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Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter?

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Abstract

Optimal escape theory predicts that animals should moderate their flight responses according to the level of risk represented by a potential predator. This theory should apply even when organisms are habituated to disturbance, and how animals respond to human presence is likely to determine their success exploiting urban habitats. Therefore, urban animals should be sensitive to cues that inform them about levels of risk, allowing them to reduce costs by not overreacting to innocuous stimuli, while ensuring that they are nevertheless reactive to genuinely threatening stimuli. We tested this at a highly urbanized site in New York City, where eastern grey squirrels appear to pay little attention to humans. Squirrels were approached tangentially on a trajectory that took the observer within ~2 m of them and we measured alert distance, flight initiation distance (FID), and distance fled for each focal individual. Squirrels showed little sign of being alerted to the pedestrian if he remained on the footpath and did not look at them (only 5% of individuals moved away), but 90% of squirrels moved away, with longer FID and flight distance, when approached by a pedestrian that moved off the footpaths and looked at them. Squirrels therefore modulate their reactions when pedestrians behave in a predictable manner (i.e. remaining on the footpaths) and are also sensitive to the direction of attention of humans, reducing unnecessary responses, and are thereby likely to be increasing their ability to persist in this urban environment. Previous studies have emphasized the behavioural plasticity of successful urban wildlife species. In this study, we emphasize the importance of disturbance monitoring by successful urban exploiters, allowing them to vary their behavioural responses according to the level of risk to which they are exposed.

Introduction

Cities are challenging environments for many species of wildlife, presenting a loss of natural resources (i.e. habitat and food) and high levels of anthropogenic disturbance, that is pedestrian traffic, vehicular traffic and industrial noise (Lowry, Lill & Wong, 2012). Despite this, some species do extremely well in urban environments. Successful 'urban adapters' (sensu McKinney, 2006) are generally species that show high levels of opportunistic behaviour (i.e. are habitat or trophic generalists and can exploit novel niches; Bateman & Fleming, 2012, Lowry *et al*., 2012), or, in the case of birds, are also more gregarious or sedentary (Kark *et al*., 2007) or have large breeding ranges, high fecundity, dispersal and survival (Møller, 2008). Behavioural flexibility and adaptive adjustments are therefore identified as a feature of successful urban species and are likely to be important in facilitating resource use, avoiding disturbance and enhancing communication (Slabbekoorn & Peet, 2003; Patricelli & Blickley, 2006; Baker *et al*., 2007; Evans, Boudreau & Hyman, 2010; Lowry *et al*., 2012; Sol, Lapiedra & Gonzalez-Lagos, 2013).

A major aspect of behavioural flexibility in urban adapters is how such animals are able to modify their antipredator behaviour towards humans, which may be regarded as 'predation-free predators' (Beale & Monaghan, 2004). Models of optimal escape theory predict that individuals should flee when costs of staying outweigh costs of flight, based on the variables of risk posed by the predator, the cost of fleeing, the potential to rely on other defensive tactics, and the size of the prey group (i.e. increased vigilance and predator dilution) (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). Animals should, therefore, assess the degree of risk represented and dynamically adjust their antipredator behaviour accordingly.

In urban environments, where there is a high level of background disturbance, the success of urban wildlife may rely on their abilities to clearly distinguish between genuinely threatening and non-threatening stimuli and become habituated to some human activity. Although animals still need to be sensitive to the level of threat because of human presence, living without fear in the vicinity of humans is identified as a key behavioural trait of urban adapters (Kark *et al.*, 2007).

Ideally, successful urban adapters should be able to ignore non-threatening stimuli, minimizing opportunity and energetic costs, and also potentially allowing exploitation of additional resources. There are subtle cues that could inform fleeing decisions by organisms, which they could use to reduce costs associated with fleeing when unnecessary and hence influence flight initiation distance (FID). For example, being sensitive to the direction of attention of an approaching human ('looking at' or 'looking away') has been demonstrated recently to influence escape responses of birds (Bateman & Fleming, 2011; Clucas *et al.*, 2013; Lee *et al.*, 2013) and reptiles (Burger, Gochfeld & Murray, 1991, 1992; Cooper, 1997, 2011). Another cue to risk perception that has received little attention is the predictability of the behaviour of humans – a human who behaves in a way that diverges from 'usual' human behaviour (e.g. approaches from a different direction to most pedestrians) may be perceived as a higher risk and therefore influence escape responses, even if their behaviour is not more threatening *per se*. Sensitivity to such 'unusual' behaviour would be dependent on long-term habituation of the animal to predictable human behaviour.

Eastern grey squirrels *Sciurus carolinensis* are extremely successful urban adapters, and can be found in high densities in urban parks where they face reduced predation and become habituated to human presence, to the point where they show minimal avoidance behaviour of people (Cooper *et al.*, 2008; McCleery, 2009; Engelhardt & Weladji, 2011). Eastern grey squirrels also have a lower giving-up density (i.e. take more seeds from localized sources) in urban areas than non-urban areas, possibly indicating lower sensitivity to predation (Bowers & Breland, 1996). We examined the behaviour of a population of eastern grey squirrels in a highly urbanized area – the lower east side of Manhattan, New York. We predicted that squirrels would show highly reduced antipredator behaviour because of habituation to human presence (as demonstrated by Cooper *et al.*, 2008, Engelhardt & Weladji, 2011), but should still discriminate between different levels of threat posed by people, and appropriately dynamically upgrade their antipredator response. We therefore tested two experimental treatments. First, as urban squirrels have become used to humans by exposure to normally unvarying behaviour (walking on footpaths), we tested what happens when pedestrians show 'unusual' behaviour (walking on the grass between footpaths). Second, we tested whether these squirrels retain the ability to discriminate between a pedestrian who passes by without looking directly at them, and a pedestrian who has their attention directed towards the animal.

Methods

The eastern grey squirrel has the widest range and distribution of all tree squirrel species, being found across eastern North America with introductions elsewhere in North America, Europe and Africa. Eastern grey squirrels show plasticity in habitat preferences, foraging activities (Wauters *et al.*, 2002), population densities (Fisher & Merriam, 2000; Parker & Nilon, 2008) and social grouping, that is home range size and group size (Don, 1983; Koprowski, 2005), all of which are likely to be modified by living in cities.

Urban eastern grey squirrels can reach high population densities: from 3–10 to 51.5 individuals per ha (Parker & Nilon, 2008). A large population of eastern grey squirrels (estimated in excess of 800, based on count transects) lives around Peter Cooper Village/Stuyvesant Town (PCVST) (40.7317°N, 73.9778°W), a residential complex (~30 ha) in Manhattan, New York City, where apartment buildings are set in a matrix of access roads, footpaths (2.5–5 m wide), grassed areas, playgrounds, garden beds and trees (Supporting Information Appendix S1). Within PCVST, apart from a central lawn, most grassed areas and bushy areas about the bases of the apartment buildings and are ~6 m wide, with some larger areas. Trees of various sizes are planted beside footpaths, but most squirrels forage on the ground and will readily cross footpaths and access roads to reach patches of grass and bushes. No cats were observed loose in PCVST and dogs are all required to be restrained on leashes. Red-tailed hawks *Buteo jamaicensis* will predate on the PCVST squirrels, although they do not seem to be resident in the complex. Squirrels appear to be highly habituated to humans, and are rarely observed running from them unless the humans are accompanied by dogs; even then, the squirrels rarely ascend >1 m up trees (P. W. Bateman, pers. obs.). The squirrels are fed by some residents, and should the person stop and rummage in pockets or bags, squirrels will often approach pedestrians expectantly.

The study was carried out in mornings in December between 9.00 AM and 12:00 noon, that is when there was human activity in PCVST. Squirrels were approached by one of us (PWB) on foot at a set pace (1 m s^{-1}). The observer maintained a trajectory that, if the squirrel did not move, would take him past it at a distance of ~2 m. We alternated our approach to these squirrels, either (1) looking directly at the squirrel at all times and tracking it with our eyes and face; or (2) looking ahead and observing the squirrel through perifoveal vision (Bateman & Fleming, 2011). We approached squirrels that were foraging (i.e. sitting eating, or moving slowly) on the plant beds and lawns that we could pass by staying on the footpath, or alternatively, approached squirrels such that our trajectory would take us off the footpaths and onto the grass or plant beds. Squirrels initially averaged 6.8 ± 2.0 m (±1 standard deviation; range 2–12 m) off the footpaths, but were still passed at a distance of ~2 m. We endeavoured to minimize the chances of re-sampling the same individuals by walking in a single direction around the complex each day. There are over 800 eastern grey squirrels at this site, reducing the likelihood of re-sampling the same individual over successive days.

Most areas of PCVST are open to human access; that is, people are allowed to walk on these grassy areas or between the plants. However, in the space of two weeks, apart from on the large central lawn, only a few people with dogs and small children were observed to go off the footpaths – these people represent a tiny percentage of the total number of humans walking around the complex (~25 000 residents plus others who can walk through the complex).

For every focal individual approached (animals that were not running: i.e. foraging slowly or motionless), we recorded whether the animal fled or not ('yes' or 'no'). Animals that did not flee were recorded as having an FID of 0 m (the minimum distance from the observer passing by 2 m away). The proportion of animals that fled was compared by Pearson's χ^2 analysis, with expected values calculated assuming an equal proportion of animals either fled or did not flee across all the treatments. Separate analyses were also carried out to test for the effects of approach trajectory and direction of attention.

The observer also measured:

(1) Start distance – the distance from observer to squirrel when the observer began moving towards it.

(2) Alert distance – the distance between squirrel and observer when the squirrel demonstrated awareness/vigilance towards the observer, usually sitting up straighter, ceasing eating or orienting towards the observer. Animals that showed no evidence of being alerted to his presence were scored as 0 m.

(3) FID – the distance between the observer and the squirrel when the squirrel began moving away from the observer, that is began moving or changed direction and speed of slow foraging movement. Scored as 0 m for animals that did not move away.

(4) Distance fled (the distance the squirrel fled before either stopping or resuming foraging behaviour). Scored as 0 m for animals that did not move away.

Distances were measured by dropping coloured pen lids at each point and recording the distances afterwards (with a practiced, measured pace; ±1 m). Although previous studies have indicated that start distance may influence FID, we had no significant difference in start distance (averaged 13 ± 4 m; range 7–27 m) for our four treatment categories (median test, $\chi^2_3 = 1.86$, $P = 0.603$) and start distance was not significantly correlated (Spearman rank–order correlations) with alert distance, FID or distance fled for any of the four treatments. We therefore have not further considered the effect of start distance on FID (which allowed us to use one-way non-parametric analyses, which were required on account of the nature of the escape behaviour data). Alert distance and FID were not normally distributed because of the high proportion of animals (57%) that did not flee the approaching observer. These data were therefore analysed by non-parametric median test for the four approach treatments for each measure (alert distance, FID and distance fled) independently followed by *post hoc* multiple comparisons (using Kruskal–Wallis H-tests). If focal animals are used to people, as in the present case, and a tangential approach has been used, then animals can be passed-by without them moving at all (e.g. Bateman & Fleming, 2011). We have recorded these animals as having an FID and distance fled of 0 m (although the FID values could also be scaled up, making the minimum value 2 m). Individuals that do not move are central to the data on the repertoire of responses seen in habituated animals, and therefore should not be omitted or ignored. Using non-parametric analyses allows the analysis of these data, where attributing a minimum value to these animals will not affect their ranking in the calculation of statistically significant differences.

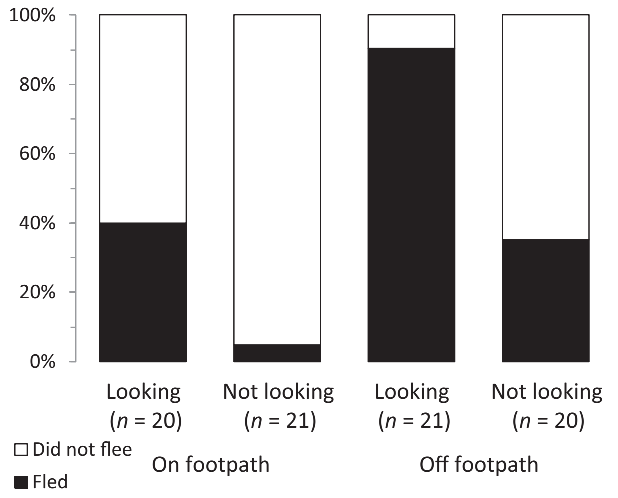

Figure 1 Proportions of eastern grey squirrels in each of four approach treatments that either fled or did not flee an approaching pedestrian.

Values are presented as medians (range).

Results

We recorded significant differences in whether the focal squirrel would move away or not between our four experimental treatments (Chi-test: $\chi^2_3 = 18.49$, $P < 0.001$) (Fig. 1). When the observer remained on the footpath, only 22% of individuals (9 of $n = 41$ approached in this manner) moved away from the observer, contrasting with 63% (26 of $n = 41$) of squirrels approached when the observer left the footpath ($\chi^2_1 = 8.20$, $P = 0.004$). Squirrels were also more reactive when he was looking at them ($\chi^2_1 = 10.24$, $P = 0.001$). When the observer was looking at them, 40 and 90% (on footpath and off footpath, respectively) of squirrels moved away compared with only 5 and 35% when the observer was not looking at them (the remainder of individuals remained where they were).

There was a significant treatment effect upon alert distance (Median test: $\chi^2_3 = 30.66$, $P < 0.001$), FID ($\chi^2_3 = 32.49$, $P < 0.001$) and distance fled ($\chi^2_3 = 33.32$, $P < 0.001$). For alert distance (Fig. 2), squirrels showed little change in behaviour when the pedestrian remained on the footpath and did not look at them (median alert distance 0 m, 0–4 m); there was no significant difference in alert distance for the other three treatments (5 m; 0–8 m). For FID and distance fled (Fig. 2), squirrels were most reactive (longer distances) when approached by a pedestrian that moved off the footpaths and looked at the squirrel as he approached (FID: 4 m; 0–6.5 m; distance fled: 6 m; 0–13 m); the other three treatments were not significantly different from each other (FID: 0 m;, 0–5.5 m; distance fled: 0 m; 0–10 m).

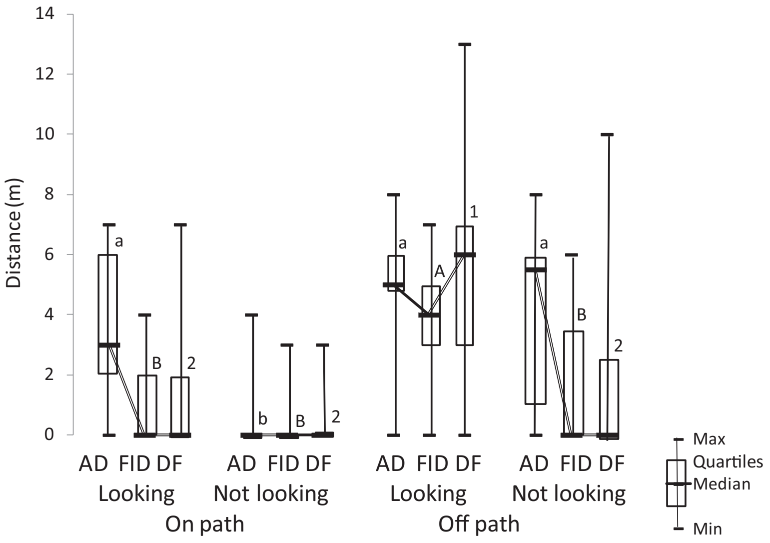

Figure 2 Alert distance (AD), flight initiation distance (FID) and distance fled (DF) for squirrels approached by a pedestrian that was either looking or not looking at them, and either remained on footpaths or approached the squirrels directly (moving off the footpaths). Letters/numerals indicate the results of *post hoc* analyses for each distance measure independently.

Discussion

In the urban environment, the mark of a successful animal species is likely to be its ability to distinguish between innocuous stimuli and genuine risk. Eastern grey squirrels have established populations in the many cities across the globe. In this study, we show that eastern grey squirrels living in a Manhattan park show behavioural flexibility towards pedestrian activities. Squirrels allow pedestrians to approach closely compared with conspecifics in rural areas (e.g. FID 10.4 ± 6.65 m; Cooper *et al.*, 2008). PCVST squirrels are mostly exposed to pedestrians acting in a benign, predictable manner, but show different responses towards pedestrians showing more irregular behaviour, presumably because they perceive it as more risky.

First, PCVST squirrels were more reactive when the pedestrian was looking directly at them as he approached, as has been observed in urban birds (increasing FID or other escape reactions, e.g. ceasing foraging or alarm calling, Bateman & Fleming, 2011, Clucas *et al.*, 2013, Lee *et al.*, 2013). Second, PCVST squirrels were more reactive towards a person that diverged from 'normal' behaviour by not keeping to the footpaths. Similar responses have been recorded in Alpine marmots *Marmota marmota* (Mainini, Neuhaus & Ingold, 1993) and for American robins *Turdus migratorius* (Eason *et al.*, 2006), which demonstrate longer FID in response to hikers that have moved off established trails than hikers that were on trails. One possible explanation for these findings may be that bolder individuals are more likely to be present closer to the roads/paths, as has been noted for burrowing owls *Athene cunicularia* (Carrete & Tella, 2010). Bolder individuals may be able to exploit resources closer to paths/roads despite exposure to greater amounts of human traffic.

Our study emphasizes the importance of monitoring for urban adapters. Most people represent a low risk to the squirrels in PCVST, and the squirrels consequently continue to forage when approached. However, being sensitive to subtle cues in the behaviour of their human co-inhabitants is likely to contribute to the success of eastern grey squirrels in highly urbanized habitats. There is nothing that should be inherently less 'risky' about a pedestrian that is 2 m away and moving on a footpath than one that is the same distance away, but moving on the grass, except that people rarely walk on the grass at PCVST. Rodriguez-Prieto *et al.* (2009) found that blackbirds *Turdus merula* in urban parks in Madrid with high exposure to humans had short FIDs, but these increased when approached by a novel 'predator' in the form of a radio-controlled vehicle. These data suggest that urban animals will modify their assessment of risk according to familiarity of behaviour and objects.

We have identified cues that are likely to be important for risk perception by an urban animal species monitoring its environment. Together with direction of attention of people, urban squirrels were more reactive to pedestrians that showed a divergence from 'usual' behaviour (e.g. pedestrians entering areas which are usually human-free), even when not associated with closer approach or changes in speed. In addition to being arboreal (which can include use of anthropogenic structures), which minimizes vulnerability to diurnal terrestrial 'predators' (see Herr, Schley & Roper, 2009), general trophic and social flexibility (Baumgartner, 1943; Don, 1983; Koprowski, 2005) may help explain why eastern grey squirrels are successful urban adapters.

Further research should consider how, despite habituation to human presence, urban taxa modulate their reactions according to subtle differences in human behaviour. Assessment of, and potentially habituation to, human activity is an important criterion for successful urban adapters and urban exploiters. In the face of increasing urbanization across the globe, the life history and behavioural attributes of those taxa that are good urban adapters warrants further study (Bateman & Fleming, 2012).

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References

Baker, P.J., Dowding, C.V., Molony, S.E., White, P.C.L. & Harris, S. (2007). Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behav. Ecol.* **18**, 716–724.

Bateman, P.W. & Fleming, P.A. (2011). Who are you looking at? Hadeda ibises use direction of gaze, head orientation and approach speed in their risk assessment of a potential predator. *J. Zool. (Lond.)* **285**, 316–323.

Bateman, P.W. & Fleming, P.A. (2012). Big city life: carnivores in urban environments. *J. Zool. (Lond.)* **287**, 1–23.

Baumgartner, L.L. (1943). Fox squirrels in Ohio. *J. Wildl. Manage.* **7**, 193–202.

Beale, C.M. & Monaghan, P. (2004). Human disturbance: people as predation-free predators? *J. Appl. Ecol.* **41**, 335–343.

Bowers, M.A. & Breland, B. (1996). Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. *Ecol. Appl.* **6**, 1135–1142.

Burger, J., Gochfeld, M. & Murray, B.G.J. (1991). Role of a predator's eye size in risk perception by basking black iguana, *Ctenosaura similis*. *Anim. Behav.* **42**, 471–476.

Burger, J., Gochfeld, M. & Murray, B.G. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *J. Comp. Psychol.* **106**, 97–101.

Carrete, M. & Tella, J.L. (2010). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**, 167–170.

Clucas, B., Marzluff, J.M., Mackovjak, D. & Palmquist, I. (2013). Do American crows pay attention to human gaze and facial expressions? *Ethology* **119**, 296–302.

Cooper, C.A., Neff, A.J., Poon, D.P. & Smith, G.R. (2008). Behavioral responses of eastern gray squirrels in suburban habitats differing in human activity levels. *Northeast. Nat.* **15**, 619–625.

Cooper, W.E.J. (1997). Threat factors affecting antipredatory behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia*. **1997**, 613–619.

Cooper, W.E.J. (2011). Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology* **117**, 620–629.

Cooper, W.E.J. & Frederick, W.G. (2007). Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67.

Don, B. (1983). Home range characteristics and correlates in tree squirrels. *Mamm. Rev.* **13**, 123–132.

Eason, P.K., Sherman, P.T., Rankin, O. & Coleman, B. (2006). Factors affecting flight initiation distance in American robins. *J. Wildl. Manage.* **70**, 1796–1800.

Engelhardt, S.C. & Weladji, R.B. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can. J. Zool.* **89**, 823–830.

Evans, J., Boudreau, K. & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* **116**, 588–595.

Fisher, J.T. & Merriam, G. (2000). Resource patch array use by two squirrel species in an agricultural landscape. *Landsc. Ecol.* **15**, 333–338.

Herr, J., Schley, L. & Roper, T.J. (2009). Socio-spatial organization of urban stone martens. *J. Zool.* **277**, 54–62.

Kark, S., Iwaniuk, A., Schalimtzek, A. & Banker, E. (2007). Living in the city: can anyone become an 'urban exploiter. *J. Biogeogr.* **34**, 638–651.

Koprowski, J.L. (2005). The response of tree squirrels to fragmentation: a review and synthesis. *Anim. Conserv.* **8**, 369–376.

Lee, S.-I., Hwang, S., Joe, Y.-E., Cha, H.-K., Joo, G.-H., Lee, H.-J., Kim, J.-W. & Jablonski, P.G. (2013). Direct look from a predator shortens the risk-assessment time by prey. *PLoS ONE* **8**, e64977.

Lowry, H., Lill, A. & Wong, B. (2012). Behavioural responses of wildlife to urban environments. *Biol. Rev. Camb. Philos. Soc.* **88**, 537–549.

Mainini, B., Neuhaus, P. & Ingold, P. (1993). Behaviour of marmots *Marmota marmota* under the influence of different hiking activities. *Biol. Conserv.* **64**, 161–164.

McCleery, R.A. (2009). Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landsc. Ecol.* **24**, 483–493.

McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260.

Møller, A. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* **63**, 63–75.

Parker, T.S. & Nilon, C.H. (2008). Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosyst.* **11**, 243–255.

Patricelli, G.L. & Blickley, J.L. (2006). Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* **123**, 639–649.

Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J. & Regis, Y. (2009). Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* **20**, 371–377.

Slabbekoorn, H. & Peet, M. (2003). Ecology: birds sing at a higher pitch in urban noise. *Nature* **424**, 267.

Sol, D., Lapiedra, O. & Gonzalez-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* **85**, 1101–1112.

Wauters, L.A., Gurnell, J., Martinoli, A. & Tosi, G. (2002). Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur? *Behav. Ecol. Sociobiol.* **52**, 332–341.

Ydenberg, R.C. & Dill, L.M. (1986). The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Map of PCVST.