

Avian Risk Assessment: Effects of Perching Height and Detectability

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Abstract

We studied two components of predator risk assessment in birds. While many species are limited to seeking safety under cover or under ground, some birds can fly away from their predators and escape to trees. If birds in fact ‘feel’ safer (e.g. perceive less risk) in trees, we would expect them to tolerate closer approach by a potential terrestrial predator. Another component of safety is at which point the animal detects an approaching threat, which we expected to increase with eye size, assuming eye size is a surrogate for visual acuity. We used the distance birds moved away from an approaching human [flight initiation distance (FID)] as a metric to determine whether birds associated a lower risk of predation by being in trees, and we used the distance at which birds first displayed alert behaviors from an approaching human (alert distance) to determine if birds with larger eyes had higher detection distances. Although some species were affected by tree height, we found no clear pattern that birds assessed themselves to be at a lower risk of predation when they were ≥ 3 m above the ground compared with being < 3 m above ground. In the 10 species for which height had any significant effect on FID, birds ≥ 3 m off the ground had greater FIDs in six species, but the remaining three species had the opposite response. While we found a significant positive relationship between eye size and alert distance in 23 species, the relationship was not present in a phylogenetic analysis using independent contrasts, which suggests that the apparent relationship was influenced strongly by the association between the studied species. Together, these results suggest that birds do not obviously associate being in a tree with safety, and that variations in visual acuity, per se, cannot be used as a general indicator of differences in alert distances, as previously suggested in the literature.

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Introduction

Non-humans perceive the world through their own perceptual window, or *Umwelt* (von Uexküll 1934), but such perceptions may not match our own. For instance, for any given species, vegetative cover may be protective (i.e. animals seek safety in cover) or obstructive (i.e. predators hide in cover and individuals therefore avoid it), and understanding how each species perceives cover is essential to understand how it uses space (Lima 1987; Blumstein & Daniel 2002). Birds may escape predators by flying up trees. There have been suggestions that birds perceive less risk (e.g. 'feel' safer) as a function of height in trees, because in areas with human disturbance they place their nests higher in trees (Knight & Fitzner 1985; Datta & Pal 1993). Another little-studied component of safety is at which point the animal detects an approaching threat. Previous studies have hypothesized that detection could be enhanced by the location of prey (greater detectability higher in the perch, Swarthout & Steidl 2001; Fernández-Juricic et al. 2004a) and by the degree of visual perception of the animal (greater detectability with higher visual acuity, which is the ability to detect two points in the visual field as distinct; Kilde 2000; Fernández-Juricic et al. 2001). But, is *our* perception of bird safety in fact commonly used by birds?

We ask the following two questions: (a) do semi-arboreal birds associate a lower risk of predation when in trees? and (b) do birds with greater visual acuity detect threats sooner? We address these questions comparatively, by studying an indicator of perceived risk (flight initiation distance), and an indicator of detectability (alert distance) in birds from Australia, Europe, North America and South America. While species may vary in their *Umwelt*, a more comprehensive understanding of avian predation hazard assessment requires a comparative approach. Flight initiation distance (FID), the distance at which an animal initiates escape when approached by a potential predator, is a common metric in predation risk assessment (e.g. Ydenberg & Dill 1986; Bonenfant & Kramer 1996). Alert distance, the distance birds first oriented toward an approaching threat, has been used previously as an indicator of detectability (Rodgers & Smith 1997; Fernández-Juricic et al. 2001; Fernández-Juricic & Schroeder 2003). We used eye size as an indicator of visual acuity (Brooke et al. 1999; Kilde 2000). Following previous studies we used humans as surrogates for predators (e.g. Blumstein et al. 1997; Martin & Lopez 1999; Louis & Le Berre 2000).

We predicted that if birds associated safety with height, then they should allow an approaching human to get closer to them when they are out of arm's reach (e.g. smaller FID when perching higher). An alternative hypothesis is that if detectability is more important in risk assessment, then birds should flush at greater distances when they are relatively higher in trees (e.g. greater FID when perching higher), assuming they flush as soon as they detect the threat. These

contrasting predictions would uncover the behavioral mechanisms used for risk assessment when perching in trees. Finally, we predicted that eye size should be positively correlated to alert distance, because visual acuity increases with eye size (Kilte 2000).

Methods

General Methods

To estimate alert distance and FID, we identified individual birds and then walked at a steady pace of approx. 0.5 m/s towards them (e.g. Blumstein et al. 2003; Blumstein 2003). We focused on birds that were foraging or engaged in ‘relaxed behaviors’, such as preening or roosting. Highly vigilant and obviously alarmed birds were not approached, nor were nesting birds, or endangered species. To our knowledge, our experimental approaches did not harm the birds; most resumed their previous activity in a different location within 30 s of initially moving (D. T. Blumstein, unpublished data). The species lived in a variety of habitat types in California, Colorado, Eastern Australia, Spain, and Tasmania, and there were a broad range of starting distances, both within and between species (Table 1). We noted the distance we started walking towards birds (starting distance), the distance the bird displayed alert behaviors (e.g. looking or orienting towards the approaching person—alert distance). Our estimates of alert behavior are dependent on a bird moving its head. It is likely that individual birds were alerted to our approach before we could detect an external sign of their response. Nonetheless, we feel that this is consistent measure of responsiveness to our approach (see Fernández-Juricic & Schroeder (2003) for methods to estimate alert distance).

We also scored the distance the focal bird moved away ($FID_{\text{horizontal}}$) either on foot or by flight. FID was scored when a bird began moving away in response to our approach. This was typically obvious, with the exception of some species that actively move while foraging (practically, this was mostly a problem with shorebirds). When birds were already moving, we focused on obvious departures from their typical movement (e.g. a double step or movement in another direction) to score flight initiation. This problem applied only to situations in which the bird walked away, instead of flying away, as they usually did. Finally, we noted the height the bird was off the ground (if it was off the ground). Distances were measured in paces and converted to meters. Height in tree was estimated by visually rotating the location of the bird in the tree onto the ground, and then measuring the ground distance. From the horizontal FID measurement and the perching height in the tree measurement, we used the Pythagorean theorem to calculate the ‘direct’ FID [$FID_{\text{direct}} = \sqrt{FID_{\text{horizontal}}^2 + \text{perching height}^2}$], and used this FID_{direct} measurement in subsequent analyses. Most of the birds we studied were perched somewhere near the periphery of the tree. However, we did not systematically record where in the tree the bird was located, nor did we record the type of tree or whether it had leaves or not. We acknowledge that location in canopy and leafiness could influence predation risk, visibility and

Table 1: ANCOVA results testing for the effect of height in tree on variation in FID after accounting for variation explained by starting distance and the interaction between them

Latin name	Species	Family	n		FID		Interaction	
			< 3 m	n ≥ 3 m	< 3 m	≥ 3 m	p-value	p-value
<i>Dacelo novaeguineae</i>	Laughing kookaburra	Halcyonidae	22	37	10.5	14.7	0.337	0.337
<i>Cacatua galerita</i>	Sulphur-crested cockatoo	Psittacidae	22	22	9.8	19.1	< 0.001	< 0.001
<i>Platycercus elegans</i>	Crimson rosella	Psittacidae	18	35	8.5	9.6	0.039	0.039
<i>Calypte anna</i>	Anna's hummingbird	Trochilidae	43	11	6.7	7.2	0.193	0.193
<i>Macropygia amboinensis</i>	Brown cuckoo-dove	Columbidae	12	11	8.9	4.6	0.380	0.380
<i>Zenaidura macroura</i>	Mourning dove	Columbidae	71	9	15.8	23.8	0.274	0.274
<i>Ptilonorhynchus violaceus</i>	Satin bowerbird	Ptilonorhynchidae	15	15	8.4	9.8	0.522	0.522
<i>Malurus cyaneus</i>	Superb fairy-wren	Maluridae	86	9	6.1	8.8	0.016	0.016
<i>Meliphaga lewinii</i>	Lewin's honeyeater	Meliphagidae	27	20	8.2	6.8	0.032	0.032
<i>Lichenostomus chrysops</i>	Yellow-faced honeyeater	Meliphagidae	17	15	4.5	4.9	0.206	0.206
<i>Lichenostomus penicillatus</i>	White-plumed honeyeater	Meliphagidae	10	14	8.9	9.5	0.230	0.230
<i>Philemon corniculatus</i>	Noisy friarbird	Meliphagidae	28	36	11.5	8.9	0.115	0.115
<i>Phylidonyris noveboracensis</i>	New Holland honeyeater	Meliphagidae	38	12	6.6	8.7	< 0.001	< 0.001
<i>Acanthorhynchus tenuirostris</i>	Eastern spinebill	Meliphagidae	26	16	5.6	3.6	0.031	0.031
<i>Manorina melanophrys</i>	Bell miner	Meliphagidae	25	22	2.7	5.5	0.507	0.507
<i>Anthochaera chrysoptera</i>	Bush wattlebird	Meliphagidae	24	18	6.7	5.4	0.095	0.095
<i>Eopsaltria australis</i>	Eastern yellow robin	Petroicidae	70	14	9.5	8.8	0.216	0.216

<i>Aphelocoma californica</i>	Western scrub-jay	Corvidae	130	71	15.8	13.8	0.474
<i>Corvus coronooides</i>	Australian raven	Corvidae	48	21	23.8	29.6	0.001
<i>Gymnorhina tibicen</i>	Australian magpie	Dicruridae	75	20	9.3	14.9	0.002
<i>Strepera graculina</i>	Pied currawong	Artamidae	18	14	15.5	13.9	< 0.001
<i>Pipilo maculatus</i>	Spotted towhee	Emberizidae	106	13	9.4	10.1	0.812
<i>Rhipidura leucophrys</i>	Willie wagtail	Dicruridae	42	12	11.7	10.9	0.490
<i>Rhipidura fuliginosa</i>	Grey fantail	Dicruridae	29	16	5.6	7.4	0.112
<i>Turdus migratorius</i>	American robin	Turdidae	71	19	11.8	9.1	0.239
<i>Baeolophus inornatus</i>	Oak titmouse	Paridae	15	12	11.7	9.4	0.529
<i>Psaltriparus minimus</i>	Bush-tit	Aegithalidae	49	9	7.4	8.5	0.094
<i>Pycnonotus jocosus</i>	Red-whiskered bulbul	Pycnonotidae	12	14	17.3	17.0	0.205
<i>Carpodacus mexicanus</i>	House finch	Fringillidae	60	8	9.6	10.8	0.002
<i>Melospiza melodia</i>	Song sparrow	Emberizidae	85	13	8.3	7.5	0.084
<i>Zonotrichia leucophrys</i>	White-crowned sparrow	Emberizidae	121	34	8.6	6.2	0.537
<i>Pipilo crissalis</i>	California towhee	Emberizidae	486	22	11.9	13.9	0.054
<i>Dendroica petechia</i>	Yellow warbler	Parulidae	26	24	6.5	9.6	0.324
<i>Dendroica coronata</i>	Yellow-rumped warbler	Parulidae	18	15	8.0	9.4	0.442

All models were highly significant ($p < 0.001$) including the covariate starting distance ($p < 0.001$). Significant interaction p-values are in bold.

detectability (Suhonen 1993a,b; Krams 1996, 2001). We think this is unlikely to confound our interpretations because of the large number of species studied, but location in tree might obscure some effects of height.

We paid particular attention to ensuring that all observers were collecting data consistently. New observers were trained until their observations were identical to a trained observer. Additionally, all observers were trained to discard a potential flush if there was any doubt about any of the variables collected.

Subjects were not marked; however, we avoided re-sampling individuals by focusing on birds in different geographic locations and not re-sampling the same location repeatedly. Birds were studied in both 'pristine' environments with few visitors, if any, and in areas with human activity. Analyses excluded observations on individuals in highly visited city parks, and individuals that approached humans (for handouts) rather than fleeing. To our knowledge, none of the species included in our analyses were actively hunted at the locations where we studied them.

Studying more than a single species raises potential problems not typically encountered in single-species studies. For instance, application of our standardized methods was, nonetheless, somewhat variable because species were studied in different habitats. In forests it was difficult to see animals from a great distance, thus limiting our 'starting distance'.

Does Height in a Tree Influence Risk Assessment?

From a database of over 350 species, we selected 34 species for which we had ≥ 9 observations of animals being approached when they were < 3 m off the ground, or ≥ 3 m off the ground. We selected 3 m for two reasons. First, this is about the reach of a tall person; if birds perceived safety in trees, then we predicted that they should feel safe when out of reach of a human. Secondly, empirically, if birds were < 3 m off the ground, the difference between FID_{direct} and $FID_{\text{horizontal}}$ was not substantial.

The distance a human begins walking towards a bird explains significant variation in FID and must be incorporated into subsequent analyses (Blumstein 2003). Importantly, this relationship logically should be forced through the origin. This is because a person beginning to approach a bird at 0 m could only elicit a 0 m FID. Removing intercepts from general linear models (GLM), however, has ramifications for interpreting both main effects and interactions. To study the effect of height off ground, we modeled variation in FID as being explained by starting distance and the interaction between starting distance and height (< 3 m; ≥ 3 m). We eliminated the main effect of height from this model because when there is no intercept, the hypothesis being tested with a categorical factor is whether or not the intercept for each categorical factor is significantly different from 0 (this is an artifact of dummy coding algorithms in GLM routines). Thus, to study the effect of the bird's initial height on the expected relationship between starting distance and height, we focused on the interaction, forcing the model through the origin. If the interaction was significant, we could

interpret this as meaning that initial height was responsible for the divergence. A number of variables could obscure our results because they too influence predation risk. We collected data on the distance a focal bird was from cover when the experimental flush began (cover was defined as a dense bush or tree), each individual's initial behavior (most commonly perched and looking or singing, or foraging), and the number of conspecifics within 10 m of the focal subject. These factors or covariates were added to the 'basic' model (i.e. the model with starting distance and the interaction between starting distance and height) by adding interactions between the factor (or covariate) and starting distance. In one instance, distance to cover changed a result: the interaction between height and starting distance became significant in California towhees. The addition of the group size interaction did not change any results, but the addition of the starting behavior interaction generated four changes: the interaction between starting distance and height became significant in robins and California towhees while the interaction became non-significant in Australian magpies and eastern spinebills. For clarity, we do not report these detailed analyses, but rather focus on the basic model.

Analyses were conducted using SPSS 10 and linear models were fitted using the GLM univariate method (SPSS Inc. 2000). We interpret p-values < 0.05 as significant. Residuals from GLMs were visually scrutinized and were typically normally distributed.

Does Eye Size Influence Alert Distance?

To estimate alert distance, we included 23 species where we had ≥ 7 estimates of the distance a bird first oriented toward an approaching human (Table 2). Body size was tabulated from Dunning (1993), and log transformed for analysis. Eye size was tabulated from Garamszegi et al. (2002). We first regressed the log of body size against eye size and used the residuals in subsequent analyses. We then regressed the residual eye size against alert distance in a non-phylogenetic analysis. We then calculated phylogenetically independent contrasts (Harvey & Pagel 1991) to study the effect of residual eye size on alert distance. We used the Sibley & Ahlquist (1990) phylogeny, assumed a punctuational model of evolution, calculated contrasts using Compare 4.5 (Martins 2003), and, as required by the method, forced the regression through the origin (e.g. Harvey & Pagel 1991).

Results

Does Height in a Tree Influence Risk Assessment?

There were significant interactions between starting distance and height for 10 species (Table 1). Specifically, this means that the expected relationship between starting distance and FID was influenced by the height a bird was off the ground. Of these, seven species flushed at greater distances when ≥ 3 m off the ground.

Table 2: Species included in the analysis of alert distance

Latin name	Common name	Family	Log (body size g)	n	Alert distance (m)	Eye size (cm ³)
<i>Picus viridis</i>	Eurasian green woodpecker	Picidae	2.25	24	12.6	14.45
<i>Alisterus scapularis</i>	Australian king parrot	Psittacidae	2.37	7	10.9	14.70
<i>Trichoglossus haematodus</i>	Rainbow lorikeet	Psittacidae	2.09	13	13.1	7.32
<i>Columba palumbus</i>	Common woodpigeon	Columbidae	2.69	100	18.6	16.69
<i>Tringa nebularia</i>	Common greenshank	Scolopacidae	2.24	7	55.1	13.05
<i>Calidris ruficollis</i>	Red-necked stint	Scolopacidae	1.56	61	22.9	2.48
<i>Calidris acuminata</i>	Sharp-tailed sandpiper	Scolopacidae	1.80	28	23.2	5.14
<i>Pica pica</i>	Magpie	Corvidae	2.22	100	18.7	19.77
<i>Corvus monedula</i>	Eurasian jackdaw	Corvidae	2.39	100	27.0	14.94
<i>Turdus merula</i>	Blackbird	Turdidae	2.05	100	14.9	9.28
<i>Erithacus rubecula</i>	European robin	Muscicapidae	1.26	16	18.6	4.02
<i>Sturnus unicolor</i>	Spotless starling	Sturnidae	1.92	15	18.0	4.22
<i>Parus ater</i>	Coal tit	Paridae	0.96	15	5.9	0.93
<i>Parus major</i>	Great tit	Paridae	1.28	15	10.2	2.51
<i>Parus caeruleus</i>	European blue tit	Paridae	1.12	15	9.5	1.41
<i>Phylloscopus collybita</i>	Eurasian chiffchaff	Sylviidae	0.88	15	12.6	1.37
<i>Passer domesticus</i>	House sparrow	Passeridae	1.44	100	13.0	2.69
<i>Passer montanus</i>	Tree sparrow	Passeridae	1.34	15	13.4	1.97
<i>Motacilla alba</i>	White wagtail	Motacillidae	1.32	17	15.6	2.5
<i>Fringilla coelebs</i>	Chaffinch	Fringillidae	1.33	15	15.5	2.7
<i>Carduelis chloris</i>	European greenfinch	Fringillidae	1.44	15	11.3	2.14
<i>Carduelis carduelis</i>	European goldfinch	Fringillidae	1.19	17	13.7	1.31
<i>Zonotrichia capensis</i>	Rufous-collared sparrow	Emberizidae	1.30	100	12.6	3.37

Does Eye Size Influence Alert Distance?

After explaining significant variation in eye size accounted for by body size ($R = 0.906$, $p < 0.001$), we found that birds with larger eyes first reacted towards an approaching human at a significantly greater distance in a non-phylogenetic analysis (adjusted $R^2 = 0.147$, $p = 0.040$; Fig. 1a). This relationship persisted following the removal of an outlier (adjusted $R^2 = 0.174$, $p = 0.031$), but was not detected in a phylogenetic analysis of independent contrasts (adjusted $R^2 = 0$, $p = 0.538$; Fig. 1b). Importantly, there were no significant relationships between these residuals and the number of conspecifics within 10 m (adjusted $R^2 = 0$, $p = 0.423$), distance to trees (adjusted $R^2 = 0$, $p = 0.320$), or more generally distance to cover (adjusted $R^2 = 0$, $p = 0.615$). We then considered only the 16 passeriforms in the analysis, because previous evidence of the relationship between eye size and alert distance considered mainly species from this order (e.g. Fernández-Juricic et al. 2001). For passeriforms only, we found an even more significant relationship between eye size and alert distance (adjusted $R^2 = 0.55$, $p < 0.001$) that again was not significant in a phylogenetic analysis (adjusted $R^2 = 0.007$, $p = 0.310$).

Discussion

Following previous suggestions (Knight & Fitzner 1985; Datta & Pal 1993), we reasoned that birds, because of their ability to be active in three dimensions, should be sensitive to their relative location above the ground, and therefore either tolerate a closer approach if they perceived less risk, or be less tolerant (by flushing immediately after detecting the threat), if they detected threats earlier. We did not find strong support for either hypothesis: while 29% of the species were affected by perching height, they were not influenced consistently. A recent study, which focused on five species, also found species-specific variation in the relationship between FID and perching height (Fernández-Juricic et al. 2004a). Overall, both studies support the lack of a general trend in terms of safety in trees. A possibility for future studies is to develop a data set including birds perching much higher than we were able to record. However, to do so, one must work in an area where birds are found and can be seen in *very* tall trees, which was not the case in our study areas. Nevertheless, we believe our data set (which contains representatives of 20 avian families) is large enough to properly address this question. It is possible that height-independent risk assessment is shaped by the risk of predation from aerial predators, which is likely to be height independent. It is also likely that birds flush from approaching threats, regardless of their location, to reduce the cost of ongoing predation hazard assessment (Blumstein 2003), and, as a result, height would not influence risk assessment. We, thus, conclude that, for birds in trees, the perception of risk does not decrease with height.

Birds with greater visual acuity tended to react toward approaching human threats at a greater distance. However, this trend between alert distance and eye

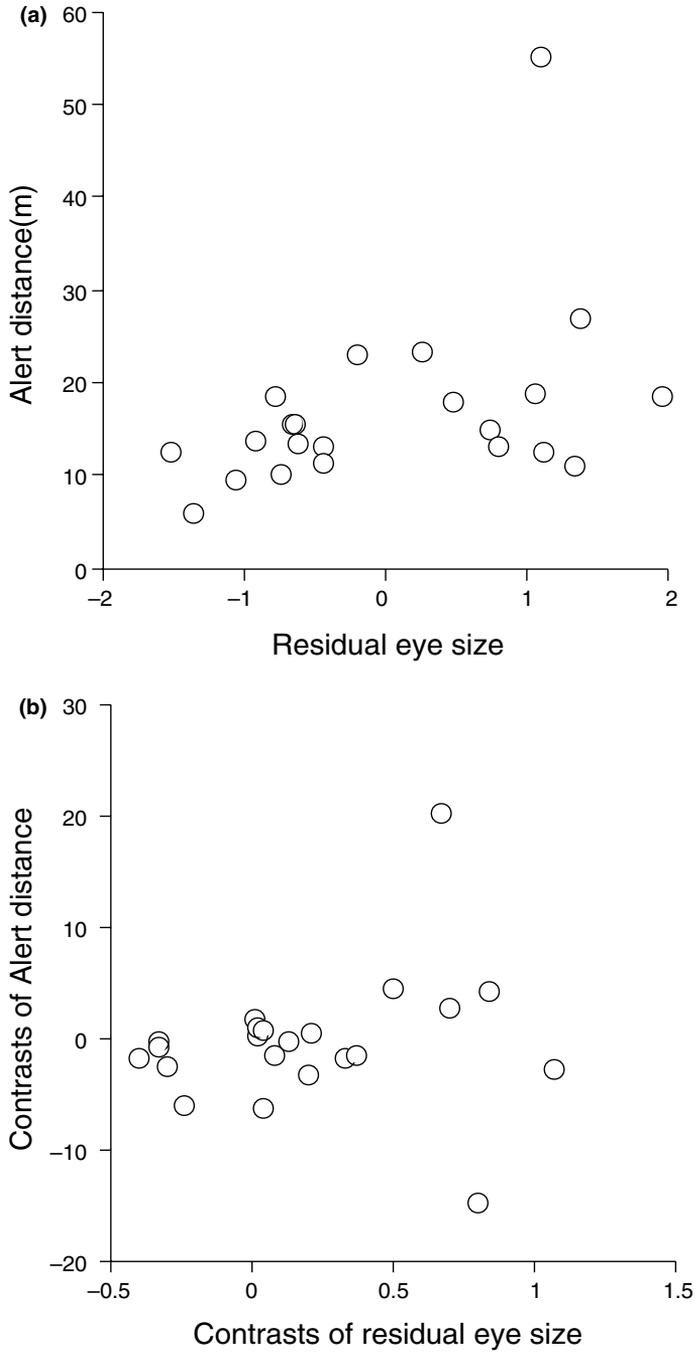


Fig. 1. The relationships between: (a) residual eye size variation and alert distance; (b) standardized independent contrasts of residual eye size variation and standardized independent contrasts of alert distance

size became non-significant, after we controlled for expected phylogenetic similarity. The results of both alert distances and FID are consistent, in that avian responses to a simulated threat are affected by neither morphological features (eye size), nor a habitat-related feature (the height they were in trees). Hence, our results contradict previous suggestions in birds and mammals that both features are involved in the process of predator detection, as well as the costs and benefits of leaving a patch after detection (Ydenberg & Dill 1986; Dill 1990; Smith & Laitvaitis 1999; Randall et al. 2000; Fernández-Juricic et al. 2001). It is possible that our results that focused on responses of birds to humans may not reflect the response of birds to other types of predators. Humans have often been used as a surrogate predator (Frid & Dill 2002), but it is clear that prey respond differently to different types of predators (Evans et al. 1993).

We are unable to eliminate the possibility that birds detected us before orienting toward us. Our measure of detection distance, alert distance, is typically correlated with both the distance we initiated our approach, and the distance the bird flushed (D. T. Blumstein unpublished observations). While alert distance is a standardized way to measure the distance at which the behavior of individuals is disrupted by disturbance (e.g. Fernández-Juricic et al. 2001), it may not be a good indicator of visual acuity.

One potential confounding factor that could account for the lack of relationship between eye size and alert distance is the size of avian visual fields. The visual field can be defined as the limits of the space around an animal from which visual information can be obtained (Martin 1993). Some species have wide visual fields, which allow them to scan for threats while foraging (head-down) (reviewed in Fernández-Juricic et al. 2004b), and empirical work has demonstrated that birds can detect threats when their head is down (Lima & Bednekoff 1999). That means that an animal may not necessarily display alert behaviors when detecting an approaching threat; which could have underestimated our measure of visual acuity. Our results call for a reassessment of the role of alert distance as indicator of visual acuity, and the need to find alternative, and empirically feasible, measures of visual resolution in birds.

Taken together, our results suggest that: (1) birds in general do not perceive less risk from an approaching human when relatively far above the ground, and (2) the relative eye size is not a surrogate of the distance at which birds display alert behaviors. In addition to gaining insight into the avian Umwelt, the results of this study have important implications for management of protected areas and birds. FID is often used to help estimate set-back distances to reduce human impacts on wildlife (Rodgers & Smith 1995). Our study suggests that measures of $FID_{horizontal}$, which are typically used by those estimating FID, are valid, even for semi-arboreal birds. We cannot generalize the relationship between eye size and alert distance, because it was mostly a phylogenetic artifact. Nevertheless, from a management viewpoint, using eye size as an indicator of tolerance to set aside buffer areas (Fernández-Juricic et al. 2001) might still be useful if the relationship holds in any particular family (e.g. possibly in raptors – Holmes et al. 1993; or

some passeriforms – our results). Identifying those families is an important research objective for managers trying to balance the increasing levels of human visitation to protected areas, with the reduction in the number of local wildlife species because of human disturbance.

Acknowledgements

We thank L. Anthony, L. Antolin, J. Craanen, J. Daniel, M. Edgerton, K. Gilmour, C. König, C. Madrileo, N. Murillo, and S. Robertson for help collecting data; L. Ikuta, P. Parvinchiha, and M. Seymour for help with data entry; J. Daniel for help with data analysis, and L. Anthony, J. Daniel, R. Fernandez, R. Harcourt, L. Ikuta, P. Nonacs, and E. Tarlow for discussions about flight initiation distance. Research protocols were approved by the Macquarie University Animal Research Committee (no. 99021) and the UCLA Animal Research Committee (no. 2000-147-01). Field research permits were issued by the New South Wales National Parks and Wildlife Service (no. A2712), the Queensland Parks and Wildlife Service (no. FA/000379/00/SA), and the Parks and Wildlife Service of Tasmania (no. FA 00060). Support for this project was from the Macquarie University (2001 Research Discovery Scheme grant with R. Harcourt), the University of California Los Angeles Division of Life Sciences, and The University of California Los Angeles Council on Research. Editorial comments by Scott Forbes and three very constructive reviewers helped us improve a previous version of this paper.

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Received: October 10, 2003

Initial acceptance: November 11, 2003

Final acceptance: January 21, 2004 (S. Forbes)