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Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris*

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Animals should adapt their escape behaviour to both physical and social surroundings in order to maximize their probability of survival. Cover can be both obstructive, reducing the visibility of the surroundings and hindering escape, and protective, providing refuge. We investigated how the provision of cover (long grass) affected (1) the escape behaviour and (2) the alarm call behaviour of Common Starlings *Sturnus vulgaris* responding to a model hawk during a simulated attack. Starlings always retreated away from the predator and sometimes alarm-called. Their escape trajectory was close to the ground when escaping in long grass, which could be explained by either tall swards hindering take-off or such swards being used as protective cover. On short grass their escape trajectory was much steeper (> 45°). We also investigated the use of alarm calls in Starlings according to predictions arising from the costs and benefits to callers and receivers. Callers could benefit from using alarm calls through dilution or confusion if their use initiates flock departures, thus reducing their probability of being targeted. If there is no cost to the producer of alarm calls we predicted that detectors should call at all times to gain these benefits (i.e. irrespective of grass length), but if their use is costly we predicted that they would be used only when the benefits outstrip the costs. In this case we would predict that alarm calls would be given when other (visual) signals were impaired on long grass but not when they were effective on short grass. Starlings used alarm calls on long grass when visibility was reduced more frequently than on short grass, suggesting that calling has a cost to the producer. The contrasting escape strategies of Starlings in relation to a relatively small (10 cm) change in grass height demonstrates the potential importance of habitat structure in determining predation risk.

Keywords: escape strategy, Eurasian Sparrowhawk *Accipiter nisus*, predation risk, protective cover, visibility.

When animals are attacked by predators they must make split-second decisions about how to adjust their escape behaviour to the prevailing situation. Prey responses may vary in relation to the type and behaviour of predators (Cresswell 1993, Kullberg *et al.* 1998), flushing distances or speeds (Lind *et al.* 2003), perceptual limits (Quinn & Cresswell 2005) and habitat types (Lima 1993). For example, lapwings (*Vanellus* spp.) peck at reptilian predators but mob and feign injury when under attack from raptors (Walters 1990). Redshanks *Tringa totanus* not only react differently when attacked by Eurasian Sparrowhawks *Accipiter nisus* and Peregrine Falcons *Falco peregrinus* (flying and freezing, respectively), but their chance of survival depends on making the correct response (Cresswell 1993).

The initial response of an escaping bird is critical to its probability of survival (Kenward 1978). Several studies have shown that responding rapidly with a

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steep, fast ascent can minimize the chances of capture (Lima & Dill 1990, Cresswell 1993). However, speed declines with increasing take-off angle due to the effects of gravity, so that birds face a trade-off between climbing and accelerating. For example, take-off angle can be mass-dependent. Small mass increases such as daily variations appear to have little effect but larger increases, for example gravidity and experimentally induced increases, lead to decreased angles (Witter *et al.* 1994, Lee *et al.* 1996, Kullberg *et al.* 1998).

Escape behaviour should also vary to enhance survival in different habitat types. Habitat cover can obstruct the detection of predators (Krause 1994, Poysa 1994), but also can function for protection and consequently many small birds flee to cover when attacked (Elton 1939, Lazarus & Symonds 1992). Protective cover can influence the escape angle of birds that use such cover for refuge. In an experiment where distance to cover remained constant with take-off angle, Great Tits *Parus major* reduced their angle of ascent, increasing their speed, when cover was present compared with when no cover was available (Kullberg & Lafrenz 2007).

Flocking is an effective anti-predation strategy for many species inhabiting open environments (Hamilton 1971, Roth *et al.* 2006). The anti-predation benefits of group living to individuals arise through the dilution effect, confusion of the predator, and collective detection (reviewed by Krause & Ruxton 2002). Two of these mechanisms, confusion of the predator and collective detection, require that individuals within the group respond to cues or signals from group members as a threat may not be detected by all individuals. In open habitats a rapid escape response to visual cues, such as flock-mate departures, may be the optimal strategy to avoid predation. Detection of anti-predator visual cues from flock-mates may be more problematic in complex environments (e.g. forests), and signals, such as alarm calls, may be necessary for information about predators to be transmitted through the flock (Cresswell 1994).

Common Starlings *Sturnus vulgaris* make a number of alarm calls when approached by a predator (Cramp & Perrins 1994). Callers benefit if their signals cause group responses through dilution and/or confusion effects or a combination of both and reduce their own probability of capture (e.g. Cresswell 1994). Alarm signal production may carry costs, be that calorific or because they draw further attention to the signaller and increase personal risk.

The aim of the present study was to assess the effects of habitat structure on signal use and escape responses in a flocking species living in open habitats. Most previous experimental studies have investigated escape strategies in woodland species (e.g. Kullberg *et al.* 1998, Lind *et al.* 2003, Kullberg & Lafrenz 2007, but see Cresswell 1993). In open habitats dashing to nearby cover is rarely feasible and individuals may rely on other mechanisms such as flocking to reduce risk. We investigated whether small differences in sward height affected the escape behaviour of Common Starlings that inhabit open grass swards. Starlings naturally prefer short grass habitats (Whitehead *et al.* 1995) that allow improved predator detection and intake rates (Devereux *et al.* 2004, 2006). In addition to concealing predators, longer swards may hinder take-off. Alternatively, Starlings may use taller grass for concealment when attacked. In a previous study we showed that Starlings were quicker at detecting Sparrowhawk attacks when foraging on short grass compared with on long grass (Devereux *et al.* 2006). We re-analysed this dataset to test whether sward height affected their escape strategies. We predicted that escape trajectory of the individual targeted by an attacking predator would be adjusted to sward height and on short grass Starlings would take off at an increased angle. Next we investigated the use of alarm calls. If there is no cost to the producer of alarm calls we predicted that individuals detecting a hawk should call at all times to gain these benefits (i.e. irrespective of grass length), but if their use is costly we predicted that they would be used only when the benefits outstrip the costs. In this case we would predict that alarm calls would be given when other (visual) signals were impaired on long grass but not when they were effective on short grass.

Finally, we examined whether individuals that could not see an attacking hawk but could see the response of a targeted flock-mate (non-detectors) used this information to escape in an adaptive manner. We predicted that if non-detectors infer the hawk's attack trajectory from the escape behaviour of flock-mates they should flee in a non-random manner, either in the same direction as the detector or at a tangent to it (see Bednekoff & Lima 1998). By doing so non-detectors would avoid putting themselves in the direct line of attack and maximize their own distance from the predator, which may serve to prevent target-switching by the predator (Bednekoff & Lima 1998).

METHODS

Experimental set-up and procedure

Seventy-six adult (fledged 2002 or before) and first-winter (fledged 2003, hereafter termed juvenile) Starlings were captured at University Farm, Wytham, Oxfordshire, UK, during November and December 2003 under licence from English Nature. At capture, basic biometric measurements were taken and birds were ringed with a unique combination of two plastic colour rings and one metal BTO numbered ring. They were housed in groups of two and three in 0.9-m-high × 0.7-m × 0.6-m indoor cages under a light/dark cycle that reflected prevailing conditions. Cages contained perches, a water bath, drinkers and a food bowl and had a newspaper substrate. Groups were in visual and auditory contact with other groups. They received a diet of turkey starter crumb and Orlux softbill pellets *ad libitum* and a daily ration of 2.5 cm^3 of live mealworms per bird, given after trials were completed. Individuals remained in captivity until their trial (median = 3 days of captivity) and were released from their capture site in pairs in good weather conditions thereafter. Each bird was used for one trial only.

The experiment was performed in a large greenhouse that was divided into two halves by an opaque wall and doorway (Fig. 1). A taxidermic model of a juvenile female Sparrowhawk mounted in flight position was suspended from a wire from the ceiling in the eastern half. The wire ran downhill at a 40% gradient for 10 m, before running beneath the table upon which the detector enclosure was placed in the western half of the greenhouse. The hawk was released only after both Starlings had foraged for at least 2 min, and whilst both were still actively foraging. The hawk travelled at speeds of approximately 13–14 km/h after it was released by a remote mechanism. This is within the normal range of *Accipiter* hawk attack speeds (5–25 km/h; Goslow 1971, Hilton *et al.* 1999). The hawk made very little noise when moving. White noise was played through two speakers placed either side of the doorway between the rooms during the experiment to reduce any disturbance from external noise and ensure that Starlings were responding only to visual signals. A screen hid the hawk from the detector bird until it was 5 m away and after it reached the detector enclosure it disappeared from sight.

Two 0.5-m^3 cubic mesh enclosures (side length 0.5 m) were placed on top of a 1-m-tall table in the western half of the greenhouse (Fig. 1). The left cage was designated the detector cage and was placed across the door opening and the non-detector cage was placed 1 m to its right behind the wall. Each enclosure sat on a fresh grass turf square that covered a tray containing a base of wet sand topped with 50 live mealworms. Starlings were able successfully to forage on the mealworms by probing through the root layer (1 cm thick). The grass on both turfs was cut to either 3 or 13 cm height prior to each trial to vary cover.

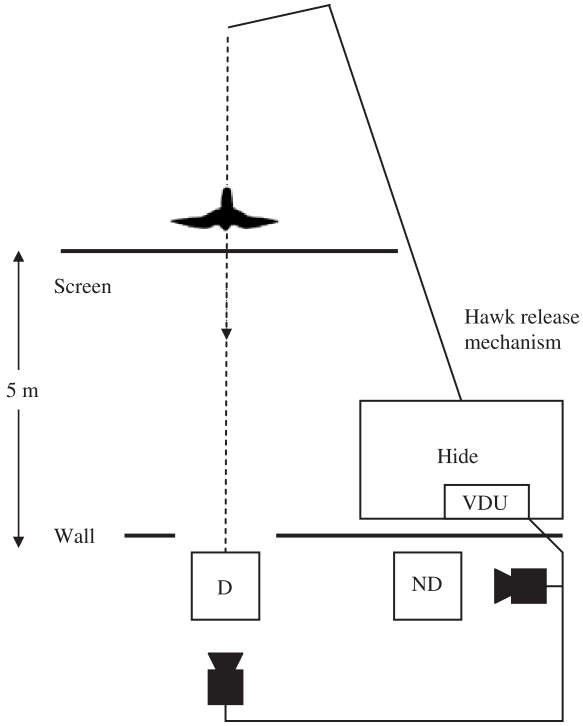

Figure 1. Experimental set up. Two Starlings, the detector (D) and non-detector (ND), were allowed to forage for buried mealworms on grass turfs in individual enclosures. The hawk flew down a wire towards the detector at approximately 13.5 m/s and appeared once it passed a screen. The non-detector could not see the hawk at any point but could see the detector. The subject's behaviour was monitored on a VDU by the experimenter and recorded on two video cameras placed behind the focal bird and to the side of the companion bird. Figure not to scale.

At testing, birds were removed from their home cage and transferred to the experimental enclosures in soft cotton bags. One bird was released into each cage (thereafter called the detector and non-detector). Their behaviour was recorded using two digital video cameras. Same-sex pairs of Starlings were used for all trials. The detector was either an adult or a juvenile (first-winter) and the non-detector was always an adult, producing two age combinations (adult–adult;

juvenile–adult). The non-detector could see the detector but could not see the hawk, and the detector could see both hawk and the non-detector. The simulated attack caused an escape reaction in both birds.

Behavioural coding and data analysis

Behavioural data were extracted from videotapes by reviewing them frame by frame (digital 8-mm video, 25 frames/s). The detector camera recordings were used to determine hawk speed and the detector's behaviour. The non-detector camera recordings were used to determine the non-detector's behaviour and to co-ordinate the timing of tapes. The following explanatory variables were determined from plumage and biometric measurements: age (adult/juvenile), sex (male, female) and body condition on day of experiment (body mass/wing length). Only trials where both the detector and the non-detector were on the ground at the time of attack were used for analysis, reducing our sample size to 23 trials. The response variables for the detector were alarm (yes or no) and escape trajectory (low, head height below 25 cm; high, head height 25 cm and above). The response variable for the non-detector was escape direction. Escape direction was taken relative to the direction taken by the detector and was grouped into four categories (Fig. 2a). In all cases the detector flew towards the rear of the cage but not to a fixed point (e.g. towards the back left corner, centre or back right corners). In 19 of the 23 trials escape direction of the non-detector could be clearly classified into one of these categories and these form the dataset for non-detector analyses. The remaining four trials had responses where the non-detector either did not flee or the direction taken could not be categorized (e.g. flew vertically to cage roof).

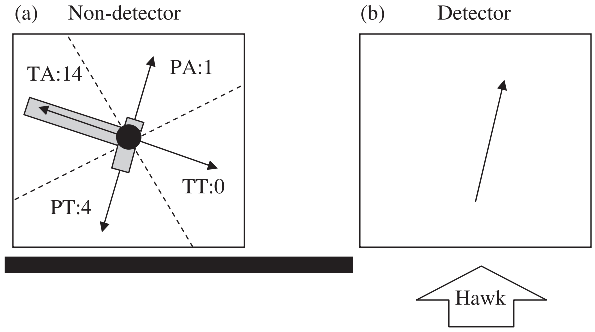

Figure 2. Classification of escape directions of non-detectors relative to the direction taken by detectors. Parallel away (PA) escapes followed the same direction as the detector (i.e. away from the hawk). Tangent away (TA) escapes took a direction approximately 270° to the detector. Parallel towards (PT) escapes took a line away from the detector at approximately 180° (i.e. towards the hawk). Escapes in the tangent towards (TT) direction were at approximately 90° to the detector. Lines are drawn dashed to represent the non-fixed nature of the quadrants, because the directions are classified relative to the detector's trajectory and are not fixed or determined by the cage or room dimensions. Bars and numbers represent the number of times each direction was recorded ($n = 19$).

We tested the hypotheses that escape trajectory and alarm calls are dependent on habitat complexity by performing binary logistic regressions on the response variables escape trajectory and alarm call (Minitab v. 14). In the models, we included the explanatory variable grass height, and the potentially confounding effects of age, body condition and detection latency (equivalent to hawk distance at detection). We fitted full models including all four predictors and assessed the significance of each by removing each in turn from this full model (see Whittingham *et al.* 2006). We analysed the escape direction of non-detectors using a G-test with William's correction (Sokal & Rohlf 1995).

RESULTS

Escape behaviour and grass height

All detector birds performed escape behaviour that consisted of some or all of the following elements: crouch, fly, run, alarm call. They moved towards the rear of the enclosure, away from the direction of the approaching hawk, but the initial trajectory of individual birds took two forms: some birds flew straight up to the top of the enclosure back (9/23), whilst others ran (6/23) or flew just above ground level (8/23) to the lower back of the enclosure. The trajectory (low or high) that detectors took when escaping from the hawk was dependent on the height of the grass in which they were foraging, but not on detection latency, age or body condition (Table 1a). On short grass most birds flew high (6/8 high) compared with long grass (3/15 high), where most birds had a low trajectory.

Escape direction of non-detectors

Escape direction of non-detectors (Fig. 2) differed significantly from chance ($G_{\text{adj } 3} = 24.28$, $P < 0.001$). Non-detectors moved away at a tangent from the detector's escape direction (TA, 270° to detector) more often than expected (14/19 responses), and escapes

Table 1. (a) Escape trajectory and (b) alarm-calling responses of a detector bird to a simulated hawk attack, analysed using binary logistic regressions ($n = 23$). Birds were more likely to have a high trajectory and to alarm call on long grass.

(a) Escape trajectory (binary response = low)

Explanatory variable	Coefficient	*Z*	*P*
Constant	0.528	0.06	0.95
Age (juvenile)	2.042	1.53	0.13
Grass height (short)	–3.126	–2.37	**0.02**
Body condition	–0.093	0.01	0.95
Detection latency	–0.243	–0.10	0.92

Log-likelihood = –10.57
Test that all slopes are zero: $G_4 = 9.66$, $P = 0.05$.

(b) Alarm (binary response = yes)

Explanatory variable	Coefficient	*Z*	*P*
Constant	–18.68	–1.75	0.08
Age (juvenile)	0.601	0.49	0.62
Grass height (short)	–2.800	–2.10	**0.04**
Body condition	30.983	1.66	0.10
Detection latency	1.504	0.71	0.48

Log-likelihood = –10.32.
Test that all slopes are zero: $G_4 = 11.21$, $P = 0.03$.

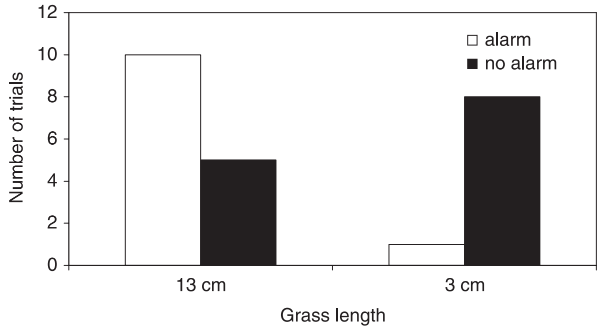

Figure 3. The effect of grass sward height on alarm-calling in Starlings under attack by a Sparrowhawk model. Starlings called more frequently on 13-cm swards than they did on 3-cm swards.

in the other categories occurred fewer times than expected by chance (PA, 180° to detector: 1/19 responses; PT, 0° to detector: 0/19 responses; TT, 90° to detector: 4/19 responses).

Habitat and alarm calls

Starlings uttered 'chip' and 'spit' alarm calls in response to the predator during escape, either singly or as a rapid short sequence of 2–3 of either call. These calls are of the type referred to by Cramp and Perrins (1994) and Feare (1984) as mobbing calls (chip-calls) and are short, metallic sounding with a wide frequency range. Alarm calling in detectors was dependent on grass height (Table 1b, Fig. 3). Birds were more likely to alarm-call on long grass than on short grass [$G_1 = 7.73$, $P < 0.01$ excluding other variables, significant at $\alpha = 0.05$ in full model (Table 1b)].

DISCUSSION

The type of escape behaviour used by Starlings that detected a hawk attack was dependent upon grass height. When using long grass patches, Starlings remained close to the ground whilst escaping and alarm-called. Non-detectors minimized their chances of being captured by fleeing sideways from their flock-mate and away from the attack line of the hawk, relying on inferring the hawk's attack angle from the behaviour of the targeted bird only.

Habitat complexity and the use of cover for concealment

We found marked differences in the escape trajectory of Starlings foraging on long and short grass swards. There are at least four explanations for this dichotomy. First, grass may have obstructed the view of the approaching predator, causing the hawk to be detected later in long swards (Whittingham *et al.* 2004; Devereux *et al.* 2006). Take-off angle was greater for tits *Parus* spp. that detected a predator at a shorter distance (Lind *et al.* 2003). However, detection distance was controlled for in our statistical modelling (through detection latency), discounting its role in determining escape trajectory in this case. Secondly, the risk of predation is known to be mass-dependent in birds; flight is impaired as fat reserves increase (Cuthill & Houston 1997). The take-off angles of Starlings carrying small lead weights are lower than in controls (Witter *et al.* 1994), and similarly gravid females take off at lower angles than post-laying females (Lee *et al.* 1996). Subordinate wintering Great Tits, which carry greater reserves to avoid starvation, have impaired flight ability when reserves are laid down in the evening, but this effect disappears in the morning after reserves are utilized (Krams 2002). However, we did not find a significant effect of body condition in our models.

Thirdly, the long swards may have impeded the angle of escape. High trajectories in long grass swards were possible but less common (3/15 trials). In addition, Starlings often appeared to run and weave through the long sward when escaping from the hawk (5/12 low trajectories on long grass), rather than trying to take off. The final reason why Starlings in long grass may have remained low when escaping from the hawk relates to their use of the sward as protective cover. Habitat cover has contrasting effects on predation risk depending on the perception of risk by different prey species (Lazarus & Symonds 1992). On the one hand, cover may provide concealment and protection from predators, but on the other, it obstructs views of approaching threats (Elton 1939). Many species of small birds flee to cover under threat, and habitats close to cover are often perceived as safer habitats (Lima & Dill 1990, Whittingham & Evans 2004). Starlings, on the other hand, prefer to occupy open habitats such as grass fields and are often found away from obstructive boundaries (Atkinson *et al.* 2005). Recent evidence shows that Starlings perceive long swards as obstructive cover because they increase their vigilance in these habitats (Devereux *et al.* 2006). However, the results of the present study suggest that Starlings could use the long grass for concealment.

It is not possible to distinguish between the final two hypotheses in the current experiment and it is probable that the lower escape trajectory of Starlings on long grass is a result of the interplay of both. Starlings usually crouch then leap to take-off (Witter *et al.* 1994, Bonser *et al.* 1999) and tall grass may hinder this and their ability to open their wings for the initial wing flaps of flight. Starlings foraging on the tall grass would be to a greater degree on top of the sward and would lose leg thrust power to the compliant substrate (Bonser *et al.* 1999). Thus, attempting a take off on tall swards may be inefficient or ineffective and the best compromise may be to use the sward for concealment whilst running (at least initially) to escape. Starlings are usually found foraging on short swards and avoid tall grass (Atkinson *et al.* 2005). In addition to increasing food accessibility and reducing the visibility of predators (Devereux *et al.* 2004, 2006), tall swards could increase predation risk by reducing escape efficiency.

Non-detector escape responses

In the present study, non-detectors escaped at a tangent away from the targeted individual in the absence of direct cues from the hawk, suggesting an adaptive behavioural response to minimize predation risk. It is possible that our escape direction result simply represents a preference for escaping towards a certain area of the greenhouse room rather than an adaptive response to reduce predation risk. We think this is unlikely because we measured escape angle relative to the direction taken by the detector. Whilst the detector always moved away from the hawk its angle varied by approximately 90°, from the back left corner to the back right corner of the cage. If non-detectors had a positional preference, for example, for moving away from the doorway of the greenhouse, this would have affected the categorization of their responses. In this case, we would have expected an equal split between the directions TA (when detector flew to back right corner, Fig. 2, 14/19 responses) and PT (when detector flew to back left corner, Fig. 2, 0/19 responses). Furthermore, there were no refuges in the greenhouse that may have made any particular area more attractive than others. Instead we assert that the non-detectors were able to extract information from the detectors about the attack trajectory of the predator without themselves seeing the predator.

Sideways movement by the non-targeted bird may confer survival advantages for at least two reasons. First, moving perpendicular to the hawk's attack line might prevent the hawk from switching target and would reduce the chances of a non-targeted individual crossing paths with the hawk. Although the non-detector could not see the hawk it could see the targeted bird's escape trajectory, which was always in the same direction as that of the hawk. Casual observations of small birds in flocks when under attack have revealed that non-targeted birds in flocks often flee sideways or freeze (Bednekoff & Lima 1998). Moreover, Blue Tits *Cyanistes caeruleus* that detect a predator late in its attack also dodge sideways (Lind *et al.* 2003). Secondly, the success of raptor attacks on prey moving sideways is less than for prey moving in any other direction (Shifferman & Eilam 2004). This could reflect postural constraints in predator head movements when tracking prey (e.g. Tucker 2000).

Alarm use and function

Different anti-predator benefits to individuals in groups rely on a co-ordinated response amongst group members based on the transmission of social information (Powell 1974, Elgar 1989). In habitats where visual cues are less effective, such as forests or rocky shores, alarm calls may have evolved to alert the non-detector to the presence of a threat and so may increase co-ordination between group members (Cresswell 1994). Starling alarm calling was significantly related to obstructive qualities of the habitat in this study, which may suggest that it functions in flock cohesion when visual signals are impractical. Starlings rarely gave alarm calls on short grass when visual signals were effective, but alarm-called when long grass obstructed visual communication.

An alternative explanation for the function of alarming is that it is used to manipulate flock-mates into making an inappropriate response to danger (Charnov & Krebs 1975). The detector, by the very nature of its name, has knowledge of the position, attack angle and speed of the predator. Foraging flock-mates do not have this, especially when vision is obstructed by long grass (Devereux *et al.* 2006). In response to an alarm call, non-detectors may startle and take off inappropriately before gaining sufficient information about the hawk, as a swift response is usually optimal for survival (Kenward 1978). This puts the non-detector at an increased risk relative to the detector, especially if the detector does not take off or is part of a small group when the benefits of confusion are small.

The question arises as to why alarm calls are not used on short grass alongside visual signals of flock departures. It is possible that calling is energetically or neurally expensive, or that it increases the risk of predation by attracting predators or by improving a predator's ability to home in on prey (Krams 2001). Individuals detecting a predator in open habitats may then avoid the increased cost of being targeted by relying on flock departures to signal an attack, whilst still benefiting from being attached to the flock (Roth *et al.* 2006).

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