	-0.163	0.197	-0.831	0.407
No. conspecifics	0.001	0.007	0.082	0.935
No. people	0.239	0.098	2.445	0.016
Environment	-0.265	0.185	-1.438	0.153
Interaction: No. people x Environment	-0.278	0.119	-2.327	0.021
SEARCHING FORAGING				
Intercept	0.011	0.188	0.060	0.952
Distance to road (m):				
1-5	0.454	0.217	2.095	0.038
6-20	0.285	0.189	-1.506	0.134
21-50	-0.215	0.199	-1.081	0.281
51-100	-0.226	0.194	-1.165	0.246
100+	0.198	0.192	1.030	0.305
No. conspecifics	0.006	0.007	0.851	0.396
No. people	-0.091	0.055	-1.656	0.100
Environment	-0.080	0.175	-0.458	0.648
CONTACT-FORAGING				
Intercept	-0.115	0.178	-0.649	0.517
Distance to road (m):				
1-5	0.261	0.218	1.199	0.233
6-20	0.029	0.190	0.153	0.878
21-50	0.032	0.200	0.162	0.871
51-100	0.135	0.195	0.695	0.488
100+	0.135	0.193	-0.475	0.635
No. conspecifics	-0.005	0.007	-0.793	0.429
No. people	0.031	0.055	0.564	0.574
Environment	0.442	0.176	2.509	0.013
VIGILANT FORAGING				
Intercept	-0.144	0.120	-1.244	0.231
Distance to road (m):				
1-5	-0.065	0.236	-0.277	0.782
6-20	-0.232	0.235	-0.989	0.324
21-50	0.056	0.238	0.234	0.815
51-100	0.282	0.244	1.153	0.251
100+	-0.261	0.248	-1.055	0.293
No. conspecifics	-0.013	0.006	-2.255	0.026
No. people	-0.016	0.047	-0.348	0.728
Environment	0.554	0.156	3.553	0.001
OTHER BEHAVIOURS				
Intercept	-0.238	0.184	-1.536	0.127
Distance to road (m):				
1-5	-0.473	0.262	-1.805	0.073
6-20	0.373	0.261	1.430	0.155
21-50	-0.351	0.265	-1.321	0.189
51-100	-0.279	0.273	-1.020	0.309
100+	0.261	0.273	0.955	0.341
No. conspecifics	-0.004	0.006	-0.565	0.573
No. people	0.003	0.052	0.057	0.955
Environment	0.553	0.172	3.209	0.002

environment by a factor of 1.4; however, this was not reflected in a correspondingly smaller percentage of searching-foraging. Vigilant foraging and 'other behaviours' comprised significantly greater components of urban than nonurban GABs (Tables 1 and 2), but together they comprised, on average, only ~7% of an urban and ~3% of a nonurban GAB.

Influence of co-variables on ground activity bout composition

Distance (m) of focal ravens from the nearest road was as follows: 0-5 - 41.9%, 6-20 - 12.4%, 21-50 - 18.5%, 51-100 - 11.1% and 100+ - 16.1%. Urban focal ravens tended to be closer to roads than did nonurban individuals ($\chi^2_{(3)} = 28.777$, $P < 0.001$, with pooling of two categories). The mean number of conspecifics in flocks containing focal ravens was 7.7 ± 1.0 ($n = 162$) and this metric was statistically similar in urban (6.4 ± 1.2 , $n = 83$) and nonurban (9.1 ± 1.5 , $n = 79$) environments ($t_{(160)} = 1.422$, $P = 0.157$). The mean number of people within 30 m of a focal raven (measured instantaneously) was 0.6 ± 0.1 , but not surprisingly there were fewer people nearby in the nonurban (0.2 ± 0.1) than in the urban (1.0 ± 0.2) environment ($t_{(160)} = 3.623$, $P < 0.001$).

Linear Mixed Effects models indicated that: (a) the number of people in a focal raven's immediate vicinity (measured instantaneously) had a significant positive effect on its vigilance effort, (b) the number of conspecifics in a focal raven's flock had a significant negative effect on the percentage of time it allocated to vigilant foraging, and (c) the time allocated to vigilance by a focal raven was less, but that spent in searching-foraging was more, within 5 m of roads. (Table 2).

Ambient traffic volume and urban ground activity bout composition

Pedestrian and vehicular traffic presence (measured over 10 min) at 73 urban sites where GABs were recorded averaged $20.5 \pm 2.9\%$ and $52.9 \pm 3.9\%$, respectively; pedestrian and vehicular traffic presence were not correlated ($r_{(71)} = 0.072$, $P > 0.05$). Linear-mixed effects models indicated that there was no significant effect of either pedestrian or vehicular traffic volume on the composition of GABs (Table 3 and Fig. 3).

DISCUSSION

On average, urban and nonurban adult ravens allocated similar percentages of a GAB to vigilance. Variation in ambient pedestrian and vehicular traffic volumes had no effect on the vigilance allocation within a GAB of urban ravens.

Factors influencing urban and nonurban vigilance time allocations

Two factors likely to influence antipredator vigilance effort in birds are (a) predator abundance, and (b) the frequency of human disturbances.

Theoretically, a greater abundance of nonurban than urban predators (Diaz *et al.* 2013; Samia *et al.* 2017) could lead to a greater prey vigilance effort in nonurban areas. Some evidence supports the hypothesis that predation risk for birds, particularly from raptors, is sometimes greater in nonurban than urban environments (Sorace and Gustin 2009; Møller 2011; Diaz *et al.* 2013; Fischer *et al.* 2012), but how widespread this trend is

Table 3

Linear-mixed-effects models examining influence of traffic volume on the composition of raven ground-foraging bouts in the urban environment. Models included all co-variables, but only outputs for traffic co-variables presented here, plus the significant fixed effect Number of Conspecifics for vigilant foraging (in bold). Degrees of freedom = 60 in all models. Value indicates effect size. SE = standard error.

Response variable and traffic volume co-variables	Value	SE	t-value	p-value
VIGILANCE				
Pedestrian	0.003	0.006	0.412	0.682
Vehicular	-0.001	0.004	-0.266	0.791
SEARCHING-FORAGING				
Pedestrian	-0.001	0.001	-0.967	0.923
Vehicular	0.003	0.004	0.629	0.532
CONTACT-FORAGING				
Pedestrian	-0.000	0.006	-0.026	0.979
Vehicular	-0.001	0.004	-0.226	0.822
VIGILANT FORAGING				
Pedestrian	-0.006	0.005	-1.165	0.249
Vehicular	0.001	0.004	0.369	0.714
No. conspecifics	-0.039	0.014	-2.759	0.008
OTHER BEHAVIOURS				
Pedestrian	-0.000	0.006	-0.023	0.982
Vehicular	-0.002	0.004	-0.578	0.565

remains unclear. Certainly, apex predatory raptors that require large home ranges and have specialised diets are largely absent from urban cores (Fischer *et al.* 2017). However, some birds-of-prey, particularly hunters of small birds, are increasingly becoming established in even the most urbanized parts of cities, which provide them with abundant food (Chace and Walsh 2006; Mazumdar *et al.* 2016), and some of them reach greater urban than nonurban densities (Kettel *et al.* 2017; Fischer *et al.* 2012). The issue is further complicated by the fact that other bird predators, such as cats *Felis catus*, are commonly more abundant in urban than nonurban environments (Møller 2011; Fischer *et al.* 2012).

Not surprisingly then, whether an avian prey species is subject to differing urban and nonurban predation pressures is likely to depend on the *specific* identity of its principal predator(s). Focusing on the relative magnitude of entire urban or nonurban predator communities when trying to predict vigilance trends for specific prey species may be unfruitful.

Adult ravens are large (425-650 g) and therefore probably only susceptible to large avian predators, particularly eagles (Rowley 1973; Lill 2019). Although eagles are increasingly being recorded in urban Australia, particularly during drought, they are still much more abundant in rural areas than cities. However, the effect of this disparity on the relative vigilance efforts of urban and nonurban ravens is complicated by the fact that ravens are also vigilant towards nest predators, such as Pied Currawongs *Strepera graculina* and Australian Magpies

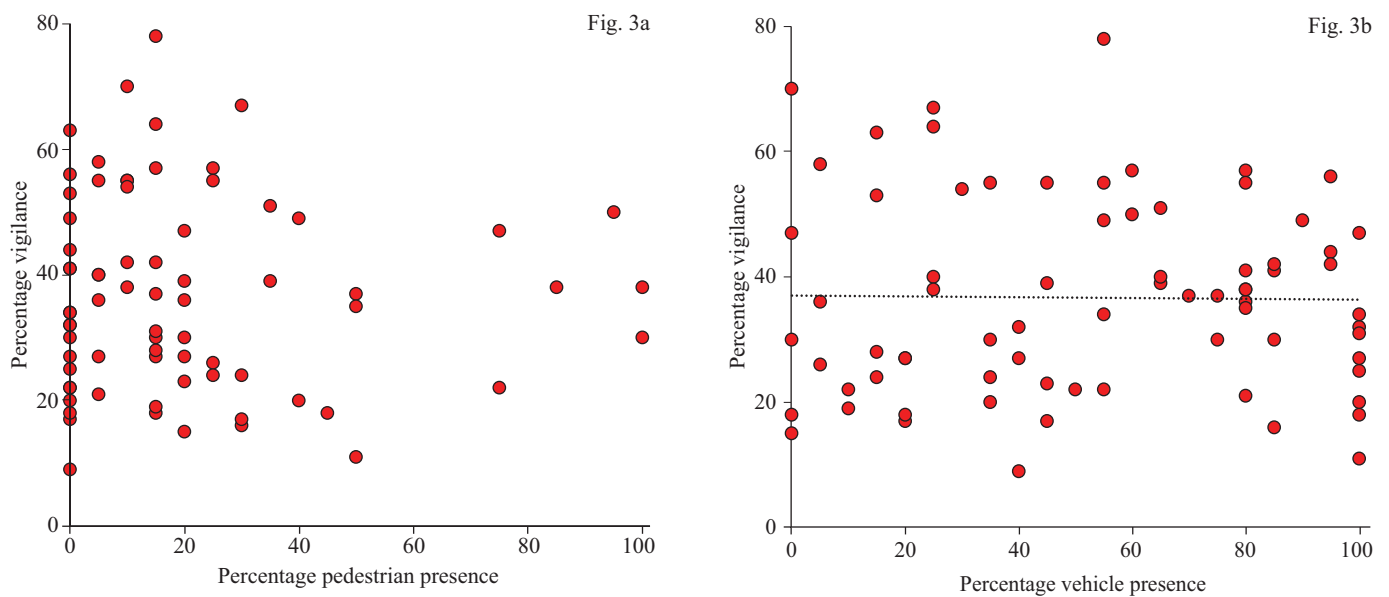


Figure 3a and 3b. Pedestrian and vehicular traffic volumes and vigilance time allocations of focal ravens at urban sites. Dashed line is a fitted linear trend line.

Cracticus tibicen (Lill 2019), both of which are common in urban and nonurban raven habitats. The limited volume of data for the breeding season in the present study did not permit meaningful examination of whether vigilance effort changed seasonally.

Frid and Dill's (2002) RDH argues that prey animals treat usually nonlethal, anthropogenic disturbances as they do real predation risk, responding in a manner that can involve diverting time and energy away from other fitness-enhancing activities, such as foraging (a 'trade-off effect'). The theory predicts that animals should monitor short-term changes in such disturbances and respond appropriately to the alterations in perceived risk that they pose, and vigilance is important in this monitoring. Although urban prey species are usually more tolerant of human proximity than nonurban conspecifics (Magle *et al.* 2005; Diaz *et al.* 2013; Samia *et al.* 2015), if the RDH is correct they should still probably expend considerably more time and energy monitoring human disturbances than do nonurban conspecifics. This might counteract any possible effect on vigilance effort of a lower natural predator abundance in the urban environment. However, Vines and Lill (2016) showed that nonurban ravens approached by a human were far less tolerant than urban conspecifics (i.e. they had a 6-fold longer flight initiation distance, escaped $1.4 \times$ more by flying than by terrestrial locomotion and fled > 10 m $3.4 \times$ more often). This greater intolerance of human proximity may reflect the fact that ravens are persecuted by some sections of the rural farming community because of their alleged predatory attacks on livestock and their consumption of crops, and are consequently very wary of humans (Rowley 1973; Vines and Lill 2016). Thus, despite the nonurban environment typically having far fewer human disturbances than urban areas, human disturbance may conceivably play a disproportionately large role in shaping the vigilance effort of nonurban ravens.

We cannot presently identify precisely why urban and nonurban ravens exhibited similar vigilance efforts. Nonurban adult ravens probably have more natural predators and

experience fewer human disturbances, but they are much more sensitive to human proximity and may therefore conceivably allocate a disproportionate amount of time to vigilance directed at people. Urban conspecifics probably have fewer natural, but more domesticated, predators and experience many more anthropogenic disturbances, but are more tolerant of human proximity. Quantifying the abundance of potential predators of adult ravens and their nest contents in urban and nonurban environments would help to elucidate the role that predator abundance has in shaping the vigilance effort of rural and city ravens, and there may be relevant survey data available for examination.

Relatively few studies have compared urban and nonurban vigilance effort within a wildlife prey species (Beauchamp 2015). Other species in which, like ravens, vigilance effort is similar under differing degrees of urbanization include Woodchucks *Marmota monax* (Lehrer *et al.* 2012) and Common Mynas *Acridotheres tristis* (McGiffin *et al.* 2013). However, there are species in which urban individuals are substantially less vigilant than nonurban ones (e.g. Swan Geese *Anser cygnoides*, Randler 2003; Fox Squirrels *Sciurus niger*, Mcclleery 2009, and American Wigeon *Anas americana*, Berl 2013), and some exhibiting the opposite trend (e.g. Grey Squirrels *Sciurus carolinensis*, Sarno *et al.* 2015; Black-tailed Prairie Dogs *Cynomys ludovicianus*, Ramirez and Keller 2010; Eastern Grey Kangaroos *Macropus giganteus*, Hume *et al.* 2019).

Magnitude and measurement of the vigilance time allocation

The 36-40% mean vigilance time allocation within GABs of foraging ravens is among the higher values recorded in the literature for birds and mammals, but our definition of vigilance (the beak's long axis at or above the horizontal and the beak not contacting food or substrate) necessarily encompassed walking between foraging sites in a head-up posture (Locomotion 1 and 2, Fig. 2), which would have inflated this mean value. However, walking in this posture would probably still facilitate vigilance

even if it was not the primary function of the behaviour. Several investigations have shown that some wildlife can be vigilant even in a head-down feeding posture or while handling or processing food in a head-up posture, although visual scanning may be less efficient under these circumstances (Kaby and Lind 2003; Cowlshaw *et al.* 2004; Baker *et al.* 2011). This reflects the broader issue that the best vigilance markers are those that can be demonstrated to be consistently associated with threat detection (Beauchamp 2015). We acknowledge that our definition of vigilance, like many others, did not meet this criterion. Moreover, we do not know how much of raven vigilance was social vigilance. However, this does not detract from the validity of our main finding of a similar vigilance effort in urban and nonurban environments, particularly in the absence of a group size effect on vigilance.

Traffic and vigilance

Roads carrying heavy traffic have profound adverse effects on the ecology of many bird species (Trombulak and Friswell 2000) through, *inter alia*, collision-related mortality, optical disturbance and acoustic interference (Pocock and Lawrence 2005; Orłowski 2008; Parris and Schneider 2009). In accordance with the RDH, some wildlife species in nonurban sites are more vigilant near to than further away from roads, sometimes with a compensatory decrease in foraging time (Speziale *et al.* 2008; Lian *et al.* 2011; Ciuti *et al.* 2012). That this is primarily a response to the presence of traffic is suggested by the fact that temporary road closure dampened the pattern in Elk *Cervus canadensis* (St. Clair and Forrest 2009). A direct response to higher vehicular and pedestrian traffic volumes with increased vigilance and reduced foraging has also been demonstrated in several wildlife species (Riddington *et al.* 1996; Gavin and Komers 2006; Griffin *et al.* 2007; Li *et al.* 2011). However, there are some exceptions, as Elk and Pronghorn Antelopes *Antilocapra americana* foraging near busy roads were less vigilant than those foraging near roads with less traffic (Brown *et al.* 2012; Shannon *et al.* 2014).

Ravens were less vigilant and foraged more within 5 m of roads than when further away. Urban individuals did not respond in vigilance terms directly to ambient pedestrian and vehicular traffic volumes, although it should be noted that urban pedestrian traffic volumes were generally low anyway. Vines and Lill (2016) also found little effect of traffic volume on tolerance of human proximity in urban Little Ravens. The lack of a response to traffic volume in urban ravens could indicate that most of them are habituated to heavy traffic or that, through a sorting process, only the more traffic-tolerant individuals occur in areas with high traffic volumes. The presence of pedestrian traffic might also buffer the risk of predation by natural predators (Møller 2012, Shannon *et al.* 2014). Alternatively, it is possible that the lack of a response reflects a measurement limitation; perhaps our 'snapshot' estimates of traffic volumes were simply too circumscribed. However, we sampled 73 urban sites at times spread throughout the day, which should have been sufficient at least to detect a strong relationship, and the data scatter in Figure 3 shows no indication of any association. It is also possible that ravens are responsive to traffic but adjust to traffic parameters that we did not measure, such as peak volumes; this might be feasible during breeding when they are territorial and could become familiar with local traffic trends. If measurement limitation was not involved, the findings are

important in indicating that ravens can inhabit even those parts of the urban environment where vehicular and pedestrian traffic volumes are particularly high (Kitchen *et al.* 2011). The fact that urban focal ravens foraged closer to roads than nonurban conspecifics may simply have reflected that either: (a) we could typically see ravens from our observation vehicle further away from roads in the nonurban environment because there were fewer visual obstructions, or (b) there are many more roads in the urban environment.

Future research

Additional research that could enhance our understanding of vigilance in urban and nonurban ravens includes:

1. Further sampling of GABs: this might be worthwhile because although our sample was sizable, there was considerable inter-individual variation in time allocations to specific behaviours (Table 1), especially the less frequently occurring ones. There were also some puzzling findings e.g. despite the overall time allocation to foraging being the same in urban and nonurban environments, the significantly greater urban time allocation to contact foraging was not reflected in a lesser time expenditure on searching-foraging.
2. Analysing vigilance bout frequency and duration in GABs: this could provide a more in-depth understanding of the value of vigilance during ground foraging.
3. Examining vigilance in contexts other than GABs. Although ravens spend much of the daytime on the ground, they also perch and forage to a lesser extent above ground level in vegetation and on infrastructure.

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