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Tolerance of human approaches by Common Mynas along an urban-rural gradient

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Abstract. Successful urban colonisation by birds requires tolerance of many disturbances and avoidance of chronic stress and major disruption to critical activities. Habituation may be involved in acquiring tolerance of human proximity, in which case tolerance should vary with the degree of opportunity to learn that most humans do not present a threat and should therefore vary with human population density. We studied Common Mynas (*Acridotheres tristis*) in the urban, suburban, peri-urban and surrounding rural zones of Melbourne, Australia, to determine whether flight-initiation distance (FID) and time allocated to anti-predator vigilance increased along this gradient from the urban to the rural zone. This gradient encompassed a 143-fold variation in average human population density during daylight hours. Urban and suburban Mynas had a 2.3–5.7 times shorter FID, were 1.6–2.5 times less likely to retreat by flying and were 1.9–3.1 times more likely to flee >5 m than their peri-urban and rural conspecifics. Fleeing behaviour was not strongly correlated with estimated human population density, but exhibited an apparent 'step' in response at the suburban–peri-urban divide. Vigilance effort did not vary significantly between zones. This suggested that habituation did not occur with respect to surveillance for people, although surveillance presumably encompassed other predators too. Similar foraging effort and rates of food acquisition among zones could suggest that food abundance per individual was similar in urban and rural environments for Common Mynas, although this requires direct measurement.

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Introduction

Cities and towns commonly have a much greater proportion of exotic birds than exurban (peri-urban and rural environs surrounding urban areas) environments (McKinney 2002). Understanding how exotic species adapt to and survive in the urban environment ('synurbanisation'; Parker and Nilon 2012) is essential in any attempt to determine and, if necessary, manage their effect on urban native biodiversity and human urban economics and health (Duncan et al. 2003; Catterall 2009). Human presence can negatively affect many aspects of a bird's life history, including behaviours, such as foraging and reproduction (e.g. Ward and Low 1997; Price 2008), and stress levels (Ruiz et al. 2002; Walker et al. 2006), and could therefore affect fitness. Thus, a key prerequisite for successful colonisation of the urban environment is the ability to tolerate human presence (Møller 2012). Given the potential negative effects of human presence, natural selection for reduced sensitivity to human presence may occur over time in populations that persist in the urban environment (Møller 2008).

Flight-initiation distance (FID) is defined as the distance at which a bird retreats from a perceived threat (Blumstein 2006; Weston *et al.* 2012). Several alternative mechanisms can potentially explain variation in FID as a function of human population density, and a commonly invoked mechanism for birds is learning (Weston *et al.* 2012). When FID is reduced at high human densities, the behaviour is termed habituation. If habituation is instrumental in each generation of urban birds acquiring tolerance

of human presence, we might predict that conspecifics exposed to widely differing human population densities would show disparate degrees of tolerance to human proximity (Glover et al. 2011). Urban birds experiencing a high rate of contact with humans that in most circumstances are harmless to them would have to habituate to some extent to their presence to function optimally, but rural birds might not have sufficient levels of contact with people for habituation to occur and it may be less critical, except in reserves heavily used by visitors for recreation. Thus members of a species occurring in rural, peri-urban, suburban and urban areas might exhibit progressively greater tolerance of human proximity and activity along this gradient. This increase in tolerance could be reflected in, among other behavioural variables, a decrease in the FID and in the percentage time allocation to vigilance (T_{vig}) (Lima 1998). The latter could, in turn, lead to a compensatory increase in percentage time allocated to other important behaviours, such as foraging (T_{forage}) (Ward and Low 1997).

The Common Myna (*Acridotheres tristis*) occurs naturally in southern and south-eastern Asia. It was successfully introduced to Australia, and has colonised many cities and towns in eastern Australia, and occurs commonly along roads, around farms and in open woodland in exurban environments (Feare and Craig 1999). It is an urban exploiter (*sensu* Blair 2001) that lives commensally with humans, consumes some human food waste and commonly nests in buildings. It is widely regarded as an undesirable pest because of the noise it makes in its communal roosts, its nesting habits, its alleged competition with native birds for nesting sites

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and possibly food, its exploitation of domestic fruit crops and potential to spread disease (Pell and Tidemann 1997; Lowe *et al.* 2011; Grarock *et al.* 2012). Consequently there has been a recent movement to cull populations (Tippet 2012).

The aim of our study was to determine whether the FID and $T_{\rm vig}$ of Common Mynas increased along an urban-rural gradient in parallel with a decrease in human population density. To do this, we measured both variables in urban, suburban, peri-urban and surrounding rural zones of Melbourne, Australia. In parallel, we also measured time allocated to foraging to determine whether any reduction in vigilance (T_{vig}) in the city was reflected in a compensatory increase in foraging time. Although a few studies have compared the FID of urban and rural conspecifics, to the best of our knowledge only Valcarcel and Fernández-Juricic (2009) have compared the FID of urban and exurban conspecific birds in a similarly spatially fine-grained manner to that which is examined here and we could find no study that compared vigilance effort of free-living urban and rural conspecifics. Although our focus was a single species of bird in one Australian city and its exurban hinterland, the findings have relevance for other cities that have been colonised by this and other exotic species of bird.

Methods

Study species and study area

Common Mynas were deliberately introduced to Australia in the 1860s. They now occur along the eastern seaboard from Cairns to Adelaide and inland to west of the Great Dividing Range and may have the potential to spread even further inland. They are omnivorous and mostly forage on the ground, either singly, in pairs or in small flocks, but they assemble nocturnally in large, communal roosts (Feare and Craig 1999).

The study was conducted in Melbourne, Australia (37°47′S, 144°58′E), and its rural hinterland, in early spring to mid-summer (September-January), 2010-11, which covers the main breeding months for the species. Melbourne has a human population of >4 million people. Our study area was split into four demographic zones: (1) urban zone, comprising the central business district (CBD), with a high density of commercial buildings and a mean daytime human population density of 10 000 people km⁻²; (2) suburban zone, the surrounding suburbs characterised by a fairly high density of mainly residential buildings, with an estimated residential population density of 2600 people km⁻²; (3) peri-urban zone, abutting the suburbs, with more diverse land-use, a low density of housing, much open land and an estimated residential population density of 150 people km⁻² and (4) the rural zone, abutting the peri-urban zone, comprising mainly agricultural land with a very low density of housing and an estimated residential population density of only 70 people km⁻² (Fig. 1). Observations were made at 39–40 sites within each of these zones, mainly in open parkland, on roadsides and footpaths and in farmland. Sites were chosen randomly, although we avoided sampling near the boundaries of each zone.

Behavioural measures

Observations were made in the mid-morning (0900–1100 hours Australian Eastern Standard Time, AEST) and mid-afternoon (1400–1600 hours AEST) on fine days. Birds were not individually recognisable, so observations were made at each site only once. Observations were made of a single bird at a location within each site, and focal birds had to be at least 30 m apart to increase statistical independence of the data. Focal birds were always on the ground and were given 2 min to acclimatise to the presence of the observer before observation began. All behavioural measurements were made by the same researcher, who wore similar and dull-coloured clothing during all observations.

Flight-initiation distance

To measure the FID of a focal bird, it was approached by the observer walking in a straight line at a speed of 0.5– $1.0\,\mathrm{m\ s^{-1}}$. Using coloured marker discs and a Bushnell laser rangefinder (accuracy $\pm 1\,\mathrm{m}$; Bushnell Yardage Pro Sport 450, China), the observer recorded: Starting Distance (SD), which is the distance between the observer and the focal bird when the approach was initiated (Blumstein 2003); and FID, the point at which the bird fled, either by flying, walking or running (including hopping). The mode of retreat (flight, walking, running) and the distance to which the bird retreated (visually estimated as 0– $5\,\mathrm{m}$) were also recorded.

Time allocated to vigilance and foraging

Time-activity budgets of focal Common Mynas were recorded by instantaneous sampling (from a distance that did not elicit alert behaviour; Fernández-Juricic *et al.* 2001) at intervals of 10 s for 2–8 min. The three behavioural categories recorded were: (*a*) vigilance, standing erect with head up and visually scanning the environment; (*b*) foraging, standing or walking with head down, visually examining and pecking at the substrate and (*c*) pecking rate (PR), the number of pecks at the substrate during foraging, recorded for the first 10 s of each minute of continuous foraging.

Co-variates that could potentially influence FID, $T_{\rm vig}$, $T_{\rm forage}$ and PR were recorded for each focal bird observed (distances visually estimated): the presence of conspecifics within 10 m, presence of people within 20 m, vehicles passing within 10 m and distance to nearest refuge (DNR), such as tall vegetation or buildings (<10, 10–20 or >20 m).

Data analysis

Statistical analyses were conducted with Systat version 13 (Systat Software: Bangalore, India). Chi-square tests were used to explore differences among zones in mode of retreat and distance retreated from an approaching researcher. We used Analysis of Covariance (ANCOVA) and post hoc Tukey tests to examine differences in FID, T_{vig} , T_{forage} and PR among the four zones. The other factors listed above that could potentially have influenced the dependent variables were included in the ANCOVAs as covariates as appropriate. Time-allocation data were arcsine-transformed and FID, SD and PR log-transformed to help meet the assumptions of ANCOVA. We also checked that the ANCOVA assumption of linearity was met. We obtained approximate counts of the number of people, conspecifics and vehicles close to focal Mynas, but the occurrence of these variables was analysed just on the basis of presence or absence. This was done because their values could change during a researcher's approach or during time-allocation observations, both of which were of varying

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Fig. 1. Aerial view of typical areas in the four demographic zones: (a) urban; (b) suburban; (c) peri-urban; (d) rural.

duration. (The mean duration of time-allocation observations was $4 \min \pm 0.1$ s.e., range 2–6 min.) We interpret the F ratios and P-values generated for the co-variates conservatively because ANCOVA just controls for the influence of the co-variates on the dependent variable (Quinn and Keough 2007).

Results

Flight-initiation distance

Overall mean FID for all zones combinedwas 16.8 m (s.e. 0.9, n = 160) Mean FID was significantly shorter in the urban zone than the suburban zone, and in the suburban than the peri-urban zone, but did not differ between the peri-urban and rural zones (Table 1). Humans other than the researcher (maximum 5) were within 20 m of the focal Myna on 19% of occasions and conspecifics (maximum 6) within 10 m on 46% of occasions; the F ratios for these two co-variates were not significant (Tables 1, 2). The DNR for most FID (71%) were <10 m and the F ratio for this co-variate was not significant (Table 2). Mean SD ranged from 19 (urban zone) to 42 m (rural zone) (Table 1) and SD was positively correlated with FID (r = 0.786; P < 0.001, n = 160), explaining 80% of the variance in this distance.

Retreat mode and distance

When retreating from the approaching researcher, Mynas flew on 40% of occasions in the urban zone and 62.5% of occasions in the suburban zone, but flew on all occasions in the peri-urban and rural zones ($\chi^2_{(3)} = 57.063$, P < 0.001) (Table 1). Common Mynas retreated >5 m from the approaching observer on only ~33 and 50% of occasions in urban and suburban zones, whereas Mynas in the peri-urban and rural zones always (100%) retreated >5 m ($\chi^2_{(3)} = 51.282$, P < 0.001) (Table 1).

Allocation of time to vigilance and foraging and the pecking rate

Overall, Common Mynas spent ~25% of observation time in vigilance and ~70% in foraging and the two allocations were negatively correlated (r = -0.870, n = 159, P < 0.001). The allocation of time to these two behaviours did not vary significantly among the four zones (Tables 1, 2). Humans other than the researcher were close to the focal Myna on 28% of occasions (maximum of 11 people), conspecifics were close to the focal bird on 59% of occasions (maximum of 12 conspecifics) and vehicles close in 47% (maximum of 25 vehicles) of occasions.

| Table 1. | Fleeing behaviours and time allocations of Common Mynas in four demographic zones in and around Melbourne |
|----------|---|
| | Figures are means \pm s.e. or percentages, and all sample sizes were 40 per zone for all measured variables |

| | Zone | | | | | |
|--------------------------------------|----------------|----------------|----------------|----------------|----------------|--|
| | Urban | Suburban | Peri-urban | Rural | All zones | |
| FID | | | | | | |
| Starting distance (SD) (m) | 18.6 ± 1.7 | 23.7 ± 1.7 | 36.7 ± 2.0 | 42.3 ± 2.5 | 30.3 ± 1.3 | |
| Flight-initiation distance (FID) (m) | 4.7 ± 0.5 | 10.7 ± 1.1 | 24.9 ± 1.1 | 26.8 ± 1.6 | 16.8 ± 0.9 | |
| Retreats by flying (%) | 40 | 63 | 100 | 100 | 76 | |
| Retreats >5 m (%) | 33 | 53 | 85 | 100 | 68 | |
| Behaviour | | | | | | |
| Percentage of time spent vigilant | 24.1 ± 0.0 | 26.5 ± 0.0 | 25.0 ± 0.0 | 27.3 ± 0.0 | 26.0 ± 0.8 | |
| Percentage of time spent foraging | 71.6 ± 0.0 | 69.4 ± 0.0 | 70.1 ± 0.0 | 68.1 ± 0.0 | 69.8 ± 0.9 | |
| Pecking rate (pecks per 10 s) | 3.5 ± 0.1 | 3.7 ± 0.1 | 3.4 ± 0.1 | 3.6 ± 0.1 | 3.5 ± 0.1 | |

Table 2. Analyses of co-variance for the variation in FID and time allocations (percentage) of Common Mynas in the four demographic zones in and around Melbourne

Significant values (*P*<0.05) are in bold; d.f., degrees of freedom. Error d.f.=152 for all analyses. Pairwise comparisons of log(FID) for the four zones (urban, suburban, peri-urban, rural) are presented in Table 3

| Dependent variable, | F ratio | d.f. | P | Multiple R ² | |
|--------------------------|---------|------|---------|-------------------------|--|
| factor and co-variates | | | | • | |
| log(FID) | | | | 0.669 | |
| Zone | 93.813 | 3 | < 0.001 | | |
| log(SD) | 22.083 | 1 | < 0.001 | | |
| Distance to refuge | 1.495 | 1 | 0.223 | | |
| Presence of humans | 0.951 | 1 | 0.331 | | |
| Presence of conspecifics | 1.481 | 1 | 0.226 | | |
| $arcsine(T_{vig})$ | | | | 0.039 | |
| Zone | 1.653 | 3 | 0.180 | | |
| Presence of humans | 2.155 | 1 | 0.144 | | |
| Presence of conspecifics | 0.002 | 1 | 0.966 | | |
| Presence of vehicles | 0.807 | 1 | 0.370 | | |
| $arcsine(T_{forage})$ | | | | 0.027 | |
| Zone | 1.028 | 3 | 0.382 | | |
| Presence of humans | 0.145 | 1 | 0.704 | | |
| Presence of conspecifics | 0.002 | 1 | 0.964 | | |
| Presence of vehicles | 0.773 | 1 | 0.381 | | |
| log(PR) | | | | 0.034 | |
| Zone | 0.784 | 3 | 0.504 | | |
| Presence of humans | 0.575 | 1 | 0.449 | | |
| Presence of conspecifics | 1.111 | 1 | 0.294 | | |
| Presence of vehicles | 0.273 | 1 | 0.602 | | |

None of these covariates (analysed on basis of presence or absence) had a significant F ratio within the $T_{\rm forage}$, $T_{\rm vig}$ or PR ANCOVA models (Table 2). Approximate counts of the number of conspecifics within 10 m of the focal bird during recording of vigilance behaviour were similar among zones (means $U=1.4\pm0.3$, $S=1.9\pm0.4$, $P=0.9\pm0.2$ and $R=1.3\pm0.2$; $F_{3,\ 154}=2.473$, P=0.064). Overall, Common Mynas pecked at food items ~21 times min⁻¹ of foraging, but PR did not vary significantly among the four zones (Tables 1, 2).

Table 3. Pairwise *post hoc* Tukey contrasts in log(FID) between the four zones

Estimate for these comparisons is the effect size. Significant probabilities are in bold

| Zone comparison | Estimate | P | |
|-----------------------|----------|---------|--|
| Urban × Suburban | 0.230 | 0.001 | |
| Urban × Peri-urban | 0.602 | < 0.001 | |
| Urban × Rural | 0.573 | < 0.001 | |
| Suburban × Peri-urban | 0.372 | < 0.001 | |
| Suburban × Rural | 0.343 | < 0.001 | |
| Peri-urban × Rural | -0.029 | 0.964 | |

Discussion

Variation in FID and fleeing behaviour among zones

The mean FID in this study was $1.4 \times$ longer than the mean (11.6 m) reported for this species in Blumstein's (2006) study. FID of Common Mynas in the breeding season studied here was significantly shorter in the urban and suburban zones than in the peri-urban and rural zones. However, the 3.9-fold increase in human population density between the suburban and urban zones and the 2.1-fold decrease between the peri-urban and rural zones did not affect the tolerance of human proximity by Mynas. Periurban and rural Mynas always flew away from the approaching researcher, usually more than 5 m, whereas suburban and urban individuals commonly walked or ran away, often less than 5 m. This variation in fleeing behaviour between zones suggested that there was a 'step change' in the tolerance of human proximity around the suburban–peri-urban divide, where human population density declined, on average, ~17-fold and the rate of human encounters by Mynas presumably declined in parallel.

The flight response of Mynas in the city (urban and suburban zones combined) can be characterised as 'later, inexpensive and less far' and in the exurban environment (peri-urban and rural zones combined) as earlier, expensive and farther. One interpretation of the contrasting fleeing behaviours is that they reflect different perceptions of risk resulting in differing optimal fleeing strategies. Exurban Common Mynas may have perceived the threat posed by the approaching researcher as great, and so readily abandoned the site and adopted the quickest strategy for getting to a new feeding site (flying >5 m). In contrast, city

Mynas may have perceived the threat as small, retreating in an energetically less expensive manner (walking or running <5 m) (Tatner and Bryant 1986) and thus retained the option of a swift and energetically economical return to the site after the source of disturbance had gone. Kitchen *et al.* (2010) observed a comparable contrast in the fleeing behaviour of native urban and rural Magpie-larks (*Grallina cyanoleuca*) in the same general area. In some species of bird, encounters with humans may occur much less often but be more threatening in exurban than in urban environments (e.g. when the species is subject to hunting pressure in rural areas). However, this is unlikely for the Common Myna, which is not commonly hunted and whose designation as a pest species is not a strictly rural perspective.

The observed spatial variation in FID did not accord with the original prediction that tolerance of human proximity would increase progressively from the rural to the urban zone if habituation was involved. It is possible that there is a threshold level of exposure to human proximity that must occur before habituation happens in the Common Myna. The ability of Common Mynas to rapidly habituate to harmless human presence may reflect a high level of cognitive buffering (Guay et al. 2012) and phenotypic plasticity, but the possibility that the observed spatial pattern in tolerance resulted from differential survival or dispersal of individuals with differing characteristics, particularly levels of boldness, cannot be excluded (Bonier et al. 2007; Heil et al. 2007; Møller 2008, 2009; Garamszegi et al. 2009; Evans et al. 2010; Lowry et al. 2011; Atwell et al. 2012; Weston et al. 2012). Weston et al. (2012) point out that comparisons of tolerance among sites with differing disturbance regimes may be confounded by habitat disparities. Exurban sites tended to have greater visibility than urban sites in our study area. Longitudinal studies with individually marked Mynas are needed to resolve definitively whether the difference in tolerance between urban and exurban Mynas shown here involves learning.

Broadly, our FID results, showing urban Mynas to be more tolerant of human proximity than their exurban conspecifics, agree with the results of several of the few other published studies comparing urban and exurban birds (Cooke 1980; Rollinson 2003; Møller 2008, 2009; Evans *et al.* 2010; Kitchen *et al.* 2010; Atwell *et al.* 2012), but not all such studies (Valcarcel and Fernández-Juricic 2009; Møller 2008). This may therefore be a common, but not universal, trend among birds that colonise cities, although these other studies, like our investigation, focussed on just a single city and its rural surrounds.

Lack of variation in time allocations among zones

Contrary to the initial prediction, time spent in vigilance (i.e. $T_{\rm vig}$) did not decrease progressively from the rural to the urban zone. Anderies $et\,al.\,(2007)$ have concluded that, on balance, the weight of evidence suggests that natural predation pressure on adult birds is lower in cities than in rural areas. If this is true, perhaps the most plausible explanation for the similar vigilance allocations of city and country Mynas is that the lower density of natural predators in the city was counteracted by the higher population density of humans (Valcarcel and Fernández-Juricic 2009). Although urban birds would not be expected to respond at an un-adaptively high rate to human proximity, they appear to treat humans as potential predators (Frid and Dill 2002). Thus the vigilance of urban and

exurban Common Mynas may have had substantially differing foci. Ward and Low's (1997) finding that urban American Crows (Corvus brachyrynchos) were more vigilant in areas of high human disturbance than in areas with low levels of disturbance is consistent with this interpretation. The Crows also showed a compensatory increase in foraging effort when vigilance was reduced. Thus it may be advantageous for Common Mynas in Melbourne to maintain a high level of surveillance when encounters with humans are frequent, but to learn not to retreat until a human is very close to them if the person appears not to be a threat. The size of groups also influences vigilance of members of the group in many birds (Beauchamp 2008), but is unlikely to have affected the similarity in vigilance among zones in the present study because approximate counts of the number of conspecifics within 10 m of the focal bird during T_{vig} recording were similar among zones.

There is much evidence that disturbance by humans can influence the foraging efficiency of birds, including the time spent foraging (Burger 1994; Burger and Gochfeld 1998), selection of foraging patches (Fernández-Juricic 2000a, 2000b) and giving-up net energy intake (Gyimesi et al. 2012). However, in our study there was no difference in T_{forage} and PR of Common Mynas across the urban-rural gradient, which may have indicated that the abundance of food per Myna was similar in the two environments. If correct, this does not necessarily contradict the widely held view (Marzluff 2001) that urban areas have a greater abundance of food than exurban environments for urban-colonising birds (owing to higher primary productivity, longer growing seasons and the presence of anthropogenic food emanating from waste and deliberate feeding; Møller 2009) if the population density of Common Mynas was also higher in the city. The mean population densities of Common Mynas in urban Melbourne and its rural hinterland (S. Taberner and A. Lill, unpubl. data) in the non-breeding season were similar (1.9 and 1.4 birds ha⁻¹), although Crisp and Lill (2006) recorded a mean density of 2.5 Mynas ha⁻¹ across a broader suite of habitats in the city during the breeding season. Contemporaneous measurement of abundance and dispersion of food and abundance of Mynas across the urban-rural interface are needed to clarify this issue, although it would be difficult to determine the former.

Two caveats apply to our foraging data. First, they were obtained in the mid-morning and mid-afternoon when rates of foraging are usually lower than in the early morning and late afternoon (Mahabal 1991). However, many Mynas were feeding nestlings at high rates, so this disparity was possibly reduced. Second, and more importantly, because Common Mynas mostly forage on the ground but often rest above ground level, time allocations to above-ground level resting really need to be measured to determine whether Mynas in the various demographic zones allocate similar percentages of total daytime to foraging. As Mynas resting in vegetation are probably often somewhat concealed from predators, this caveat is less problematic for $T_{\rm vig}$ comparisons.

Starting distance – a cautionary note

Starting distance was strongly positively correlated with FID and explained 80% of the variance in this distance. The researcher subconsciously increased her SD in the peri-urban and rural zones

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relative to that in the suburbs by a factor of 1.6–1.8, probably for two reasons. Firstly, Mynas were visible to the researcher from a greater distance in the more open peri-urban and rural zone habitats, making it possible to begin the experimental approach from further away and, secondly, Mynas in these zones tended to flee from the researcher at a greater distance, probably stimulating the researcher after some experience to subconsciously begin her approach sooner. However, these adjustments by the researcher were not sufficient to obscure the effect of zone on FID.

Blumstein (2006) noted that birds that detect threats at a greater distance also initiate fleeing at a greater distance, thus keeping the costs of fleeing low by avoiding precipitous, energetically expensive retreat. If this is true of the Common Myna, conceivably peri-urban and rural individuals were not inherently less tolerant of human proximity than urban and suburban birds, but simply tended, on average, to detect the approaching threat at greater distances because of the greater visibility in their environments. However, in contrast with city individuals, exurban Mynas tended to retreat from the researcher mostly by energetically expensive flying and to retreat >5 m, so it is not obvious that their costs of fleeing would be greatly reduced by having a longer FID.

Whatever the explanation of the longer FID of exurban Mynas, clearly researchers using the FID paradigm need to be very aware of the potential influence of SD on FID and actively strive to prevent it confounding other interesting sources of variation in FID. It is still not clear, however, why SD and FID are strongly correlated in many, but not all, species (Blumstein 2003; Kitchen *et al.* 2010; Evans *et al.* 2010; Glover *et al.* 2011), perhaps because there are potentially several ways in which the two parameters could interact. Weston *et al.* (2012) outline several possible explanations for the correlation, including an inability to assess distance efficiently, monitoring of the persistence of an approach, and making judgements about the value of a patch of habitat under increasing perceived risk from the approaching human.

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