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The importance of indirect cues for white-browed sparrow-weaver (*Plocepasser mahali*) risk assessment

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Abstract Both direct cues that provide information about the actual presence of a predator and indirect environmental cues that provide information about the probability of encountering a predator may be used by animals assessing predation risk, but relatively few studies manipulate both simultaneously to study their relative importance. We conducted two experiments to study the foraging decisions of white-browed sparrow-weavers (*Plocepasser mahali*). The first experiment manipulated both direct and indirect cues in a feeding array by simultaneously placing feeding stations at different distances from humans (to manipulate direct risk) and from protective cover (to manipulate indirect risk). Weaver foraging was influenced more by indirect risk than by direct risk. The second experiment aimed to determine if weaver's indirect risk assessment was sensitive to variation in benefits. We set two feeding stations at different distances from cover but the same distance from the human observers and systematically increased the amount of food at the station farther from cover. Weavers far from cover initially foraged at higher rates than those close to cover, but the addition of food reduced the foraging rate. Together, our results illustrate that weaver foraging decisions are sensitive to variation in risk and that indirect cues are relatively more important than direct cues.

Keywords Indirect cues · Direct cues · Predation risk assessment

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Introduction

We assume that the decisions that dictate how, when, and where an individual will forage are sensitive to both energetic gain and predation risk (Abrahams and Dill 1989). Animals utilize both indirect and direct cues to assess predation risk and make their foraging decisions (Grubb and Greenwald 1982; Thorson et al. 1998; Orrock et al. 2004; Schmidt 2006). Indirect cues are those environmental factors that might be somehow related to the probability of predation (Thorson et al. 1998). Direct cues are olfactory, auditory, visual, or tactile stimuli produced by a predator (Thorson et al. 1998). Compared to the number of studies that focus on a single cue (Schneider 1984; Blumstein et al. 2000; Mandelik et al. 2003; Mikheev et al. 2006), there are relatively few studies that focus on multiple cues simultaneously. Thus, how these indicators of risk interact and their relative effect in the decision-making process is relatively unknown.

A number of studies have explored the effects of direct cues on prey foraging behavior. By presenting two types of direct cues (auditory and visual), Blumstein et al. (2000) found that tammar wallabies (*Macropus eugenii*) were unresponsive to direct auditory cues but foraged less and looked more when exposed to direct visual cues. The importance of visual cues to elicit behavioral responses was demonstrated by Mikheev et al. (2006), who found that olfactory cues alone were not sufficient to significantly change food intake rate of juvenile perch (*Perca fluviatilis*), but when combined with visual presentation of the predator, food intake rate was greatly reduced. This combinatory effect demonstrates the importance of analyzing multiple features of the predator–prey system to describe the dynamic interactions that may occur. Fernandez-Juricic and Kacelnik (2003) showed that animals may use conspecific behavior to assess direct risk.

Many studies have shown that indirect cues, such as distance to cover, can affect prey behavior. For instance, we know that cover may either be protective or obstructive. When cover is obstructive, it increases the vulnerability of foraging animals because it hinders their ability to visually detect predators (Blumstein et al. 2004; Whittingham and Evans 2004; Ebensperger and Hurtado 2005). By contrast, cover may also be protective. For instance, Schneider (1984) found that white-throated sparrows (*Zonotrichia albicollis*) preferentially foraged in areas closer to cover even when areas farther from cover offered greater energy intakes and only foraged in areas farther from cover when food in the area closer to cover was depleted. Similarly, Guillemain et al. (2000) showed that mallards (*Anas platyrhynchos*) only foraged using the riskier deep-water-dabbling method when food in the shallow mud flats, which required a less risky mud-grubbing technique, was depleted. Mandelik et al. (2003) examined the feeding behavior of the common spiny mouse (*Acomys cahirinus*) under the influence of two indirect cues: moonlight and overhead cover. The common spiny mouse visited fewer food patches on moonlit nights and more food patches under overhead cover instead of the open environment (Mandelik et al. 2003).

Such studies demonstrate that both direct and indirect cues may independently influence foraging behavior. However, in nature, prey often must assess the interaction and the influence of both direct and indirect cues at the same time. Thus, we must consider both simultaneously.

Indirect cues provide vital information about potential risk independently of a predator's presence. For this reason, indirect cues may provide important background information about the risk of predation, while direct cues provide information when facing an actual predator (Thorson et al. 1998). When comparing the effects of direct cues (olfactory and visual stimuli) against indirect cues (microhabitat and background coloration), Thorson et al. (1998) found that both fox squirrels (*Sciurus niger*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) responded more strongly to the indirect cue of distance from refuge. Orrock et al. (2004) found that the oldfield mouse (*Peromyscus polionotus*) removed considerably more seeds from trays sheltered by vegetative cover and on nights where moon illumination was minimal, while they found no significant effect of predator urine (a direct cue) on mouse foraging. In contrast, Schmidt (2006) found that direct (owl vocalizations) and indirect (moonlight) cues alone had no effect, but the combination of both induced a significant reduction in movement of the white-footed mouse (*Peromyscus leucopus*). Given the contradictory results of these studies and the paucity of experiments that explicitly contrast the effects of direct and indirect cues on foraging behavior, further investigation is warranted.

We provided both direct and indirect cues to analyze their relative effect on the foraging behavior of the white-browed sparrow-weaver at the Mpala research station in Kenya. We conducted two experiments.

In the first experiment, we used a feeding array where we varied direct and indirect risk and measured the latency to initially visit a feeding plate (a demonstration of wariness), the total number of visits (a measure of preference), and the foraging behavior of those weavers who elected to forage. Given that white-browed sparrow-weavers are small social passeriformes that nest and roost in trees but forage on the ground (Ferguson and Siegfried 1989), we assumed that the cover would provide safety while foraging. Slotow and Rothstein (1995a) demonstrated that birds view adjacent vegetation as a source of protective cover from predators rather than merely as a perch. Therefore, as distance from cover increased, we predicted that perceived risk would also increase. We expected that weaver behavior would vary with this increased perception of risk such that the latency to initially visit a feeding plate would increase with increasing distance from cover, and the number of visits would decrease. We also used our presence at a specific location as a metric of direct risk. We sat quietly to simulate a stalking or waiting predator. We therefore expected that as the distance from the observer increased, the risk perceived by the weavers would decrease, and their behavior would track this decreased perception of risk. We thus predicted that latency to initially visit a feeding plate would decrease and the number of visits would increase with increasing distance from the observer.

In the second experiment, we studied whether weavers could be lured into accepting a greater indirect risk by increasing the energetic reward on a plate further from cover than one closer to cover. Since white-crowned sparrows trade off food return in the presence of predation risk (Slotow and Paxinos 1997), we predicted that indirect risk would influence behavior and that weavers would trade off cost of predation risk with benefit of extra food. While similar studies have been performed with respect to direct and indirect cues (Lima 1990; Thorson et al. 1998), few have integrated quantitative measures (latency, duration, and number of visits) with behavior (vigilance, foraging, and vocalizing). Combining these two methods to quantify behavior provides further insight into the decision-making process under both direct and indirect predation risk. Thus, our study comprehensively explores the reliability of indirect versus direct cues and how they interact to influence the foraging behavior of a granivorous passerine.

Materials and methods

In October 2007, from 0630 to 1800 hours, we established feeding arrays in a 20×20-m portion of a large meadow at

the Mpala Research Station in the Laikipia District of Kenya (36°54′E, 0°17′N). Our study site was bordered on the eastern side by a line of trees approximately 5 m tall that provide protective cover to the weavers, and we assumed that the distance from cover would be perceived as an indirect cue of risk. We assumed that the cover was perceived as a safe location because it did not inhibit visibility significantly and thus served as an effective refuge (Caro 2005). Two observers sat, quietly, at one edge of the feeding array, and we assumed that the distance from the human observers would be perceived as a direct cue of risk (Caro 2005). We focused on white-browed sparrow-weavers, social birds that live in groups of two to 11 individuals (Collias and Collias 1978; Lewis 1982). We note that weavers at this site did not normally land next to humans, and they flushed when we approached them. Thus, while they may have been somewhat habituated, they still responded fearfully to humans. Our study site contained one colony of ten to 15 weavers; strictly our inferences are limited to this colony. Weavers from this colony were not color-ringed for individual identification.

Experiment 1

Data were collected over 5 days. Observations for the first three trials were made from 0630 to 1800 hours, and for trials four and five, observations were made from 0630 to 1000 hours. Observations were made by two individuals at a time (observers rotated every 4 h). We trained (with other birds) until we were consistently recording data. Our experimental array consisted of three rows, each with four 26-cm diameter white plastic plates. The three rows were arranged along a bias so that they were exactly 5, 10, and 15 m away from the observers, and each plate within the row was 0, 5, 10, or 15 m away from cover. The human observers sat 7.5 m west of the tree line on the southern side of the array.

We placed a handful of sorghum in each plate and refilled the plate whenever depleted. The plates were large enough to allow for more than one white-browed sparrow-weaver to forage simultaneously, which occurred often. Weavers readily foraged on sorghum.

Each visit to a plate was recorded. We noted the plate visited, the weaver's arrival time to the plate, their latency to forage once they landed on the plate, and their time of departure. We also noted if other conspecifics were present on the plate. If an individual visited more than one plate during a foray into the array, each landing at a plate was scored separately. When weavers were on plates, we conducted focal observations with continuous recording to quantify time allocation (Martin and Bateson 1993). We dictated into a microcassette recorder the onset of each bout of foraging (head down and pecking at plate), vigilance

(head elevated and neck stretched), calling (weavers produced food calls when they discovered food; Valone 1996), grooming (pecking at feathers), hopping (jumping to and from plates and within study site), and when they were off the plate.

We graphically examined the number of visits to each plate and the latency for any weaver to initially visit each plate. Focal observations were analyzed using JWatcher 1.0 (Blumstein et al. 2006). After visually examining our data, we elected to focus our formal analyses on foraging rate and vigilance rate, because previous studies have demonstrated that these behaviors are sensitive to variation in predation risk (Slotow and Rothstein 1995b; Slotow and Coumi 2000). We fitted two-way general linear models in Statistical Package for the Social Sciences (SPSS) version 14 (SPSS 2005) to examine effects of indirect risk, direct risk, and their interaction on time allocation. We calculated partial η^2 values and used them as our estimate of effect size, and we report R^2 values for the models.

Experiment 2

We attempted to find the amount of food that would cause the weavers to forage farther from cover (Lima and Bednekoff 1999; Brown and Kotler 2004; Slotow and Paxinos 1997). We collected data over 4 days. The first and second trials took place from 1400 to 1800 hours on days 1 and 2, the third from 1400 to 1800 hours on day 3, and the fourth and fifth trials from 0600 to 1000 and 1400 to 1800 hours on day 4. We placed two plates 10 m away from the observers; the first plate was placed 0 m from cover, and the second plate was placed 15 m from cover. For the first trial, we placed 4 g of sorghum on each plate and replenished the sorghum when necessary. For the second trial, we placed 4 g of sorghum on the 0-m plate and 8 g of sorghum on the 15-m plate. For the third trial, we placed 4 g of sorghum on the 0-m plate and 16 g of sorghum on the 15-m plate. For the fourth trial, we placed 4 g of sorghum on the 0-m plate and 32 g of sorghum on the 15-m plate. As in experiment 1, we conducted focal observations of foraging weavers, scored these focals using JWatcher 1.0, and analyzed the data with two-way analysis of variance models.

Results

Experiment 1

There were 383 weaver visits during experiment 1. Several lines of evidence suggest that weavers were more sensitive to indirect risk than to direct risk. Weaver visits to plates were not random ($\chi^2 = 38.817$, $df = 6$, $p < 0.0001$); they

visited plates more if they were closer to cover than farther from cover, but there was no relationship between distance to the observer and the number of weaver visits (Fig. 1). Additionally, plates closer to cover tended to be first visited sooner than plates farther from cover, but again, there was no relationship as a function of distance to observer (Fig. 2).

Perhaps the most compelling evidence for the importance of indirect risk comes from the results of our focal observations. Variation in foraging rate was significantly ($p=0.047$, $\eta^2=0.061$) explained by indirect risk, though not by direct risk ($p=0.520$, $\eta^2=0.010$; Table 1). In general, we noted that foraging rate increased with increasing distance to cover. The indirect, but not direct risk, significantly ($p=0.008$, $\eta^2=0.089$) explained variation in vigilance rate. As weavers foraged farther from cover, they increased their vigilance rate. Moreover, the effect size of indirect risk, while small ($\eta^2=0.089$), was four times that of direct risk ($\eta^2=0.022$). For vigilance rate, there was no significant interaction ($p=0.263$, $\eta^2=0.058$) between direct and indirect risk.

Experiment 2

There were 77 weaver visits during the course of our feeding manipulation. We found a significant effect of indirect risk on foraging rate ($p=0.026$, $\eta^2=0.069$) and a significant effect of food at 15 m on foraging rate ($p=0.003$, $\eta^2=0.179$; Fig. 3a). Weavers foraged at faster rates when farther from cover and foraged at slower rates when
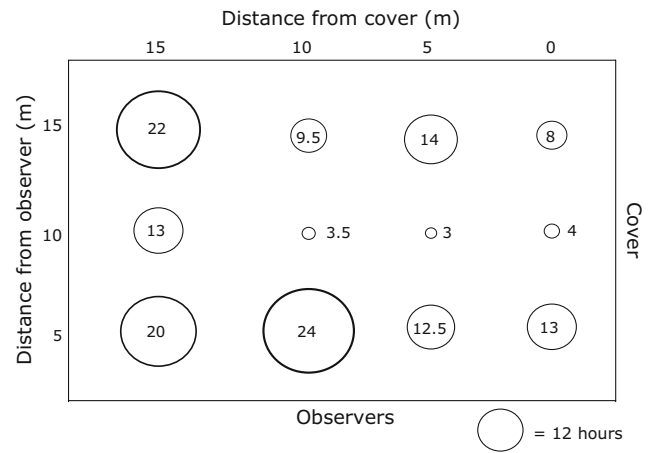
there was more food provided at the 15-m plate. There was no significant interaction between indirect risk and food at the 15-m plate ($p=0.964$, $\eta^2=0.001$), and the model significantly ($p=0.004$, $\eta^2=0.236$) explained 17% of the variation in foraging rate. No significant effect of either indirect risk or food at the 15-m plate was found for vigilance rates (Fig. 3b).

Fig. 2 The latency to arrive at each plate scaled by circle size in experiment 1. *Circles* represent the average number of hours during the time which plates were set up that it took for weavers to first visit the plate. Thus, latencies >12 h means that it took more than one experimental (12-h) day for an individual to first visit a plate. Plates closer to cover were visited by weavers sooner than plates farther from cover. There was no obvious relationship in latency to arrive as a function of distance to the observer
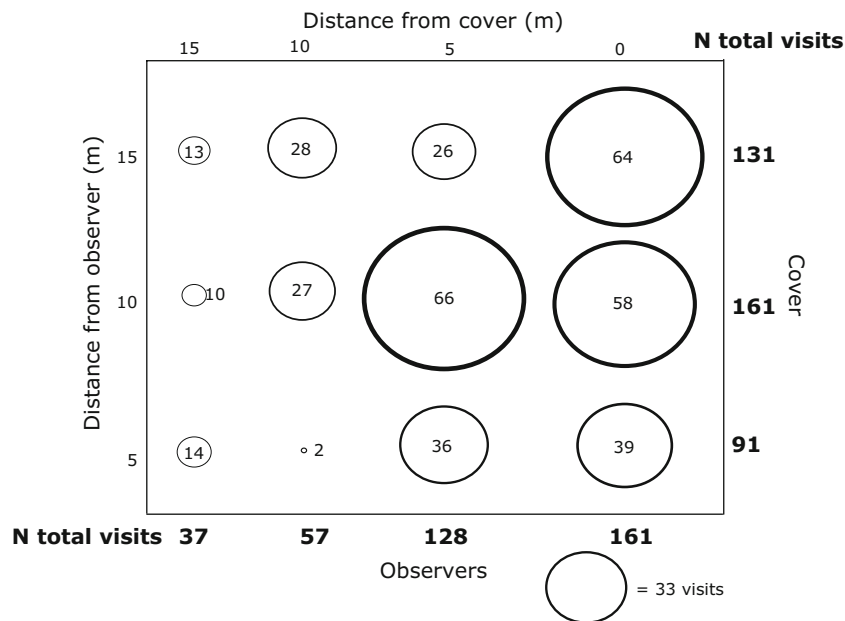

Fig. 1 The number of visits (represented by relative circle size) to each plate by weavers in experiment 1. Visits were non-randomly distributed ($\chi^2=38.817$, $df=6$, $p<0.0001$), with plates closer to cover receiving more visits by weavers than plates farther from cover. There was no relationship in total number of visits as a function of distance to the observer

Table 1 Results (*B* values, *p* values, and partial η^2) of general linear model examining the effects of direct and indirect risk on foraging and vigilance rates of 139 white-browed sparrow-weaver visits to an artificial feeding array

		B	*p*	η^2
Foraging rate	Corrected model		0.123	0.118
	Intercept	52.486	<0.001	0.916
	Direct risk		0.52	0.01
	5 m	2.869	0.632	
	10 m	8.917	0.178	
	15 m			
	Indirect risk		0.047	0.061
	0 m			
	5 m	9.271	0.169	
	10 m	1.937	0.788	
	15 m	18.389	0.031	
	Direct risk × indirect risk		0.072	0.086
Vigilance rate	Corrected model		0.08	0.128
	Intercept	44.357	<0.001	0.943
	Direct risk		0.237	0.022
	5 m	5.157	0.212	
	10 m	4.993	0.272	
	15 m			
	Indirect risk		0.008	0.089
	0 m			
	5 m	5.746	0.215	
	10 m	3.744	0.450	
	15 m	10.983	0.061	
	Direct risk × indirect risk		0.263	0.058

Coefficients for direct and indirect risk are, with tested against a reference, 15 m row for direct and 0 m from cover for indirect

Discussion

Taken together, our results strongly suggest that white-browed sparrow-weaver foraging behavior is influenced by indirect cues of predation risk. Weaver patch choice could be manipulated by food addition suggesting that benefits influence foraging decisions. Additionally, weavers foraged the most at feeding plates closer to cover, took the longest time to arrive at plates farthest from cover, and had higher rates of foraging and vigilance when farther from cover.

Conducting both experiments in the same area may have increased the likelihood of a single weaver visiting the food plates numerous times, and thus potentially allowing the weavers to habituate to humans. If so, it is conceivable that weavers at the research center did not view humans as a sufficient threatening stimulus. However, as we noted in the introduction, weavers did not land near us if there was no

food, and they flushed when we approached them. Thus, we do not infer that they had no fear of humans, and thus humans are conceivably a relevant threatening stimulus. It would be interesting to see if other predators (e.g., felids) sitting at the same distance from the array generated different results. Future experiments could study this.

Our results suggest that once weavers elected to forage on our array, they were more sensitive to the indirect cue than the direct cue. However, the lack of a strong direct effect and a relatively strong indirect effect could be explained by the weavers having assessed that there was limited danger associated with our presence, while risk associated with the indirect cue remained unchanged. Viewed this way, direct cues quickly provide information about risk and permit animals to dynamically modify their assessment. In some cases, this may mean that animals may appear unaffected by a direct cue. By contrast, indirect cues, because they are indirect, provide more probabilistic information about risk and help minimize the risk of encountering a predator (Thorson et al. 1998). The information about risk contained in an indirect cue does not get updated as quickly; being vigilant at the plates and cover does not help an individual assess the probability of
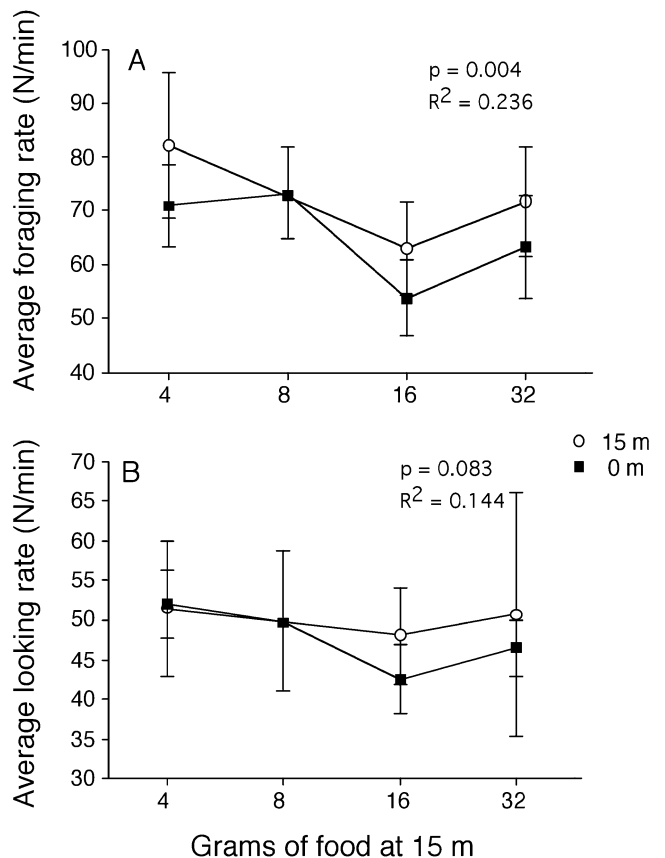

Fig. 3 The effect of food supplementation at the distant plate on: (**a**) mean (±95% CI) foraging rate and (**b**) mean (±95% CI) vigilance rate

surviving an attack. Additionally, prey may have more than a single predator, and Orrock et al. (2004) noted the greater importance of indirect cues than direct cues for prey with multiple predators.

We may also expect some interaction between direct and indirect cues. Brinkerhoff et al. (2005) found that predator urine and microhabitat had a combined effect on the foraging behavior of small mammals. Kotler et al. (1991) studied the foraging behavior of two species of gerbils (*Gerbillus allenbyi* and *Gerbillus pyramidium*) when owls were present and absent in conjunction with varying microhabitat features and illumination levels. They found a combined effect of these three indirect and direct variables. Thus, direct cues may provide important information about risk in the context of specific indirect cues. Further analyses of the relative effect sizes of both direct and indirect cues when simultaneously considered could elucidate their relative importance in a system where both cues influence foraging behavior but to different extents.

The relatively small effect sizes for significant results imply that other factors besides perceived risk influenced foraging behavior. We acknowledge that while weavers are seed-eaters, our choice of only providing sorghum may have influenced foraging behavior; providing mixed diets may increase foraging time (e.g., Randolph and Cameron 2001). Heterospecific competitors may also influence foraging behavior (e.g., Alatalo and Moreno 1987), and there were occasional visits by other granivorous birds to our array. Furthermore, intraspecific competition among the weavers may influence their foraging behavior. Previous studies have shown that aggression among individuals of the same species increases with increasing group size when individuals are at safer foraging locations (Slotow and Rothstein 1995b; Slotow and Coumi 2000; Slotow 1996). Environmental conditions could potentially influence foraging decisions. Although the weather was fairly consistent throughout our sampling period, when it was very hot or very windy, weavers did not forage. Slotow and Coumi (2000) also considered the effect of temperature on foraging distance in their study on the vigilance of bronze mannikin (*Lonchura cucullata*) groups. Formally, we did not quantify temperature, but (aside from animals not foraging during the heat of the day) we detected no obvious effects of temperature on risk taking.

Despite the relatively small effect sizes, our results are consistent: white-browed sparrow-weavers varied their foraging behavior in response to indirect cues normally associated with predation risk. Because the risk estimated by such indirect cues may not change over time, indirect cues may be generally more important for long-term assessments that individuals make about where, when, and how to forage, while direct cues may be relatively more important in deciding whether to forage in the first place.

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