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T. L. DeVault
USDA/APHIS/WS National Wildlife Research Center, Travis.L.DeVault@aphis.usda.gov

T. W. Seamans
USDA/APHIS/WS National Wildlife Research Center, thomas.w.seamans@aphis.usda.gov

Bradley F. Blackwell
USDA/APHIS/WS National Wildlife Research Center, bradley.f.blackwell@aphis.usda.gov

S. L. Lima
Indiana State University, slima@indstate.edu

M. A. Martinez
New Mexico State University

See next page for additional authors

Authors
T. L. DeVault, T. W. Seamans, Bradley F. Blackwell, S. L. Lima, M. A. Martinez, and E. Fernandez-Juricic

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Can experience reduce collisions between birds and vehicles?

T. L. DeVault[1], T. W. Seamans[1], B. F. Blackwell[1], S. L. Lima[2], M. A. Martinez[3] & E. Fernández-Juricic[4]

1 United States Department of Agriculture, National Wildlife Research Center, Sandusky, OH, USA
2 Department of Biology, Indiana State University, Terre Haute, IN, USA
3 Department of Fish, Wildlife and Conservation Ecology, New Mexico State University, Las Cruces, NM, USA
4 Department of Biological Sciences, Purdue University, West Lafayette, IN, USA

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Correspondence
Travis L. DeVault, United States Department of Agriculture, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, Ohio 44870, USA.
Email: Travis.L.DeVault@aphis.usda.gov

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Abstract

Bird collisions with vehicles cause serious safety, financial and conservation concerns worldwide, but the causes of such collisions are poorly described. We investigated how experience with vehicles influenced avian avoidance responses. We trained three groups of vehicle-naïve rock pigeons *Columba livia* with 32 near-miss vehicle approaches over 4 weeks at 60 and 120 km h^{-1}, and also included individuals that heard but did not see the approaches (control group). We subsequently measured flight initiation distance (FID) and whether individuals 'collided' with a virtual vehicle directly approaching at 120 or 240 km h^{-1} using video playback. We found that inexperienced individuals (i.e. the control group) had longer FIDs than experienced birds, although only one of 90 individuals across groups successfully avoided virtual collision. Vehicle approach speed during video playback and the interaction of approach speed and training group did not influence FID. Our results suggest that a habituation-like effect based on repeated observations of passing vehicles could contribute to ineffective vehicle avoidance responses by birds when collisions are imminent. Novel strategies should be developed to enhance avoidance responses to high-speed vehicles to minimize bird mortality.

Introduction

Aircraft collisions with birds pose serious safety and financial threats worldwide (DeVault, Blackwell & Belant, 2013). Birds are also frequently struck by automobiles (Loss, Will & Marra, 2014), and these road collisions can adversely impact populations (Mumme *et al.*, 2000; Kociolek *et al.*, 2011). Birds appear to use antipredator behaviors for vehicle avoidance (Blackwell *et al.*, 2012), although often unsuccessfully (Bernhardt *et al.*, 2010; DeVault *et al.*, 2015). Recent investigations have begun to describe how sensory mechanisms, cognitive abilities and behaviors, all of which evolved in the context of predator avoidance, are frequently inadequate for successful vehicle avoidance, given the speed and size of modern aircraft and automobiles. For example, avoidance responses vary widely across species (Blackwell *et al.*, 2009; Møller, Erritzøe & Erritzøe, 2011; Husby & Husby, 2014) and birds face a higher risk of collision as vehicle speed increases (DeVault *et al.*, 2014, 2015). These and other efforts have offered insights into the sensory and behavioral factors important to antipredator responses, and how they might be exploited to reduce bird-vehicle collisions (Blackwell *et al.*, 2009, 2012; Doppler *et al.*, 2015). Still, several important questions regarding vehicle avoidance by birds remain inadequately addressed, such as the role of experience in avoiding collisions (Legagneux & Ducatez, 2013; Husby & Husby, 2014).

Birds that regularly observe fast-moving vehicles potentially could learn to increase their flight initiation distances (FIDs) in response to vehicles over those normally used to escape slower predators, thereby increasing their likelihood of successful avoidance compared to inexperienced birds. For example, FIDs of European birds along roads were correlated with posted vehicle speed limits, suggesting that birds might adjust avoidance responses according to average vehicle speed (Legagneux & Ducatez, 2013). Also, vehicle collision mortality for Florida scrub-jays *Aphelocoma coerulescens* was lower for older and experienced individuals than for inexperienced individuals (Mumme *et al.*, 2000). Finally, some wildlife managers at airports recommend that resident hawks and other birds of prey should not be removed or relocated, suggesting that these individuals are 'airport savvy' and thus unlikely to be struck by aircraft, and that their territorial presence discourages the use of airport lands by less experienced individuals (Solman, 1981; Burger, 1985).

Alternatively, repeated exposure to stimuli perceived as non-threatening, such as distant vehicles or those not on a collision course (e.g. birds viewing passing vehicles from the road margin or airport infields), could potentially lead to habituation (Bejder *et al.*, 2009), thereby reducing the likelihood of successful escape when collisions are imminent (Lima *et al.*, 2015). Several studies have shown such habituation-like responses to frequently encountered stimuli by various taxa. Australian magpies *Cracticus tibicen* had shorter FIDs in response to an approaching human in high pedestrian-traffic areas than in areas with few pedestrians (Gravolin, Key & Lill, 2014). Li *et al.* (2011) found that yellow-bellied marmots *Marmota flaviventris* decreased FIDs in response to an approaching human as vehicle and pedestrian traffic increased. Also, elk *Cervus elaphus* and pronghorn *Antilocapra americana* became less likely to perform vigilance and escape-related behaviors as vehicular traffic increased (Brown *et al.*, 2012).

Finally, previous repeated exposure to passing vehicles might have little effect on FIDs during situations where an escape response is necessary to avoid collision. Birds can differentiate between direct and tangential approaches of threatening objects (Wang & Frost, 1992; Lima & Bednekoff, 2011; Møller & Tryjanowski, 2014). Furthermore, Raderschall, Magrath & Hemmi (2011) demonstrated that fiddler crabs *Uca vomeris* that had been habituated to a threat approaching from one direction reverted back to their initial antipredator response when that same threat approached from a new direction. Likewise, birds facing a direct vehicle approach might quickly differentiate such a threat from previous experience with passing vehicles that did not pose an obvious risk of collision, and thus use unmodified predator escape strategies for vehicle avoidance (e.g. the FID would remain unchanged).

We explored the role of experience with vehicles traveling at different speeds as it influences vehicle avoidance by birds. Specifically, we exposed vehicle-naïve, captive birds to different levels of near-miss (tangential) vehicle approaches in a field scenario over a 4-week period and then quantified their FIDs in response to direct approaches of a virtual vehicle in a video playback experiment. We sought to determine whether previous, repeated exposure to passing vehicles increased, decreased or had no effect on FIDs and the probability of successful vehicle avoidance compared to inexperienced (naïve) birds when a collision was imminent. Following inferences by Mumme *et al.* (2000) and Legagneux & Ducatez (2013), we expected experienced birds to adjust avoidance responses according to observed vehicle speed (i.e. increase FID), and therefore improve their likelihood of successful avoidance.

Materials and methods

Study animals

We obtained 105 approximately 6-month old, farm-raised rock pigeons *Columba livia*; (hereafter pigeons) from a commercial breeder (K. C. Kennels and Lofts in Champaign County, Ohio, USA) on 1 June 2015. Previous research indicated that pigeons respond well to experiments involving approaching virtual objects in a video playback scenario (Wang & Frost, 1992). Our experimental birds were hatched and raised in a barn and had never been approached by moving vehicles or experienced traffic before our experiment. We transported pigeons in covered cages via truck approximately 105 km to our holding facility and video laboratory at the National Aeronautics and Space Administration Plum Brook Station (PBS; DeVault *et al.*, 2015). Pigeons were held in three 3.6 × 3.6 × 2.0 m cages in an indoor aviary illuminated with natural lighting and provided with commercial pigeon food, water and grit *ad libitum*. They were held for 14 days before vehicle-approach training began.

Vehicle-approach training

We randomly separated pigeons into three groups of 35. Each group was held together in separate cages throughout the experiment. We exposed the three groups of pigeons to near-miss vehicle approaches (passing within 2 m of the cages) to give them different levels of experience with vehicles. The first group (T120) was always trained with a vehicle approaching at 120 km h^{-1}, the second group (T60) with a vehicle approaching at 60 km h^{-1} and the third group (control) was prevented from seeing any vehicle approaches, but was exposed to auditory cues of the vehicle approaches during training of the other two groups. We prevented pigeons from observing any other vehicle approaches.

Training occurred on four consecutive days during four consecutive weeks (15 June through 10 July 2015), for a total of 16 training days. Each group was trained four times each day during two of the four training days each week, totaling 32 vehicle approaches per group. On the morning of each training day, we first moved pigeons (always keeping groups together) from the holding cages to 1.8 × 1.8 × 1.6 m training cages and covered the training cages with a visual barrier (fabric screen) to prevent birds from experiencing visual cues from vehicles during transport. We transported birds in the covered training cages via truck and trailer approximately 2 km to a straight, flat, single-lane, closed road at PBS. Training cages were placed adjacent to each other on the side of the road in mown grass at the edge of the pavement (Fig. 1). We removed the visual barrier from the training cage in the front position (holding either the T120 or T60 group), so that birds in that group could observe the approaching vehicle during training. When present, birds in the control group were always placed in the rear position and completely shielded from the oncoming vehicle and the visually exposed birds by the visual barrier (Fig. 1). The control group was trained with the T120 group during weeks 1 and 3, and with the T60 group during weeks 2 and 4.

We made four consecutive vehicle approaches with a 2002 white Ford Ranger pickup truck, starting from a distance of 1.0 km away, during each training day. During each approach, the driver quickly accelerated to the speed (120 or 60 km h^{-1}) corresponding to the group (T120 or T60) placed in the front cage position. The driver maintained that speed until passing beyond the rear cage. The approach vehicle always passed within 2 m of the cage(s). The driver then circled around to the start point (out of view of the birds) and repeated the process until four identical approaches were conducted. The four consecutive approaches generally took about 20 min to

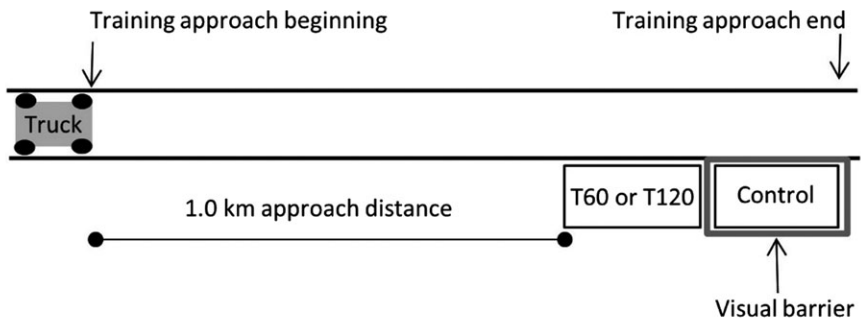

Figure 1 Diagram of vehicle-approach training for three groups of pigeons (T60, T120 and control). Each group was exposed to 32 near-miss vehicle approaches over a 4-week period.

complete. After the four vehicle approaches, the front training cage was re-covered with the visual barrier and all pigeons were transported to their holding cages in the aviary.

Video playback

We quantified avoidance responses from 13 to 16 July 2015 using video playback methodology (D'Eath, 1998). Video playback allowed us to measure FIDs and survival probabilities of the animals without causing physical harm, using direct (head-on) vehicle approaches. Direct vehicle approaches were essential to meet the objectives of our study, because many birds respond more strongly to direct approaches (Møller & Tryjanowski, 2014; Lima *et al.*, 2015), and some neurons eliciting escape behaviors in response to oncoming (looming) objects in pigeons are activated only when objects approach on a collision course (Wang & Frost, 1992). Video playback also allowed us to simulate vehicle speeds faster than those which we could safely achieve using real vehicles. Although we used a different stimulus during training (real vehicle approaches) and measurement of avoidance responses (simulated vehicle approaches), we stress that the only difference across the three groups of pigeons (T120, T60 and control) was exposure to vehicles during training, thus any differences in avoidance responses observed during video playback could be attributed to different levels of experience with passing vehicles.

To generate the videos used during playback, we video-recorded approaches of the same truck used during training with a Sony high definition (HD) Handycam video camera. The video camera was placed on the pavement in the middle of the road and we drove directly over the camera from 1.0 km away while recording at 30 frames per second. These recordings were played back at double speed during our playback experiment (see below) such that birds viewed video images at 60 frames per second. We made recordings of the truck approaching at 60 and 120 km h^{-1}, so that during playback at double speed, the truck appeared to approach at either 120 or 240 km h^{-1}. Truck approaches were recorded on a calm, sunny day (8 July 2015) on the same road section where cages were placed during training and at about the same time of day as when training occurred. As a result, when birds viewed videos of the approaching vehicle during video playback, they observed the same landscape, viewing angle (i.e. from ground level) and truck as they observed during training.

Video playback procedures largely followed DeVault *et al.* (2015). Pigeons were placed individually into an indoor viewing chamber with three walls (61 × 152 cm) and a ceiling (122 × 152 cm) of solid, composite material painted flat gray, a mesh floor (122 × 152 cm) to allow pass through of waste, and a fourth wall consisting of a 61 × 102 × 117 cm backlit, HD Samsung television monitor. A black, mesh screen similar to the holding cage material (62 × 102 cm) was positioned 50 cm from the monitor to separate birds from the monitor and thus reduce the use of non-pictorial depth cues. The top, rear and side walls of the chamber included openings for placement of video cameras used to record behavior. Lighting within the chamber was supplied by the monitor and an overhead compact fluorescent bulb producing a near-continuous light (>1000 Hz).

Upon placing a bird in the viewing chamber, the video was paused with the truck positioned at the start point 1.0 km away for 10 min to allow acclimation to the chamber. We then started the video and the truck approached at a consistent speed until it (virtually) collided with the bird. Thirty birds from each of the three groups were used (90 total trials). Fifteen birds from each of the three groups (50%) were shown videos of the truck approaching at 120 km h^{-1}; the other 15 were shown videos of the truck approaching at 240 km h^{-1}. The faster approach allowed us to test escape responses to vehicles traveling at speeds faster than those for which the pigeons were experienced. Because of difficulties in accurately reproducing sound cues during vehicle approach, all video playbacks were silent and tested responses only to visual cues (see also DeVault *et al.*, 2015). After each video presentation of the oncoming vehicle, the experimental bird was removed from the viewing chamber, returned to a holding cage and a new bird was placed in the viewing chamber. Thus, during video playback, individual birds viewed only a single video of a directly approaching vehicle.

We recorded birds with four video cameras and examined each of the 90 video recordings frame-by-frame. We defined an avoidance (flight) response as an obvious attempt to avoid the vehicle by running or flying toward the walls of the viewing chamber. We recorded the time to the nearest 1/15 s that an individual exhibited an avoidance response relative to the time of virtual collision. We then calculated FID by multiplying the time-to-collision at initiation of the flight response (TTC_{flight}) by the virtual vehicle approach speed (km h^{-1}) and a conversion factor (0.2778) used when FID is expressed in m. When pigeons exhibited no flight response prior to virtual collision, FID was scored as zero.

Estimating collision mortality

Following DeVault *et al.* (2015), we conducted a field experiment to measure the time needed for pigeons to travel 3 m (roughly the width of one lane in a standard road) from a stationary position. This time served as our estimate of the minimum time necessary for pigeons to avoid a collision with an oncoming vehicle.

Fifteen pigeons were captured at a nearby airport on 4 February 2016 in a walk-in trap baited with corn and transferred to our aviary at PBS by truck where they were provided commercial pigeon food and water *ad libitum*. In contrast to the main experiment, we used wild pigeons to measure flight speed because farm-raised birds held in captivity might have less muscle mass and not fly as quickly as wild birds, and also because naïveté to vehicles was not required for this test.

We used five groups of three pigeons each. On 5 February 2016, we released each group into a 2.4 × 3.5 × 8.5 m (height × width × length) outdoor flight cage. A sturdy, wooden sawhorse was placed inside the flight cage 1 m from one end to serve as a perch. A camera and video recorder system (the same as used in the video chamber) was positioned at one side of the flight cage to record the flights of each group. To measure flight distance, we marked the side of the flight cage at 0.5-m intervals. One person was hidden in a blind located approximately 2 m from the end of the flight cage that contained the perch. After an acclimation period of 3 min, another observer located out of sight of the pigeons (monitoring the video feed) signaled to the person hidden in the blind when all three birds were first located together on the perch. The person in the blind then quickly emerged and fired a starter pistol, causing the pigeons to fly in the opposite direction, presumably at top speed. Our intent here was not to mimic conditions associated with vehicle approach and avoidance, but only to estimate the time needed by pigeons to fly a 3-m horizontal distance. We examined the resulting videos and measured the time necessary (to the nearest 1/15 s) for each pigeon to fly 3 m (from the perch to the opposite end of the flight cage), starting at the instant when pigeons began their flights. Four of the five groups of pigeons behaved as expected, immediately flying from the perch and away from the person firing the starter pistol. Pigeons in the last group did not immediately fly and were not used in our analysis; thus, we obtained video footage sufficient to measure flight speed for 12 of the 15 pigeons used in the test. Our estimate for pigeons to fly 3 m was 0.96 ± 0.08 (SD) s.

Analyses

We used a general linear model (IBM Corporation 2014, IBM SPSS Statistics for Windows, Version 23.0; IBM, Armonk, NY, USA) to explore the effects of training group (T120, T60 or control), virtual vehicle approach speed (120 or 240 km h^{-1}) and their interaction on the avoidance response (FID) as measured in the video playback experiment. FID was square-root transformed to meet model assumptions. Post hoc analysis was conducted with LSD tests.

Results

During training, pigeons generally loafed or foraged in the grass through the bottom of the cage and most birds showed no visible reaction to vehicle approach, despite the truck passing within 2 m at 60 or 120 km h^{-1}. However, during the video playback experiment, pigeons attempted to avoid the directly approaching (virtual) vehicle before the point of collision during 83 of the 90 trials (Table 1).

Table 1 Flight initiation distances (m) of pigeons in response to video playback of a directly approaching vehicle

Training group	Virtual vehicle approach speed (km h^{-1})	Mean	SD
Control	120	13.46	10.47
	240	15.27	9.84
T60 (60 km h^{-1})	120	5.88	1.98
	240	10.63	5.70
T120 (120 km h^{-1})	120	6.89	4.67
	240	8.96	9.00

Birds were previously exposed to 32 near-miss vehicle approaches in a field scenario ($n = 15$ individuals for each training group-vehicle approach speed combination).

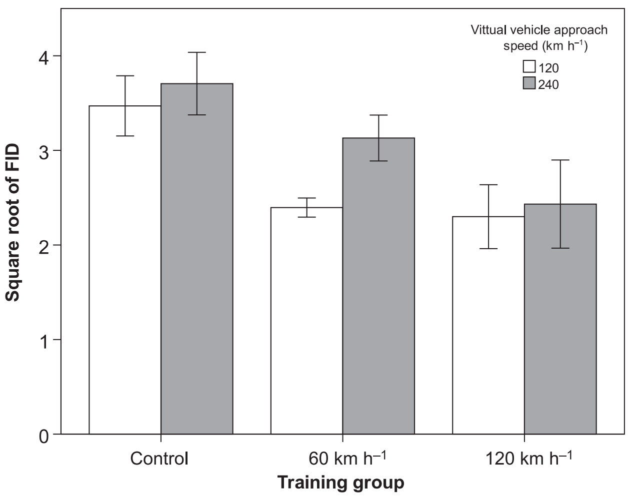

Figure 2 Pigeons that observed 32 near-miss vehicle approaches at 60 or 120 km h^{-1} over a 4-week period exhibited shorter flight initiation distances (FID; square-root transformed) than birds exposed only to the sound of the passing vehicle (control group). FID (m) was measured in response to a directly approaching virtual vehicle in a video playback scenario. Means ± 1 SE are shown.

Our model indicated that virtual vehicle approach speed ($F_{1,84}$ = 1.99, P = 0.162) and the interaction of speed and training group ($F_{2,84}$ = 0.51, P = 0.602) did not influence FID. However, training group influenced FID significantly ($F_{2,84}$ = 7.63, P = 0.001). Contrary to our expectation, the control group (naïve birds) had longer FIDs than birds exposed to vehicles traveling at 60 km h^{-1} (P = 0.011) and 120 km h^{-1} (P < 0.001) during training (Fig. 2). We found no significant difference between the T60 and T120 groups (P = 0.217).

Although naïve individuals exhibited longer FIDs compared to experienced individuals, they were not more likely to survive collision with the virtual vehicle. Only one of the 90 pigeons across training groups had a $TTC_{flight} \geq 0.96$ s, our estimate of the time needed for avoidance. We tried modeling this response with a generalized linear model, but the model did not converge due to the large proportion of virtual collisions (98.9%).

Discussion

Our study used vehicle-naïve birds and a structured training regimen to determine how experience with repeated near-miss vehicle approaches affected avoidance behavior when a collision was imminent with a directly approaching vehicle. As such, our experiment was similar to situations in which birds using airfield or roadside habitats regularly view passing vehicles that usually do not pose an immediate threat. In contrast to inferences from recent empirical findings (Legagneux & Ducatez, 2013), we found that inexperienced birds had longer FIDs in response to direct vehicle approaches than individuals that had repeatedly observed passing, fast-moving vehicles. However, even the heightened avoidance response of inexperienced birds was inadequate to cope with the high vehicle speeds tested, as nearly all birds failed to avoid virtual collision.

Given that birds vary across species with regard to avoidance of approaching threats (Blackwell *et al.*, 2009; Møller *et al.*, 2011; Husby & Husby, 2014), pigeons might adapt antipredator behaviors to vehicle avoidance differently than the suite of bird species studied by Legagneux & Ducatez (2013). In our study, experienced pigeons ostensibly learned that passing vehicles did not pose a threat, as evident by the shorter FIDs exhibited during video playback experiments compared to inexperienced birds. Furthermore, differences in behavior shown by pigeons during training (i.e. no visible reaction to the passing vehicle) and video playback (i.e. avoidance response shown in 92% of trials) may partially reflect their ability to accurately differentiate between tangential and direct approaches (Raderschall *et al.*, 2011), which is acute in pigeons (Wang & Frost, 1992).

The high rate of virtual collision found during video playback might suggest that vehicle noise is used by pigeons (perhaps as an early warning signal) to avoid vehicles, which was absent during video playback in our study. Alternatively, the high vehicle speeds we tested (120 and 240 km h^{-1}) might have overwhelmed the sensory or cognitive mechanisms used by pigeons to avoid oncoming objects, as was found in an earlier study with brown-headed cowbirds (*Molothrus ater*; DeVault *et al.*, 2015). Irrespective of the mechanism, pigeons would have needed to increase their flight speed by a factor of 3.7 (for 120 km h^{-1} vehicle approaches) or 5.7 (for 240 km h^{-1} vehicle approaches) to avoid the oncoming vehicle in our video playback tests based on the mean FIDs we observed. This highlights the challenges of mitigating bird-vehicle collisions, given the evolutionary constraints inherent to the antipredator behavior of some species.

We cannot definitively conclude that some individuals in our study became habituated to vehicle approach because we did not take multiple measurements of escape behaviors for individuals over time (Bejder *et al.*, 2009). However, of the four explanatory mechanisms that could account for evidence of habituation-like responses (learning, displacement, physiology and ecology; Bejder *et al.*, 2009), learning seems the most likely explanation for the increased tolerance (i.e. shorter FIDs) shown by the groups visually exposed to vehicle approaches during training in our controlled experiment, which suggests that habituation was occurring (see also Sztarker & Tomsic, 2011).

Across much of the developed world, birds observe many vehicles each day. These vehicles rarely, if ever, pursue the birds, but instead travel predictably along roads, flight lines and railroad tracks. Our findings suggest that (1) habituation could contribute to many of the mortalities associated with vehicle collisions, and (2) even birds with heightened avoidance responses (i.e. individuals that rarely have been exposed to vehicles) may be vulnerable to collisions with high-speed vehicles that are common worldwide. Future research should investigate the degree to which systems designed to elicit earlier avoidance responses (e.g. aircraft lights) can counteract this effect (Blackwell *et al.*, 2012; Blackwell & Fernández-Juricic, 2013; Doppler *et al.*, 2015).

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