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THE ROYAL SOCIETY
PUBLISHING

Sensory integration of danger and safety cues may explain the fear of a quiet coyote

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Sensory integration theory predicts natural selection should favour adaptive responses of animals to multiple forms of information, yet empirical tests of this prediction are rare, particularly in free-living mammals. Studying indirect predator cues offers a salient opportunity to inquire about multi-modal risk assessment and its potentially interactive effects on prey responses. Here we exposed California ground squirrels from two study sites (that differ in human and domestic dog activity) to acoustic and/or olfactory predator cues to reveal divergent patterns of signal dominance. Olfactory information most strongly predicted space use within the testing arena. That is, individuals, especially those at the human-impacted site, avoided coyote urine, a danger cue that may communicate the proximity of a coyote. By contrast, subjects allocated less time to risk-sensitive behaviours when exposed to acoustic cues. Specifically, although individuals were consistent in their behavioural responses across trials, 'quiet coyotes' (urine without calls) significantly increased the behavioural reactivity of prey, likely because coyotes rarely vocalize when hunting. More broadly, our findings highlight the need to consider the evolution of integrated fear responses and contribute to an emerging understanding of how animals integrate multiple forms of information to trade off between danger and safety cues in a changing world.

1. Introduction

Evolutionary biologists have long recognized that many animals produce, perceive and respond to multiple forms of information from their environment [1,2]. In many cases, information includes multiple sensory modalities with visual, tactile, acoustic and/or chemical components [3,4]. Sexually selected traits, for example, are widely recognized for combining visual, chemical and/or acoustic signals to attract mates [5]. Indeed, multimodal courtship displays are commonly produced and assessed for their quality by animals from beetles [6] to birds and frogs [7,8]. Moreover, prey from invertebrates [9,10] to birds [11] and mammals [12] also combine two or more signal components to deceive predators. Yet, it is striking that very few—if any—field studies have inquired about whether free-living mammalian prey integrate multiple forms of sensory information when responding to predation risk. Empirical tests examining how prey integrate multiple predator cues in ecological contexts are clearly warranted [13,14].

Theoretically, natural selection should favour the ability for prey animals to optimize decisions under the risk of predation [15,16]. Although individuals are expected to discriminate among various risky options based on multimodal information [17–19], we know comparatively little about vertebrate prey responses to non-redundant predator cues [3,14]. Non-redundant signals outside of the predator–prey context should theoretically mediate one of several different

responses. They may (i) independently trigger two or more distinct responses (e.g. spiders respond differently to acoustic versus chemical mating signals [20]), (ii) modulate each other (e.g. tadpoles beg the most when exposed to visual, chemical and tactile cues together [21]), (iii) combine to produce an entirely new response (e.g. domestic chicks were only strongly averse to yellow/red foods when paired with pyrazine; pyrazine is not inherently aversive [22]), or (iv) override each other via signal dominance (e.g. dogs signal play rather than aggression by combining a visual bow with growling [23]). A few studies have also documented the integration of conflicting or complementary predator cues used by prey to assess predation risk [24]; these reveal signal dominance (e.g. visual cues dominant to acoustic cues [25]) and enhancement (e.g. acoustic and visual cues combine to promote stronger responses [26]). Moreover, in a rapidly changing world, there is growing interest in understanding the extent to which human presence alters risk perception by wildlife, particularly by small mammalian prey [27–31].

Here we applied a psychophysics approach as part of a multi-year field experiment to gain insights into the cognitive integration of indirect cues from predators by mammalian prey [13,32,33]. We focused on the free-living California ground squirrel (Otospermophilus beecheyi), an endemic in California grasslands that is a major prey species for northern Pacific rattlesnakes (Crotalus oreganus), birds of prey and coyotes (Canis latrans) [34]. California ground squirrels represent a textbook example of a species that produces a suite of multimodal, anti-predator signals—alarm calls (acoustic), tail-flagging (visual) and infrared heat (electromagnetic) [35–39]. They also respond to conspecific alarm calls [40–42]. Although there is some evidence from separate studies that the intensity of threat responses varies between rattlesnake cues [43,44], we lack an understanding of whether ground squirrels integrate multiple, non-redundant indirect cues. Moreover, information on ground squirrel responses to coyote cues is generally lacking.

Environmental constraints should theoretically influence the degree to which different sensory modalities (e.g. acoustic versus olfactory) influence risk-sensitive behaviours in nature [45]. Coyotes, for example, produce several major cues that may separately, or together, inform risk-sensitive decisions by ground squirrels. This information may or may not be redundant, depending upon its meaning to receivers. First, as the most vocal mammal in North America, coyotes use calls to communicate their motivational state to conspecifics [46] and coordinate group activities (e.g. hunting of large prey [47], territory defence [46]). Because coyotes rarely vocalize when stalking rodent prey [48], ground squirrels may perceive calls as safety cues (i.e. squirrels are not being actively stalked as prey) [49]. Conversely, any predator cue may communicate danger and thereby induce threat-sensitive responses; indeed, marmots [50] and skunks [51] exhibit heightened responses to coyote vocalizations despite only being hunted when coyotes are quiet. Second, coyotes regularly deposit urine on the landscape to advertise their presence to conspecifics [52,53], but this chemical information is also available to prey and can persist after a coyote has left an area [54–56]. Because rodents are exquisitely sensitive to predator urine from a young age [57–59], coyote urine may induce investigation followed by avoidance (across the lifespan). However, indirect predator cues (e.g. olfactory or acoustic cues conveying predator presence without visual confirmation) may also be particularly challenging because they require prey to infer risk in the absence of observing a predator [60]. Finally, human presence may increase [61] or decrease [62] the perceived risk of predation. Our major goal is therefore to assess the responses of ground squirrels to indirect cues from two study sites that differ in human and domestic dog (Canis lupus familiaris) activity. Studying coyote calls in combination with urine (in the absence of visual cues) offers a salient opportunity to inquire about multimodal risk assessment of indirect predator cues and their potentially interactive effects on prey responses between landscapes that vary in human presence.

In this study, we examined the effects of non-redundant, indirect predator cues on space use (in a testing arena) and behavioural reactivity (e.g. vigilance, fleeing, investigating). We presented ground squirrel subjects with stimuli from one or two sensory modalities: chemical and/or acoustic. Studies have focused on each cue in isolation, but few have considered their relative effects in nature or these effects in the context of human presence. First, we examined whether squirrels integrate indirect predator cues (i.e. whether subjects' responses reflect the integration of non-redundant information). Second, we investigated the extent to which individuals experiencing divergent levels of human and dog activity differed in their responses to the predator cues. At our disturbed site, domestic dogs directly kill, chase and disturb squirrels whereas dogs rarely visit the relatively pristine site [63] (see Methods for details). Because mammalian prey often respond similarly to odours from domestic dogs and wild canids [64,65], we expected squirrels at the disturbed site to be more reactive to coyote cues than those residing at the pristine site (i.e. human, dog and predator cues combine to trigger heightened risk sensitivity) [66,67]. Repeated exposure to canid urine (i.e. urine produced by domestic dogs) could also promote habituation [68], thus reducing responses to coyote urine at the disturbed site. Third, we investigated the effects of age class and sex on the behavioural responses to various stimuli. Because many animals, including California ground squirrels [69,70], learn to mount appropriate anti-predator responses across ontogeny [71–73], we predicted adults would be more reactive to predator cues than juveniles. We also expected negligible sex differences because the study was conducted outside of the breeding season. Although lactating mothers are most reactive to predation risk [74] and males tend to flee earlier than females when approached by humans [75], both sexes are equally vigilant at our study sites during the summer months [69]. Finally, we also asked if individual responses were consistent (repeatable) across tests [76].

2. Methods

(a) Field site and study populations

This field experiment was part of a long-term study of free-living California ground squirrels at Briones Regional Park in Contra Costa County, CA, USA (latitude: 37.93 north, longitude: 122.13 west, elevation: 319 m.a.m.s.l. [69]). Since 2013, we have monitored marked individuals at two distinct locations. The study sites are roughly 9500 m² each and vary in their degree of disturbances by human foot traffic and domestic dogs as well as the level of vegetation management [69,77]. Animals at the disturbed site are generally less reactive to humans, have higher glucocorticoid levels, and are in poorer body condition than
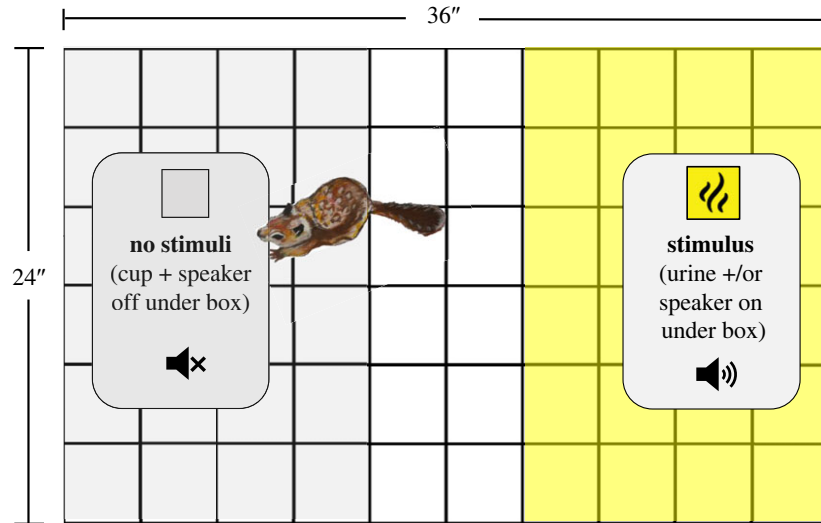
Figure 1. Behavioural testing arena for assessing integrated fear responses of California ground squirrels in field conditions. For each test, we presented a choice of two options: no stimulus (speaker off and empty cup, designated by grey shading) versus stimulus side (yellow) of either coyote cue(s) (urine ± calls) or the control (crow call + ammonia). Grey and yellow shading is only to visualize the set-up; the apparatus floor was simply white with black lines.

those residing at the relatively pristine site [69,77]. Moreover, ground squirrels at our study sites have consistent individual differences in behaviour across time and contexts [36,63,75,78].

(b) Live-trapping of free-living squirrels

We live-trapped and released ground squirrels using Tomahawk Live-Traps (Hazlehurst, WI, USA) from late May through July of each summer, the period over which juveniles and adults are most active aboveground [78,79]. We covered traps with cardboard for shade and checked at intervals of less than 30 min. Upon first capture and using a cone-shaped handling bag [80], we marked each individual with a Monel metal ear tag (National Band and Tag Co., Newport, KY, USA), fur mark (Nyanzol cattle dye, Greenville Colorants, NJ, USA) and passive integrated transponder tag (Biomark, Inc., Boise, ID, USA). Juveniles were weaned young of the year (60–365 days of age) and adults were older than 365 days [81]; age categories were assigned with high accuracy [78].

(c) Field experiments

We used a mobile testing arena modelled after that designed for the yellow-bellied marmot (*Marmota flaviventris*), a large free-living ground squirrel (figure 1; for details, see [82,83]). Briefly, our testing arena was a Midwest Life Stages Folding Metal Dog Crate (92 cm × 62 cm × 69 cm), reinforced internally with 0.15 cm thick white Poly Wall; this limited disturbance by external stimuli while allowing for sufficient ambient sunlight into the arena. We ran behavioural assays on subjects between 8.00 and 16.00 in shady areas hidden from human activity to avoid direct sunlight (heat stress) and reduce anthropic noise during the trials.

Over two summers, each individual received up to four of the conditions (predator odour, predator sound, predator odour + sound, control; tables 1 and 2); some individuals were available for fewer than four trials because of mortality, dispersal, or low trappability. Each 10 min trial was recorded from the top of the arena with a GoPro Hero 3. We used a grid pattern on the floor of the apparatus to aid in quantifying space use (figure 1). We placed two small plastic boxes (25 cm × 15 cm × 13 cm, figure 1, each with 25 different 2 cm × 2 cm holes along the side to promote airflow) on either side of the testing arena. Each stimulus was hidden under one of the boxes within a single trial to offer a choice: stimulus (predator or control) on

Table 1. Experimental treatments for examining sensory integration.

mode	treatment	modalities	stimuli
multimodal	predator	auditory, olfactory	coyote call, coyote urine
	control	auditory, olfactory	crow call, ammonia
unimodal	predator	olfactory	coyote urine
	predator	auditory	coyote call

Table 2. Principal components analysis results for ethogram.

coefficients	PC1	PC2
resting	−0.97	0.20
stimulus investigation	0.80	0.37
walking	0.74	−0.63
fleeing	0.64	−0.64
non-stimulus investigation	0.57	0.59
looking (vigilance)	0.48	−0.27
eigenvalues	3.22	1.03
s.d.	1.80	1.02
proportion of variance	0.54	0.17

one side of the testing arena versus no stimulus on the other side of the testing arena. We randomized the side of the box containing the stimulus to avoid potential spatial confounds and thoroughly wiped down the testing arena with a 70% vinegar solution between trials to prevent the accumulation of odours. Subjects were live-captured, tested and released at the site of capture across multiple days. Individuals were tested no more than once each day, never on their first day of capture, and, in some cases, in two different summers until receiving up to four treatments. We randomized treatment order for subjects. No subject received the same treatment more than once.

Olfactory and/or auditory cues were hidden under the plastic box inside the arena (figure 1). The predator odour treatment consisted of a cotton ball saturated with coyote urine (PredatorPee Brand Product from Maine Outdoor Solutions, LLC) in a small plastic cup. Audio recordings of coyote (e.g. growls, yips and barking) and control calls were played at approximately 60 or more decibels (dB) 50 cm from the centre of the testing arena and for the duration of predator auditory tests from a DG530 Portable Mini Super Bass Portable Wireless Bluetooth Speaker FM.

We used Decibel X, a noise meter app to measure sound pressure level (SPL) in dB(A) at a distance of 50 cm from the speaker (i.e. the distance of a subject in the middle of the testing arena to the speaker) with the reference quantity of 20 µP. Because an external calibrated sound meter was unavailable as a reference, we relied upon the app's internal settings and did not adjust the trimming values in the field. This approach likely reduced the precision and accuracy of target SPLs of the playbacks. Because A-weighted decibels reflect the sensitivity of the human ear, it is possible they may not fully represent the intensity at which ground squirrels perceived the playback. For context, ground squirrels typically hear pitches from 16 to 26 000 Hz, a range that is similar but not identical to that of humans [84].

Playback stimuli were broadcast at a low intensity (60 dB measured at 50 cm from speaker) to represent a distant coyote (or control) call in the study area. These SPLs are comparable with those used to elicit anti-predator responses by ground squirrels in other studies. For example, the closely related yellow-bellied marmot was played stimuli at 92–93 dB (measured 10 cm from the speaker) in a field study [85]. Based on the inverse square law for a point source at reported distances (subject 10–15 m from the speaker), this is equivalent to marmots experiencing SPLs at 49–52 dB at 50 cm from the speaker [85]. Others have played predator sounds of 55–75 dB to California ground squirrels at distances of 40–95 cm [86] and a variety of stimuli at 60–88 dB to Belding's ground squirrels (*Spermophilus beldingi*) at a distance of 2 m [72]; measurement distances for SPLs were not explicitly reported for either study, so we cannot infer the equivalent SPLs experienced by subjects at 50 cm from a speaker.

Because coyotes vocalize at a maximum of 105 dB (recorded at 1 m away) [46], a squirrel played a vocalization from 50 cm away at SPL of 60 dB should perceive the coyote to be vocalizing at a maximum distance of 177 m away (from the subject). This is equivalent to a coyote vocalizing at the edge of our study area (i.e. the longest distance from one side to the other [69]). We also selected this modest volume given the short distance of squirrels from speakers and to avoid possible eavesdropping from non-target squirrels being processed at the nearby trapping station. Coyote vocalizations played in a pilot study at 60 dB (measured at 50 cm) outside of the testing arena were audible to the human ear and the squirrels in the area.

Our control consisted of an olfactory stimulus (a cotton ball soaked in ammonia placed in a small cup) and an acoustic stimulus (recordings of American crows; *Corvus brachyrhynchos*, a common, non-threatening species), both of which were hidden under the plastic box. Ammonia is a harmless chemical stimulus often used as a control in studies aimed at testing the behavioural responses of prey [55]. We retrieved audio files from the Macaulay Library at the Cornell Lab of Ornithology and randomly played a unique sound file for each trial.

(d) Quantifying behavioural responses

Each video was scored in JWatcher version 1.0 [87] to quantify space use and behavioural responses. First, following [88], we tracked the position of each subject's snout (regardless of the position of its tail) to measure where each subject's body was located in the arena and recorded whether they were on the stimulus side (12 open squares + test box), in the middle of the arena (12 open squares), or on the non-stimulus side (12 open squares + test box; figure 1). Second, we scored each behaviour into one of six mutually exclusive categories: (1) resting (stationary posture, includes chewing seeds from cheek pouches or autogrooming when sitting or lying down), (2) looking (head moving in the air from side to side or up and down without flexing of nostrils), (3) walking (animal transverses across gridlines on the floor of the arena while at least two paws were in contact with the floor at all times), (4) non-stimuli investigation (subject sniffing side of the enclosure, middle of the arena or near the non-stimuli test box), (5) stimuli-box investigation (sniffing at or head oriented towards stimuli in a state of arousal often while moving tail from side to side in a sweeping motion), and (6) fleeing (actively climbing on, biting at and/or scratching at enclosure with teeth or paws, presumably in an attempt to escape from the testing arena). Videos were scored by two observers and mean values were analysed. Videos were muted and scorers were blind to the predator cues presented (i.e. olfactory versus auditory versus multimodal) in each trial. Videos with interobserver reliabilities of less than 85% were rescored to yield a mean ± s.e. interobserver reliability of 96% ± 0.03 (*n* = 231 trials).

(e) Statistical analysis

We used R version 4.0.3 [89] for all statistical analyses. We applied a principal component analysis (PCA) to reduce the dimensionality of correlated behaviours in FactoMineR [90] (table 1). The first principal component (PC1) explained more than half of the variation (54%; eigenvalue of 3.22) and correlated positively with behavioural arousal (e.g. investigating the stimulus box (0.80), walking (0.74), fleeing (0.64), non-stimulus investigation (0.57) and looking (0.48)) but negatively with resting (−0.97). The second principal component (PC2) explained an additional 17% of the variation, but the values of behaviours loading on PC2 were generally in the opposite direction (of those loadings for PC1) with one exception. Investigation of the non-stimulus boxes loaded positively on PC1 (0.57) and PC2 (0.59). Given that components with eigenvalues near one generally have limited explanatory value (i.e. eigenvalue PC2 was 1.03) [91,92], subsequent analyses only focused on explaining PC1 (hereafter, 'behavioural reactivity').

We ran four generalized mixed effect models (GLMMs). First, we fitted a single GLMM with a binomial distribution in lme4 [93] to examine the subject's preference for (versus aversion to) the stimulus side of the arena. Given that a subject with no preference should theoretically split its time equally among the three spatial sections of the arena (no stimulus side, middle or stimulus side), we deemed a squirrel to prefer the stimulus side if it allocated more than two-thirds of its time to that side during a trial. We used this threshold approach for the choice test rather than a proportion of time because the latter failed to meet model assumptions despite transformations. Second, we evaluated the factors explaining PC1 (behavioural reactivity) using a Gaussian distribution. To help describe two behaviours of interest, we also ran two additional models with the proportion of time (i) investigating the stimulus box and (ii) vigilant as outcome variables (see electronic supplementary material). For all models, we entered the fixed effects of a subject's characteristics (age category (juvenile/adult) and sex (male/female) as well as their interaction), trial number (1, 2, 3 or 4) to account for habituation or sensitization, and treatment (coyote calls, coyote urine, both stimuli or control) as predictor variables.

We also included the random effects of 'squirrel identity' in each model to account for repeated measures within our dataset and to examine inter-individual differences in responses. We used likelihood ratio tests (LRTs) to assess if the random effect of identity improved each model's fit. We extracted the various components using the linear mixed model method to report

Table 3. Factors predicting behavioural responses of ground squirrels. Results are from GLMM models and significant terms are shown in bold. For categorical fixed effects, the level of the variable being compared is shown in parentheses (e.g. for 'site', animals from the pristine site were compared to those from the disturbed site; a positive estimate indicates that individuals at the pristine site were more likely to prefer the stimulus side than those at the disturbed site). Significant terms are shown in bold. Non-significant interaction terms for each model, respectively, also included: olfactory × site (1.47 ± 1.05, $t = 1.40$, $p = 0.162$; -0.35 ± 0.66, $t = -0.529$, $p = 0.597$), auditory × site (0.73 ± 1.01, $t = 0.73$, $p = 0.466$; 0.76 ± 0.63, $t = 1.203$, $p = 0.230$), multimodal × site (1.45 ± 0.92, $t = 1.58$, $p = 0.115$; -0.39 ± 0.59, $t = -0.661$, $p = 0.509$).

fixed effect	estimate ± s.e.	*t*-value	*p*-value
(*a*) preference for stimulus side			
intercept	**−1.46 ± 0.47**	**−3.08**	**0.002**
olfactory predator cue (control)	**−1.11 ± 0.50**	**−2.23**	**0.026**
auditory predator cue (control)	−0.84 ± 0.48	−1.72	0.084
auditory + olfactory (control)	**−0.94 ± 0.43**	**−2.17**	**0.030**
site (pristine)	**0.94 ± 0.39**	**2.45**	**0.015**
age category (juvenile)	0.44 ± 0.39	1.13	0.260
sex (male)	0.41 ± 0.35	1.17	0.242
random effect		χ^2	*p*-value
identity		0.25	0.617
(*b*) behavioural reactivity (PC1)			
intercept	**1.51 ± 0.41**	**3.70**	**0.0003**
trial order	**−0.60 ± 0.11**	**−5.46**	**<0.009**
olfactory predator cue (control)	**0.71 ± 0.27**	**2.63**	**0.009**
auditory predator cue (control)	0.31 ± 0.28	1.09	0.276
auditory + olfactory (control)	0.24 ± 0.25	0.98	0.329
site (pristine)	−0.41 ± 0.29	−1.42	0.158
age category (juvenile)	**−0.88 ± 0.37**	**−2.42**	**0.016**
sex (male)	−0.55 ± 0.41	−1.35	0.180
age × sex	0.62 ± 0.51	1.22	0.226
random effect		χ^2	*p*-value
identity		**15.71**	**<0.0001**

repeatabilities, defined as the intraclass correlation coefficient, to measure the proportion of total variance explained by among (versus within) individual differences using the rptR package [94,95].

3. Results

Our final dataset of 231 trials on 114 unique free-living ground squirrels ($n = 59$ females and 55 males) across the four conditions ($n = 45$ calls, 50 urine, 70 calls + urine, 66 control) at the disturbed ($n = 169$) and pristine ($n = 63$) sites. On average, subjects were tested over 41 ± 10 (mean ± s.e.) days, but individuals were tested over as many as 370 days. At the time of testing, subjects included 76 juvenile females, 74 juvenile males, 43 adult females and 38 adult males.

In terms of space use, individuals—particularly those from the disturbed site—consistently avoided spending time near coyote urine, regardless of whether urine was paired with a coyote call. That is, individuals were significantly more averse to the coyote urine alone ($t = -2.23$, $p = 0.026$) or combined with coyote calls ($t = -2.17$, $p = 0.030$; table 3*a* and figure 2*a*) versus the multimodal control; their responses were comparable for urine alone versus urine combined with

coyote calls ($t = -0.17$, $p = 0.89$). Squirrels did not significantly avoid coyote calls more than the control ($t = -1.72$, $p = 0.084$), but calls alone elicited similar space to urine alone ($t = -0.13$ $p = 0.90$) or paired with calls ($t = -0.38$, $p = 0.70$).

Stimuli avoidance varied between sites. Individuals from the disturbed site were significantly more averse to the stimulus side of the testing arena than those from the pristine site ($t = 2.45$, $p = 0.015$; figure 3*a*). These patterns persisted regardless of the subject's sex (male: $t = 1.17$, $p = 0.242$), age category (juvenile: $t = 1.13$, $p = 0.260$), or identity ($\chi^2 = 0.25$, $p = 0.617$). Spatial preferences were not repeatable across treatments (repeatability ± s.e.: 0.06 ± 0.01; 95% confidence intervals: 0.00 to 0.22, $p = 0.21$). The space use model failed to converge when 'trial order' (0.34 ± 0.20, $t = 1.70$; $p = 0.089$) or 'age × sex' (0.85 ± 0.80, $t = 1.07$; $p = 0.287$) were included, so both terms were removed.

When looking at behavioural reactivity (e.g. fleeing, investigating, vigilance), PC1 was higher for individuals exposed to predator cues of any type compared with the control, but only exposure to urine alone triggered a statistically significant increase in behavioural reactivity compared with the control ($t = 2.63$, $p < 0.009$; table 3*b* and figure 2*b*). By contrast, exposure to coyote calls in the presence ($t = 0.98$, $p = 0.329$) or the absence ($t = 1.09$, $p = 0.276$) of coyote urine failed to significantly
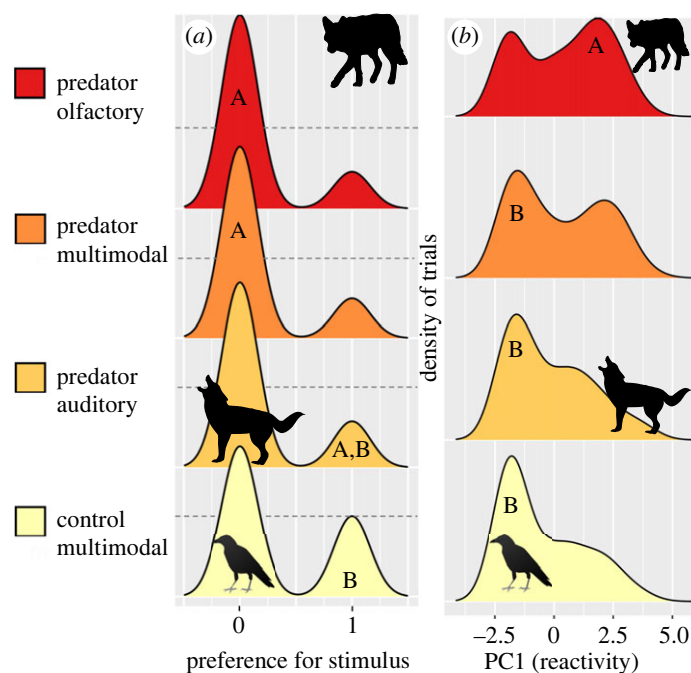
Figure 2. The effects of predator cue treatments (coyote urine and/or calls) and multimodal controls (ammonia and crow calls) on the spatial preferences and behavioural reactivity for California ground squirrels. Density (ridgeline) plots depict the proportion of all 231 trials (*y*-axis) for which individual squirrels demonstrated (*a*) a preference for (one) or avoidance of (zero) the stimulus side of the arena (*x*-axis; the dashed line represents the spatial preference for the control stimulus, reflecting a baseline value) and (*b*) low to high levels of behavioural reactivity, as reflected by the proportion of trials with various values of first principal component (PC1). Capital letters reflect statistically significant differences in the proportion of spatial or behavioural responses among testing conditions.
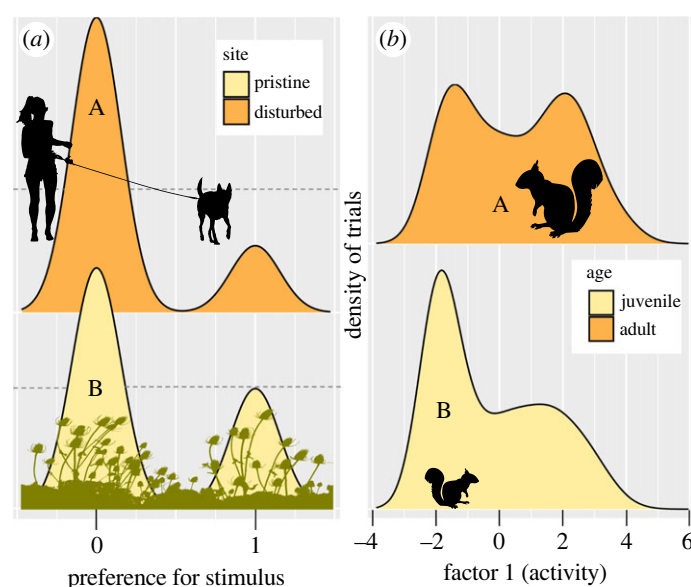
Figure 3. The effects of study site and age category on the spatial preferences and behavioural reactivity for California ground squirrels. Density (ridgeline) plots depict the proportion of all 231 trials (*y*-axis) for which individual squirrels demonstrated (*a*) a preference for (one) or avoidance of (zero) the stimulus side of the arena (*x*-axis; the dashed line represents the spatial preference for the control stimulus, reflecting a baseline value) and (*b*) low to high levels of behavioural reactivity, as reflected by the proportion of trials with various values of first principal component (PC1). Density plots are shown for individuals (*a*) residing at a pristine (top) and a more human-disturbed (bottom) site and (*b*) tested as adults (top) and juveniles (bottom). Capital letters reflect statistically significant differences in the proportion of spatial or behavioural responses among testing conditions.

increase behavioural reactivity compared to the control. Behavioural reactivity to urine alone was also statistically higher than for calls alone ($t = 2.39$, $p = 0.019$), but responses to calls or urine alone were not statistically different from the predator cues combined ($t \leq 1.57$, $p \geq 0.120$). Moreover, adults were significantly more reactive during behavioural assays than juveniles ($t = -2.42$, $p = 0.016$; figure 3*b*). Finally, although individuals' reactivity significantly declined across repeated trials ($t = -5.46$, $p < 0.009$), some individuals were significantly

more reactive than others across testing situations ($\chi^2 = 15.7$, $p < 0.0001$; figure 4). Specifically, an individual's reactivity (PC1) across trials (treatments) was significantly repeatable (repeatability $\pm$ s.e.$= 0.25 \pm 0.08$; 95% credible intervals: 0.09–0.41, $p < 0.001$), documenting consistent individual differences in the behavioural reactivity.

On average, squirrels allocated around 15% of each trial to investigating the stimulus box (mean $\pm$ s.e.: 0.15 ± 0.01, range: 0 to 0.81), but adults investigated the stimuli for a
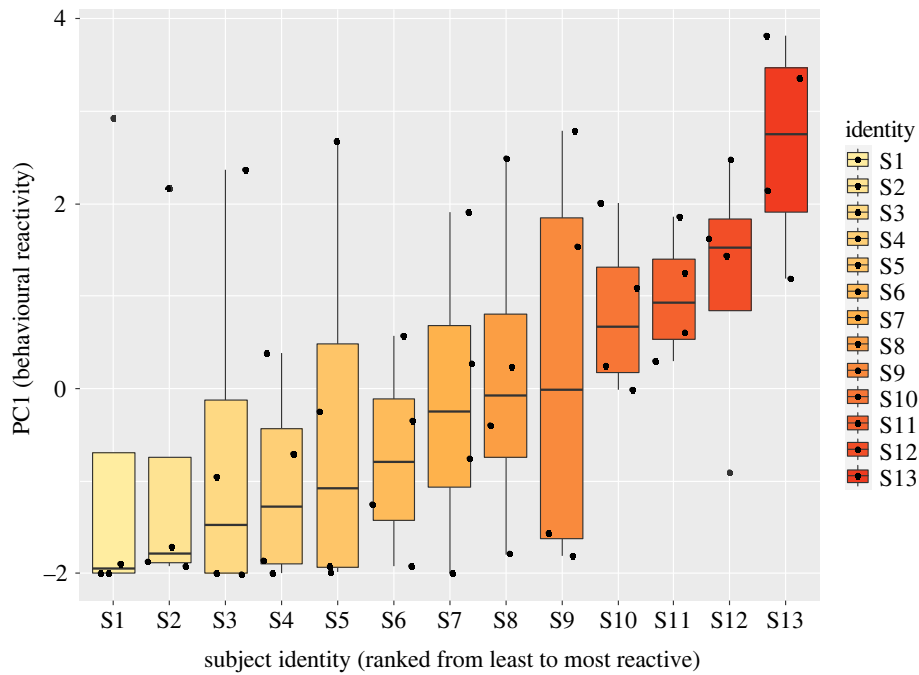
Figure 4. Box plots reflect the effects of an individual's identity on the first principal component score (PC1), reflecting low to high 'reactivity'. Although statistical models include all individuals from the study, values presented here are for the subset of individuals sampled across all conditions (3 treatments + control) while belonging to the same age category to demonstrate the effect of identity while accounting for these other main effects ($n = 7$ females and 6 males across 52 trials). The central line in each box and whisker plot shows the median value while the bottom and top edges show the 25th and 75th percentiles, respectively. Whiskers extend up to 1.5 times the interquartile range. Individual data points are overlaid using the jitter function to visualize multiple points with overlapping values for the same subject.

significantly greater proportion of time than juveniles ($t = -2.97$, $p = 0.003$; electronic supplementary material, table S1a). Although squirrels investigated coyote urine (mean ± s.e. proportion of time: 0.16 ± 0.02) for significantly longer than coyote calls (0.11 ± 0.03; $t = 2.03$, $p = 0.045$), there was no difference in the proportion of time they investigated urine alone versus multimodal predator cues (0.18 ± 0.05; $t = -0.828$, $p = 0.409$). Squirrels investigated multimodal predator cues for longer than calls alone ($t = 2.89$, $p = 0.005$) or the control (0.12 ± 0.02; $t = 2.01$, $p = 0.041$).

In general, squirrels only allocated 3% of each trial to vigilance (mean ± s.e.: 0.03 ± 0.01 proportion of time; range: 0–0.35) but were significantly more vigilant for coyote calls alone versus the multimodal control ($t = 2.20$, $p = 0.029$; electronic supplementary material, table S1b). The proportion of time vigilant was statistically similar for coyote urine (0.04 ± 0.01) and calls alone (0.05 ± 0.01; $t = -1.60$, $p = 0.873$), but subjects spent more looking in trials with coyote urine only or calls only versus those with multimodal predator cues (0.02 ± 0.01: $t \geq 2.46$, $p \leq 0.015$).

4. Discussion

(a) Sensory integration of non-redundant multimodal cues

Overall, the experiments revealed divergent patterns of signal dominance to non-redundant information from two indirect cues—coyote calls and urine. Ground squirrels avoided coyote urine (irrespective of calls) but only increased their reactivity (e.g. vigilance, fleeing, investigating) when exposed to 'quiet coyotes' (urine without calls). These findings are generally consistent with sensory integration theory [4,13,14],

supporting the prediction that animals consider information from multiple sensory channels in risky situations [19,96,97].

Physiological constraints dictate that coyotes must urinate within their home range—regardless of their motivational state—whereas calls offer specific information about predator intent because stalking predators rarely vocalize when hunting [51,98]. Thus, coyote calls could represent safety—rather than danger—cues to ground squirrels, contributing to the growing literature suggesting that prey optimize decisions by avoiding danger *and* seeking safety [99]. It is also possible that squirrels discounted the danger of calls because they could not see nearby coyotes. That is, after integrating nearby predator odour and calls, squirrels may deem this combined information as unreliable or conflicting in the absence of visual confirmation of a coyote. This second explanation was only partially supported by the data; squirrels investigated the stimulus for longer but were generally less vigilant when exposed to multimodal predators cues (than urine or calls alone). Regardless, the non-additive responses to indirect cues—in the absence of visual information—are consistent with sensory integration theory. More broadly, our experiment offers insights into the growing appreciation that multiple, non-redundant predator cues from the same species may increase accuracy in fear responses.

Our study confirms that free-living mammals are able to reconcile non-redundant information from different sensory modalities and highlights the need to consider how multimodal cues shape the evolution of integrated fear responses. Whereas the combination of two disparate sources of information (dog versus human) has previously been shown to amplify fear responses [100], our current findings extend our knowledge by suggesting that non-redundant cues from the same predator species may also act to promote accurate decisions through signal dominance. Taken together, we contribute to an understanding of how animals make accurate risk-sensitive decisions through the integration of multimodal information.

(b) Variation in responses between pristine and disturbed sites

Individuals living at the pristine site spent more time near stimuli than those residing at the disturbed site. We interpret this behavioural response to mean that individuals at the disturbed site are most risk-averse to coyote cues. Interestingly, our findings are in direct contrast to the prediction that increased exposure to humans (e.g. tourism) may increase prey vulnerability to predators by reducing their reactivity to natural predators [61]. This could be explained by site-level differences in exposure to predator cues. Although coyotes are fairly cryptic and, thus, tracking their relative abundance at our two sites is challenging, other studies show that coyotes tend to avoid areas frequented by humans and their dogs [101]. Thus, one might expect encounters by squirrels with coyotes to be less common at the disturbed than at the pristine site [77]. Moreover, subjects may integrate information from increased ambient anthropic noise with experimental stimuli since the disturbed site is near a parking lot. Ground squirrels do compensate for anthropic noise (e.g. wind turbines) by increasing their anti-predator behaviour at other sites in California [41]. Similarly, European mink (*Mustela lutreola*) increase risk aversion when confronted with anthropogenic acoustic (e.g. road traffic noise, human voices) and olfactory (e.g. dog odours) cues [100]. Thus, in a changing world, prey must often integrate information from multiple threats to make adaptive decisions.

(c) Ontogeny of risk aversion to predator cues

In our study, adults were more behaviourally reactive to predator cues than were juveniles, suggesting risk sensitivity increases with experience. Mammalian prey are naturally averse to predator-derived odours, especially urine [57,58]. Rodents in particular are exquisitely sensitive to the sulfurous metabolites, compounds that reflect the amount of meat in a coyote's diet [58], and prey species widely use chemical cues to assess risk, often from a young age [102–104]. Specifically, olfactory sensory neurons and chemosensory receptors allow rodents to detect predator odours from as early as 12 days old [59,105]. European rabbits (*Oryctolagus cuniculus*) also recognize fox (*Vulpes vulpes*) feces without prior experience [106]. Despite juvenile competency in detecting predator odours, our finding that adults were more reactive than juveniles to predator cues is consistent with earlier research in California ground squirrels [69,70] and other taxa [107]; adults are generally most reactive to threats. Similarly, adult meerkats (*Suricata suricatta*) are more likely to alarm call than juveniles when confronted with threats [71]. Ontogenetic differences may be attributed to increased experience with predators [108], stage-specific danger (e.g. offspring vulnerability) [86] and/or increased survival by reactive juveniles [107,109]. These patterns generally highlight the need to consider how an individual's experience interacts with integrated responses to threats and the associated fitness consequences of integrated responses to threats across the lifespan.

(d) Consistent individual differences in behavioural reactivity

Another major finding of our study was that individuals were consistent in their behavioural reactivity—but not in their time spent near stimuli—across treatments. This finding adds to our growing understanding of the consistent individual differences in California ground squirrels [36,63,75,78] and other animals [76,110,111]. More broadly, given that individuals residing at the human-impacted site were also consistently most reactive to predator cues, future studies should investigate the extent to which fear of predators generalizes to fearfulness of other dangers, including humans [112]. These modes of inquiry should offer key insights into how animals cope with multiple sources of information in a changing world.

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