

Can a solitary avian species use collective detection? An assay in semi-natural conditions

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ABSTRACT

Collective detection (e.g., enhanced predator detection through the vigilance of conspecifics) is expected to have evolved particularly in social species. However, we assessed the degree to which an avian territorial species (California towhee *Pipilo crissalis*) would use social cues about predation in a semi-natural assay. We also exposed a social species (house finch *Carpodacus mexicanus*) to similar conditions. California towhees increased scanning rates when foraging with conspecifics, whereas house finches increased scanning rates when foraging solitarily, suggesting that vigilance in these species is regulated mostly through interference competition and through predation risk, respectively. California towhees did not show early detection, and actually the last detector in the group delayed detection in relation to solitary individuals. House finches benefited from early detection, but the second and last detectors maintained detection at the level of solitary individuals. California towhees increased the chances of fleeing when in groups in relation to solitary conditions, but this effect was less pronounced in the last detector. House finches always fled across conditions. Overall, an asocial avian species may use collective detection, but limited to certain types of cues: responses were more pronounced to overt (conspecifics walking or fleeing) rather than subtle (conspecifics becoming alert or crouching) social cues.

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1. Introduction

Joining groups may confer individuals anti-predator benefits (Krause and Ruxton, 2002). Individuals could detect a predator not only through their own vigilance (e.g., personal information), but also through the behavior of group mates that had already detected it (e.g., social information; Davis, 1975; Lima, 1995a). Thus, the detector could cue in a non-detector, which in turn could cue in other non-detectors in a group, eventually leading to a group escape response (Treherne and Foster, 1981). The rule of thumb is that the probability of a non-detector fleeing increases with the number of group mates escaping at any given point in time (Cresswell et al., 2000; Lima, 1995a; Roberts, 1997). This type of response using social information about a predator attack is certainly adaptive in terms of reducing the chances of predator capture. However, similar responses may occur even when individuals are not attacked (Quinn and Cresswell, 2005) leading to false alarms, which may influence the energetic costs of patch exploitation (Siro, 2006, 2007) and

ultimately the mechanisms of social information transfer, such as collective detection (Beauchamp and Ruxton, 2007).

The theoretical roots of collective detection lie in the studies of Pulliam (1973) and Pulliam et al. (1982). They proposed that individuals in groups could benefit from similar or better predator detection than in solitary conditions through the vigilance of group mates, which could lower individual vigilance levels and release time for foraging (Lima, 1994; Roberts, 1996). Most of the empirical studies assessing collective detection have focused on vigilance patterns, and relatively fewer have also measured responses to predator attacks (reviewed in Fairbanks and Dobson, 2007; Roberts, 1996). Of particular importance are empirical studies considering the timing of the responses of both detectors and non-detectors (Devereux et al., 2008), as they can shed light on a key assumption behind collective detection: whether information spreads quickly enough to guarantee that non-detectors escape before the predator is too close (Lazarus, 1979; Lima, 1994, 1995b).

Evidence of enhanced predator detection in groups through collective detection has been found in social species (Cresswell, 1994; van Schaik et al., 1983; Williams et al., 2003). The degree to which collective detection is used has been associated with the sensory modality employed to spread social information (e.g., acoustic, Radford and Ridley, 2007; visual, Davis, 1975) as well as the degree

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of group cohesion (Fairbanks and Dobson, 2007). A recent study, however, showed that predator detection through conspecifics is present in temporary aggregations of a solitary frog species (Martin et al., 2006). This interesting result suggests an early stage in the evolution of collective detection (Martin et al., 2006). The implication is that social cues about predator attacks may be used in species that form either permanent or temporary aggregations. However, the existence of behavioral mechanisms in solitary species to associate these cues with predation risk, and eventually escape, may depend upon the benefits (e.g., reduced predation) and costs (e.g., interference competition) of getting close enough to conspecifics to gather predator-related social information (Krause and Ruxton, 2002).

Our study intended to establish whether a solitary avian species would use social anti-predator cues. We focused on behavioral mechanisms (vigilance and predator detection) used under solitary and social conditions through a semi-natural assay. We also used a social species to determine if these mechanisms would vary when exposed to similar experimental conditions. We took into consideration subtle (group mates becoming alert or crouching) and overt (group mates walking or fleeing) cues. Although the responsiveness to cues may vary on a gradient scale, this binomial classification allowed us to determine some threshold responses in the use of social information about predation.

We predicted that vigilance would be adjusted to the presence of conspecifics. In the territorial species, conspecifics may signal competitive interactions that could actually increase vigilance levels (Beauchamp, 2001). In the social species, scanning effort is expected to decrease in groups in relation to solitary conditions (Elgar, 1989). The territorial species is in principle not expected to use social cues about predator detection to a large degree, as mechanisms to gather and respond to social cues may have evolved in combination with group living (reviewed in Holekamp, 2007), even in birds (Scheid et al., 2007). However, given the finding that an asocial frog species has a rudimentary form of collective detection (Martin et al., 2006); we measured whether our avian territorial species would obtain any information benefit by being in an aggregation based on the type of social cues (subtle or overt) available. On the other hand, we expected that the social species would use social information about predation, which would allow it to enhance individual detection times when in groups.

2. Materials and methods

2.1. Study approach and model species

There are at least two approaches to assess the use of social cues. First, to observe anti-predator behavior under natural conditions (e.g., Martin et al., 2006), which could potentially lead to some interpretation problems due to different confounding factors. Alternatively, vigilance and predator detection could be studied in a semi-natural scenario (e.g., individuals foraging in a outdoor enclosure and exposed to a predator model). We followed the latter approach (see also Fernández-Juricic and Tran, 2007; Morgan and Fernández-Juricic, 2007), acknowledging that conclusions may not be fully generalized to natural situations. Nevertheless, our intention was to uncover behavioral mechanisms (if any) associated with the use of predator-related social cues.

We used a common assay to record anti-predator behavior and control for bird identity, food deprivation, food availability, individual space, etc., while manipulating the factors of interest (see below). We conducted the study on a fenced grassy area at the California State University Long Beach (CSULB) campus during September–October 2007.

Our territorial model species was the California towhee *Pipilo crissalis* (Family Emberizidae, Order Passeriformes), which shows territorial behavior year round, defending areas where foraging and mating take place (Kunzmann et al., 2002). Sometimes California towhees are seen in pairs, family groups, or temporary aggregations. The California towhee (52.85 g, Dunning, 2008) forages mostly on the ground, but has also been observed foraging (<30% of the time) off-the-ground (Kunzmann et al., 2002).

Originally, we captured lark sparrows *Chondestes grammacus*, which belong to the same Emberizidae Family as the California towhee, to be used as the social model species (Martin and Parrish, 2000). However, individuals did not adapt well to our experimental enclosures: they would not forage despite attempts with various design types (indoors, outdoors, mesh wire or Plexiglas enclosures, different food types, etc.). To still assess the anti-predator reactions of a social species in the same experimental conditions, we chose the house finch *Carpodacus mexicanus* (Family Fringillidae, Order Passeriformes) due to (a) its high abundance, (b) the availability of wild-caught individuals from trapping locations close to our study area, and (c) its adaptability to the experimental conditions (e.g., Fernández-Juricic and Tran, 2007). The house finch (21.4 g, Dunning, 2008) can be considered a gregarious species that tolerates conspecifics at close distances (e.g., flocks); although aggressive interactions are generally observed at foraging and roosting sites and during mating (Hill, 1993). Males become territorial during the breeding season but they defend only a female and a relatively small territory (Hill, 1993). Thus, the house finch can be considered mainly a social species that forages on- as well as off-the-ground (Hill, 1993).

We acknowledge that running a study with two species that are not closely related phylogenetically (although they belong to the same Order) could lead to interpretation problems due to the other life-history and ecological factors that could affect the responses observed. But, we simply assessed how each of them used the personal and social cues available in the experimental set-up. Therefore, in our analyses we did not compare statistically for between-species differences, but rather focused on within-species responses.

2.2. Study subjects

We caught and color-ringed 31 adult California towhees (15 males, 16 females) and 24 adult house finches (12 males, 12 females) belonging to different populations in southern California, from Orange, Riverside, and Los Angeles counties. We sexed California towhees by drawing blood and using a molecular technique (Ellegren and Fridolfsson, 1997; Griffiths et al., 1998) because of their monomorphic plumage (Kunzmann et al., 2002). House finches were sexed using plumage characteristics (Hill, 1993). Birds were housed in indoor cages (0.85 m × 0.60 m × 0.55 m), under a 12:12 h light:dark cycle (lights on at 07:00), and were in visual and auditory contact. Water and food (finch mix Royal Feeds, Leach Grain and Milling, Co., Downey, CA) were available *ad libitum* except during experimental trials. Animals were held captive for 2–4 weeks before the beginning of the experiment. Experimental protocols were approved by the Institutional Animal Care and Use Committee at CSULB.

Our experimental set-up consisted of a circular bottomless enclosure completely made of mesh wire (opening 2.4 cm, percentage open area 93%) placed over a wooden tray covered with 3 cm of sawdust (Fig. 1). Because species differed in body mass, we provided different amounts of food in the tray during trials: 3 g of finch mix seeds per each California towhee and 1 g per each house finch used. Seeds were randomly distributed and partly mixed with the substrate but ensuring that some were visible on top of the substrate to encourage foraging. Both species adapted well to the semi-

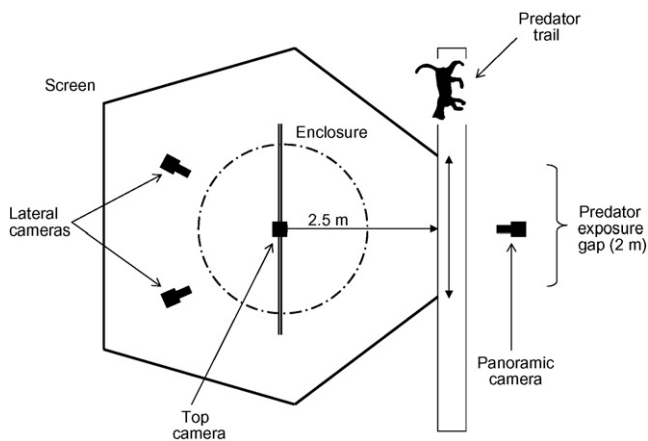


Fig. 1. Schematic representation of the experimental set-up. A stuffed cat on top of a skateboard was moved through a rubber trail and after the exposure was hidden behind the fence.

natural conditions and started foraging right after the beginning of trials.

Each species was subject to three scenarios: (a) solitary foraging, (b) foraging in a group of three birds, and (c) foraging with two blocks (each a 10 cm length \times 6 cm height \times 3 cm width piece of wood). Enclosure size was the same in scenarios (b) and (c). The scenario with the blocks was meant as a control in which individuals shared the same amount of space as in the group foraging condition but with inanimate objects. We recorded only scanning and pecking behaviors from focal individuals when foraging with two blocks. Individuals were exposed to a predator model only in the solitary and group foraging scenarios, which were applied in a random order. We used groups of 3 individuals since previous work has shown that collective detection is more likely in small rather than large groups (Dehn, 1990).

Ten minutes after the focal bird first pecked, we presented a predator model to assess detection and reaction behaviors. The predator model consisted of a natural-sized (63.5 cm nose to tail) black stuffed domestic cat mounted in walking position (Blue Russian Model, Piutrè Animal Collection; Piutrè USA, Ltd) with the head turned towards the experimental subjects. The predator model was set on top of a skateboard, which was moved in front of the experimental enclosures on a rubber trail (6 m long) via a pulley system (Fig. 1). The model was shown to the animals through a 2 m predator exposure gap at a speed of approximately 0.5 m s^{-1} . To increase the contrast between the predator and the background, we used a white cardboard behind the predator exposure gap. We covered the edge of the trail with synthetic grass to screen out the skateboard, which did not produce any noticeable noise to the human ear. We ran some preliminary trials pulling the skateboard without the cat and no obvious bird response was detected. Nevertheless, during the trials, we played white noise to minimize any auditory cues from the predator model (following Quinn et al., 2006). No bird reacted to the cat before it showed up in the predator exposure gap.

Larger species have higher spatial visual resolution than smaller ones due to the differences in eye size (Brooke et al., 1999), which can affect spacing behavior (e.g., species with larger eyes would increase neighbor distances, Kiltie, 2000). Additionally, the individual area that a bird occupies can vary between solitary and social conditions (Keeling, 1995). Therefore, we controlled for enclosure space so that the amount of individual space available would be similar between our solitary and group conditions. We also scaled the size of the enclosures to the size of each species. To establish enclosure size, we conducted a preliminary study with animals

that were not used in the experiment to assess space usage when foraging in an aggregation. The experiment comprised a 2.35 m long \times 0.9 m wide \times 0.5 m height rectangular Plexiglas cage (with one mesh-wired side) with three individual birds at a time for 15 min (3 replicates per species). We recorded the position of individuals with a Sony DCR-TRV38 digital video, and measured neighbor distances with ImageJ (<http://rsbweb.nih.gov/ij/>) every 60 s when the three animals were with their heads up. Based on neighbor distances, we calculated the diameter of the solitary and group enclosures in order to provide a minimum circular area that would allow animals to keep their individual space (calculations available from the authors upon request). We estimated the enclosure diameters as 164 cm for the group and 71 cm for the solitary conditions for California towhees, and 46.6 cm and 28 cm, respectively, for house finches. Enclosure heights were determined as four times the bird height while on the ground, which resulted in enclosures 50 cm high for California towhees and 24 cm high for house finches.

Ten individuals per species were chosen randomly as focal subjects, with an equal number of individuals of each sex. These focal individuals were exposed to all three scenarios randomly, without being used more than once per day. We used the remaining birds as companions in the group condition. We kept a 1:1 sex ratio for companions, irrespective of the focal sex. We measured scanning, foraging, and chasing behavior of the focal birds. We measured predator detection and reaction behaviors of focal and conspecific birds. We ran 60 trials (10 trials per each of the three scenarios per two species). We ran three to six trials per day between 08:00 and 13:00, excluding rainy or windy days. Focals were food deprived for 65–310 min (California towhees) and 55–310 min (house finches). Food deprivation times did not influence significantly our results: California towhee (scanning rate: $F_{1,25} = 1.37, P = 0.253$; pecking rate: $F_{1,25} = 0.34, P = 0.565$; detection time: $F_{1,14} = 2.30, P = 0.151$) and house finch (scanning rate: $F_{1,25} = 2.81, P = 0.105$; pecking rate: $F_{1,25} = 0.56, P = 0.454$; detection time: $F_{1,15} = 1.03, P = 0.327$). Body condition can influence foraging and scanning behaviors (Fernández-Juricic and Tran, 2007); so, we also recorded body mass (house finch: 16.92–22.1 g; California towhee: 36.91–47.45 g), and wing length (house finch: 79.5–89 mm; California towhee: 72.0–82.0 mm) of each individual used in the experiment. We calculated body condition as body mass/wing length.

2.3. Behavioral observations

Birds were transported from the animal-care facility to the study site in soft cloth bags and released into the enclosure through a gated opening at the side. We recorded their behavior with four PelikanCam color bullet cameras (TC855) connected to a Digital Quad Splitter (Clover Electronics, U.S.A.), which allowed for the simultaneous recording of all cameras onto a single frame. Two cameras were located on one side of the enclosure (40 cm above the ground and 2 m of separation between them; Fig. 1) to have coverage of the predator exposure gap as well as all the birds at any given point in time. A third camera was positioned (1.50 m height) just in front of the predator exposure gap to obtain a panoramic view of the entire enclosure (Fig. 1). A fourth camera was located 3 m above the centre of the enclosure yielding a top view of the enclosure (Fig. 1).

Foraging and scanning behaviors were scored on the focal birds using an event recording program, JWatcher 1.0 (Blumstein et al., 2006). We recorded the behavior only while birds were on the ground and excluded sequences when birds hung from the enclosure wall. There were no significant differences between species in the time spent on the ground (California towhee, 0.992 ± 0.004 ; house finch, 0.964 ± 0.018 ; $F_{1,36} = 2.07, P = 0.159$). While the animals

were head-up, we recorded the number and duration of scanning events and aggressive interactions (e.g., fights, displacements, etc.). Head-up scanning events included food-handling, as visual monitoring is possible in seed eaters (Beauchamp and Livoreil, 1997). When animals were head-down, we recorded the number of pecking events. With this information, we calculated the rate (events per min) of scanning, pecking, and chasing events, and also the average scan bout duration (s). Results from the proportion of time spent scanning were similar to those of scan bout duration, so we present only the latter.

When animals were foraging solitary and with conspecifics, we measured detection and response times (in frames) of the focal and companion birds. We assessed changes in the alert and reaction behaviors of each species, and classified them according to the following postures that diverged from the regular foraging and scanning motor patterns: casual alert (when an individual turned motionless), upright alert (when an individual raised its head, stretched its neck, and increased the speed of head movements), crouch (when an individual ducked down without moving from the spot it was occupying), walk (when an individual moved from its initial position by walking or hopping), and flush (when an individual moved from its initial position by jumping/flying away). A “no response” event was considered when an individual did not stop its ongoing foraging and regular scanning behavior during and after the cat went by.

We considered arbitrarily that the difference between detection and reaction was based on the movement of an individual from the position it occupied a frame before the cat was exposed. Under this classification scheme, *detection* occurred when an individual showed a *subtle* response and did not move from the detection spot (casual alert, upright alert, crouch), whereas *reaction* took place when the individual showed an *overt* response and moved away from the detection spot (walk, flush). The main reason behind this criterion was that in both species all individuals that detected the predator showed some of the three subtle behaviors used as proxies of detection before showing any of the two overt behaviors used as proxies of reaction (walking away, flushing). Furthermore, we assumed that overt cues may be easier to detect by individuals than subtle cues due to their greater degree of body motion.

It is important to clarify that detection can occur when individuals detect the predator themselves or through changes in body postures of group mates. In this study, we could not distinguish between these two sources of information, which would have required establishing the target of visual attention of each individual. Therefore, we made some assumptions regarding the cues measured (see above) and the order of the responses. We only included in the analysis data in which all three individuals in the group condition showed any of the three subtle detection behaviors *before* they showed any of the two reaction behaviors. Therefore, we met the assumption that the social cues used in the *detection* phase by the 2nd and 3rd individuals in the group did not include any overt movement behavior from the 1st individual detecting the predator, which could have enhanced detection responses.

Using Ulead VideoStudio 9, we measured detection time from the frame in which the nose of the cat became visible to the frame prior to the first of the three subtle detection responses (casual alert, upright alert, crouch). We assumed that the detection of the predator occurred immediately before the animal exhibited an alarm response (Fernández-Juricic and Tran, 2007). Likewise, we measured reaction time from the frame in which the nose of the cat became visible to the frame the individual exhibited the first overt reaction behavior (walk, flush). We did not detect the use of vocal cues during the exposure to the predator in the trials included in this study.

2.4. Statistical analysis

We used general linear models to analyze within-species responses (scan rate, scan bout duration, pecking rate, detection time) to different treatments (solitary foraging, foraging with conspecifics, foraging with blocks). To control statistically for within-individual variability, we added to models a random factor reflecting the identity of the focal bird, and body condition. Body condition could give some indication of the levels of energetic reserves that affect sensitivity to a threat (Beale and Monaghan, 2004). Differences between levels were analyzed with planned comparisons.

We used a χ^2 test to assess differences in the frequency of different subtle detection behaviors (casual alert, upright alert, crouch). We also conducted pair-wise *t*-tests to assess how detection times varied among the solitary individual and the 1st, 2nd, and 3rd individuals detecting in the group. We were interested in two sets of comparisons: (a) between the solitary and each of the individuals in the group to establish if early or delayed detection occurred in relation to individuals foraging alone, and (b) between each pair of individuals within the group to determine how information about the predator spread through the group. These comparisons are important because previous studies have found that sometimes the benefits of collective detection are restricted to some individuals in the flock (usually detectors) as information may not spread quickly enough (Hilton et al., 1999). The order in which individuals (focal or conspecifics) detected the predator varied from trial to trial; thus, we used *t*-tests for dependent samples because the levels compared (solitary individual, 1st, 2nd, and 3rd individuals detecting in the group) were dependent on one another within a given trial. We also ran these comparisons with a general mixed linear model, with bird identity included as a random factor, and obtained similar results (available upon request).

We assessed the probabilities of individuals reacting to the predator (walking, flushing) in relation to social condition upon detection (solitary individual, 1st individual in the group, 2nd individual in the group, and 3rd individual in the group) with a generalized linear model, which included bird identity as an independent factor. The dependent variable was modeled with a binomial distribution. Mean probabilities of reaction under different social conditions were calculated with Statistica 8.0. We did not analyze reaction times because not all California towhees reacted in certain conditions (2nd and 3rd individuals detecting in the group), limiting the sample size substantially.

Some variables were log-transformed to meet normality and homogeneity of variance assumptions. Sample sizes varied in the different analyses depending on the number of individuals that responded (using subtle or overt cues) or not.

3. Results

Considering all conditions, California towhees scanned 12.60 ± 0.85 times per min, with averaged scan bout durations of 4.40 ± 0.55 s, and pecked 7.57 ± 1.02 times per min. Considering the treatment in which focals foraged with conspecifics, California towhees engaged in 1.58 ± 0.68 chases per min.

Considering all conditions, house finches scanned 17.41 ± 1.21 times per min, with averaged scan bout duration of 2.48 ± 0.46 s, and pecked 14.51 ± 1.83 times per min. Considering the treatment with only conspecifics, house finches engaged in 0.31 ± 0.11 chases per min.

Scan rates showed an almost significant difference among treatments in California towhees ($F_{2,17} = 2.96$, $P = 0.078$). When foraging with conspecifics, scan rates were higher than when foraging with blocks ($F_{1,17} = 4.84$, $P = 0.043$), and almost significant than when foraging solitary ($F_{1,17} = 3.69$, $P = 0.071$), without a signifi-

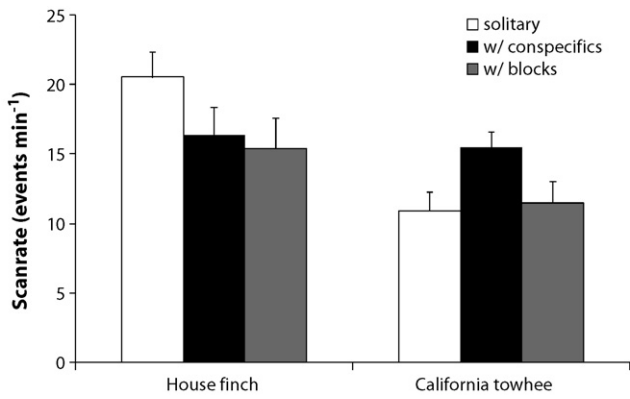


Fig. 2. Scan rates of house finches (social species) and California towhees (solitary species) under three conditions: foraging solitary, foraging with two conspecifics, and foraging with two wooded blocks.

cant difference between the latter two ($F_{1,17} = 0.11$, $P = 0.744$; Fig. 2). Body condition did not significantly affect scan rates ($F_{1,17} = 0.271$, $P = 0.609$). We did not find significant differences between individuals ($F_{9,17} = 1.37$, $P = 0.274$).

Scan rates varied significantly among treatments in house finches ($F_{2,17} = 6.17$, $P = 0.009$). House finch scan rates when foraging solitary were higher than when foraging with conspecifics ($F_{1,17} = 11.58$, $P = 0.003$) or blocks ($F_{1,17} = 6.24$, $P = 0.023$), without significant difference between the latter two ($F_{1,17} = 0.83$, $P = 0.376$; Fig. 2). Body condition did not significantly influence scan rates ($F_{1,17} = 1.66$, $P = 0.215$). We found an almost significant difference between individuals ($F_{9,17} = 2.31$, $P = 0.065$).

Scan bout duration (California towhee, $F_{2,17} = 2.17$, $P = 0.144$; house finch, $F_{2,17} = 0.71$, $P = 0.502$) did not vary significantly among treatments in either species: focals in solitary conditions (California towhee, 5.62 ± 1.27 ; house finch, 2.35 ± 0.30), with blocks (California towhee, 4.60 ± 1.10 ; house finch, 2.82 ± 0.57), and with conspecifics (California towhee, 2.97 ± 0.31 ; house finch, 2.26 ± 0.25). All other effects were not significant ($P > 0.05$).

Similarly, pecking rate did not change significantly among treatments in either species (California towhee, $F_{2,17} = 0.83$, $P = 0.452$; house finch, $F_{2,17} = 2.09$, $P = 0.153$); focals in solitary conditions (California towhee, 9.78 ± 2.22 ; house finch, 19.36 ± 2.61), with blocks (California towhee, 8.54 ± 1.49 ; house finch, 13.44 ± 3.81), and with conspecifics (California towhee, 10.72 ± 1.56 ; house finch, 18.74 ± 1.68). We found significant differences in individual pecking rates in both species (California towhee, $F_{9,17} = 2.61$, $P = 0.042$; house finch, $F_{9,17} = 3.03$, $P = 0.023$). All other effects were not significant ($P > 0.05$).

Detection behaviors were classified into three categories, which were considered as subtle cues (see Section 2): casual alert, upright alert, and crouch. Taking into account all focals and companions, we found differences in the type of detection responses within-species. California towhees used the casual alert (21) more frequently than the upright alert (13) or crouching (5) ($\chi^2_2 = 9.84$, $P = 0.007$). House finches used the upright alert (28) more frequently than the casual alert (8) or crouching (4) ($\chi^2_2 = 24.8$, $P < 0.001$). Sample sizes were not large enough to run χ^2 tests in the solitary and group conditions separately, but the trends were similar to the patterns reported for each species.

Taking into account only the focal individuals, detection time did not vary between solitary and group conditions in neither the California towhee ($F_{1,7} = 1.28$, $P = 0.295$) nor the house finch ($F_{1,7} = 0.65$, $P = 0.454$). We did not find any significant effect of body condition (California towhee, $F_{1,7} = 1.02$, $P = 0.345$; house finch, $F_{1,7} = 0.04$, $P = 0.837$) or individual variation (California towhee, $F_{9,7} = 0.97$, $P = 0.529$; house finch, $F_{9,7} = 0.778$, $P = 0.646$) on detection times.

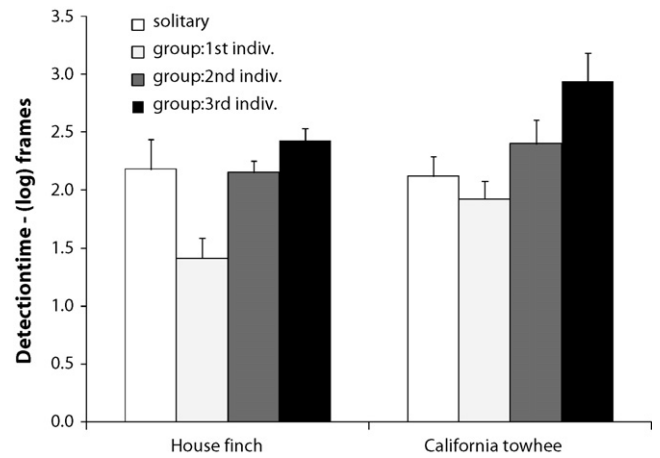


Fig. 3. House finch and California towhee predator detection times (in frames) under solitary and group conditions. Within the group condition, detection times of the 1st, 2nd, and 3rd individuals showing detection behaviors are shown.

However, the order in which focals showed detection while in groups varied from trial to trial. Therefore, we assessed differences in detection times between solitary conditions and the order in which the different individuals detected in the group. The expectation is that the detection time of the 1st individual would be shorter in groups than in solitary conditions as more individuals would be scanning.

California towhee detection times of the solitary individual did not differ significantly from that of the 1st ($t_9 = 0.76$, $P = 0.465$) and 2nd ($t_9 = 1.02$, $P = 0.339$) individuals detecting in the group (Fig. 3). However, detection times of the solitary individual were significantly quicker than those of the 3rd individual detecting in the group ($t_8 = 2.99$, $P = 0.017$; Fig. 3). Within California towhee groups, we found significant increases in detection times from the 1st to the 2nd ($t_9 = 2.86$, $P = 0.019$), from the 1st to the 3rd ($t_8 = 4.19$, $P = 0.003$), and from the 2nd to the 3rd ($t_9 = 3.01$, $P = 0.017$) individuals detecting in the group (Fig. 3).

House finch detection times of the 1st individual detecting in the group were significantly quicker than those of the solitary individual ($t_9 = 5.67$, $P < 0.001$; Fig. 3), which suggests enhanced detection

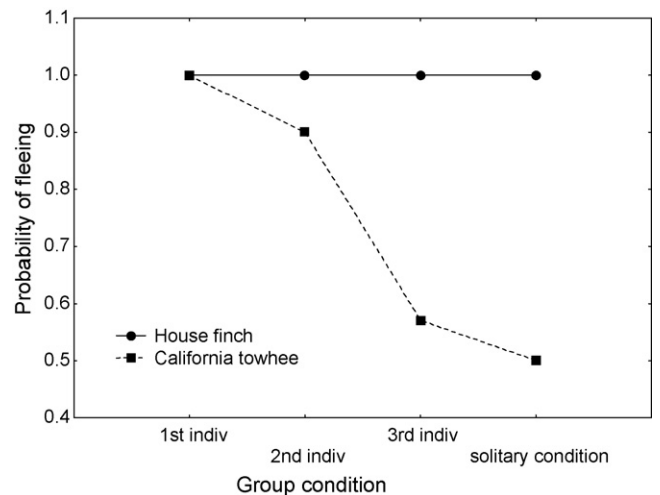


Fig. 4. Probabilities of fleeing (either flying or walking) of house finches and California towhees once the predator was detected under solitary and group conditions. Within the group condition, probabilities of fleeing of the 1st, 2nd, and 3rd individuals that had detected the predator are shown. Mean probabilities of fleeing were calculated with Statistica 8.0.

through collective detection. However, there were no significant differences between the solitary individual and the 2nd ($t_9 = 0.69$, $P = 0.507$) and 3rd ($t_9 = 0.87$, $P = 0.406$) individuals detecting in the group (Fig. 3). Within house finch groups, we found significant increases in detection times from the 1st to the 2nd ($t_9 = 3.30$, $P = 0.009$), from the 1st to the 3rd ($t_9 = 5.92$, $P < 0.001$), and from the 2nd to the 3rd ($t_9 = 4.56$, $P = 0.001$) individuals detecting in the group (Fig. 3).

The probabilities of California towhees fleeing (walking or flying away) after detection were significantly higher in the group (0.90 ± 0.10) than in the solitary (0.50 ± 0.17) conditions ($\chi^2_1 = 4.18$, $P = 0.041$). Considering the order of detection in California towhees, we found significant differences among individuals: higher probabilities of fleeing in the 1st and 2nd individuals detecting in the group in relation to the solitary individual ($\chi^2_3 = 11.56$, $P = 0.009$; Fig. 4). However, in the house finch the probabilities of fleeing (walking or flying away) after detection were 100% in both solitary and group conditions (Fig. 4). We did not detect significant variations in individual behavior ($P > 0.05$).

4. Discussion

Our results show that a territorial avian species can use social cues about predation when in aggregations, but it appears responsive to overt cues (e.g., conspecifics walking away or flushing) to a greater degree than to subtle cues (e.g., conspecifics becoming alert or crouching). California towhees increased the chances of fleeing after detection, but detection was actually delayed in some individuals within the group. Thus, collective detection in this territorial species seems possible with certain types of cues.

Both species reacted to the predator exposure, but in different ways. We cannot attribute the differences directly to their social organization because they are not closely related phylogenetically. Nevertheless, both studied species adapted well to our assay, we incorporated control treatments that allowed us to test for differences in the use of information *within*-species, and we used a stimulus (approaching predator) that is relevant to these species as they show anti-predator behavior in natural conditions (Fernández-Juricic et al., 2006). Although some of the observed strategies are consistent with those of territorial and social species (e.g., Cresswell, 1997; Lima et al., 1999), we discuss these behaviors within the ecology of each species.

California towhees tended to increase their scanning rate in the presence of conspecifics in relation to solitary conditions. Higher vigilance levels in this territorial species may have been directed towards neighbors, rather than a potential predator, as they can be sources of aggressive interactions. For instance, this species has been shown to engage in shadow-boxing when presented with reflecting images (Ritter and Benson, 1934). California towhees actually took part in chases in our study. However, their vigilance was not affected by the presence of the blocks, contrary to the house finch response. This finding may be related to the proportionally larger size of towhees in relation to the blocks (2:1 ratio), resulting in no net obstructive or protective cover effect. Thus, we suggest that California towhee vigilance behavior in aggregations may be influenced by interference competition.

House finches decreased their scanning rate when foraging in groups in relation to solitary conditions. This group size effect has been described before in many species (reviewed in Beauchamp, 1998; Elgar, 1989), and associated generally with dilution of risk, collective detection, or scramble competition (reviewed in Beauchamp, 2003; Krause and Ruxton, 2002). We provided sufficient food to avoid depletion effects; thus, we believe that the potential role of scramble competition in our system may have been minor. In addition, there was no difference in scan rate

when house finches foraged with conspecifics and with blocks, probably because blocks were perceived as protective cover due to their size or because individuals perched on top of them to increase visibility, thereby reducing perceived risk. Overall, house finch vigilance behavior in groups appears to be influenced by predation risk.

In both species, information did not spread instantaneously within groups (e.g., Hilton et al., 1999), as there was an increasing delay in detection from the 1st to the 2nd and 3rd individuals detecting in the group. A central comparison is between the 1st individual detecting in the group and the solitary conditions. California towhees did not benefit from early detection, as detection times of the 1st and 2nd detectors did not differ from those of the solitary individual. However, keeping detection times at the same level as those of individuals foraging solitarily is compatible with collective detection (Roberts, 1996). Yet, the 3rd detectors incurred a potential cost as they delayed their response in relation to solitary conditions, leading to potentially higher risks of predation. This delay is not predicted by collective detection, and it may have been caused by the 3rd detector being distracted by conspecifics or monitoring its surroundings for a predator and then responding rather than leaving immediately after observing the other detectors. Alternatively, detection delays may have been influenced by the large size of the California towhee enclosures leading to a distance effect, although the greater acuity of this species (Kiltie, 2000) in relation to the house finch should compensate for this effect. The overall implication is that temporal aggregations of California towhees could increase the chances of successful predator attacks as a result of lower time investment into predator-related vigilance (e.g., red-tailed hawks and Cooper's hawks are known predators of this species, Kunzmann et al., 2002).

House finches have been shown to use social cues about predation (Fernández-Juricic and Tran, 2007; Roth et al., 2008). In our study, individuals that first detected the predator shortened detection times in relation to solitary individuals (see also Hilton et al., 1999; Lima and Zollner, 1996), which leads to early detection. Nevertheless, 2nd and 3rd detectors in the group maintained similar detection times to those of solitary individuals, which is supported by collective detection effects (Roberts, 1996) because in the worst case scenario the 2nd and 3rd detectors can detect the predator by themselves or use information from the 1st detector. Additionally, the 2nd and 3rd detectors may have obtained other anti-predator benefits of being in a group, such as risk dilution. Overall, our findings show that group foraging benefited house finches by early detection, collective detection, and a reduction in vigilance effort.

Both species were sensitive to social information about predators that involved overt responses from conspecifics either walking or flushing. House finches always fled across all conditions. California towhees increased the chances of fleeing after detection in group in relation to solitary conditions. This result runs counter previous studies that showed that individuals actually increase the delay between detection and reaction in some species Boland (2003), Fernández-Juricic et al. (2002). We analyzed only those samples in which reaction took place after all individuals detected the predator (e.g., the 1st individual showing an overt response occurred after all three group mates showed subtle responses). Consequently, we suggest that overt conspecific responses heighten the risk perception of California towhees while in aggregations.

Interestingly, California towhees varied reaction probabilities within groups, with 3rd detectors being less likely to walk or flush than 1st and 2nd detectors. One possibility is that the perception of predation risk of the 3rd detectors may be confounded with social cues that reinforced territory membership over a dispute; particularly if fleeing is a visual cue associated with both territorial and

anti-predator contexts. Alternatively, 3rd detectors may reduce the chances of reacting right after the two conspecifics fled in order to decrease the risk of making themselves more noticeable to the predator (Bednekoff and Lima, 1998).

The fact that a mainly solitary species may use some forms of collective detection raises some interesting implications. Fairbanks and Dobson (2007) predicted that individuals that defend territories and rely on acoustic alarm signals would benefit from collective detection. However, our study shows that a territorial species can also use visual social cues about predation. Martin et al. (2006) suggested that a solitary species relying on some rudimentary form of collective detection may indicate a step towards more complex mechanisms of social information transfer. We generally agree with this view, but speculate that a territorial species may gather social cues but process them in a different way. In a social species, a subtle behavioral response to a predator may potentially signal danger to conspecifics. In a solitary species, the same response could also signal the outcome of a territorial dispute, which could lead to delays in detection and reaction, and become a cost to aggregating. Therefore, it would be interesting to assess how visual attention towards conspecifics varies between territorial and social species (Scheid et al., 2007) under the context of predator detection. Our experimental assay in semi-natural conditions offers an opportunity to study the mechanisms involved in between-individual interactions across species (Jackson and Ruxton, 2006). Future studies can use this approach to assess variations in collective detection across several species that are more closely related to establish changes in the strength of this mechanism, but controlling for phylogenetic noise (Lefebvre, 1996).

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