



Original Article

Short-term social dynamics following anthropogenic and natural disturbances in a free-living mammal

Gabriella E. C. Gall,^{a,b,c,✉} Julian C. Evans,^{d,✉} Matthew J. Silk,^{e,f,✉} Chelsea A. Ortiz-Jimenez,^{g,✉} and Jennifer E. Smith^{a,✉}

^aBiology Department, Mills College, 5000 MacArthur Blvd. Oakland, CA 94613, USA, ^bZukunftskolleg, University of Konstanz, Universitätsstrasse 10, 78467 Konstanz, Germany, ^cCentre for the Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstrasse 10, 78467 Konstanz, Germany, ^dDepartment of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8050 Zurich, Switzerland, ^eCentre for Ecology and Conservation, University of Exeter, Campus Penryn, Penryn, TR10 9FE, UK, ^fNational Institute for Mathematical and Biological Synthesis, University of Tennessee, Claxton Bldg. 1122 Volunteer Blvd., Suite 106, Knoxville, TN 37996, USA, and ^gDepartment of Environmental Science and Policy, University of California, One Shields Avenue, Davis, CA 95616, USA

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Anthropogenic disturbances are widely recognized for their far-reaching consequences on the survival and reproduction of wildlife, but we understand comparatively little about their effects on the social lives of group-living animals. Here we examined these short-term changes in affiliative behavior as part of a long-term study on a human-tolerant and socially flexible population of California ground squirrels (*Otospermophilus beecheyi*). We used social network analysis to examine short-term changes in affiliative behavior and individual consistency in response to disturbances by humans, domestic dogs, or a natural predator (the coyote). Overall, juveniles were more involved than adults in affiliative interactions, but the short-term directional effects of these acute disturbances on social cohesion varied by disturbance type. Human and dog presence reduced aboveground connectivity, particularly for juveniles, whereas disturbances by coyotes generally promoted it. Beyond these effects, we also detected non-random responses to disturbances, though individuals were not very consistent in their directional response to different disturbance types. Our results demonstrate the flexible changes in social behavior triggered by short-term disturbances imposed by humans and other threats. More generally, our findings elucidate the underappreciated sensitivity of animal social interactions to short-term ecological disturbances, raising key questions about their consequences on the social lives of animals.

Key words: anthropogenic disturbance, California ground squirrel, group dynamics, social network analysis, social dynamics.

INTRODUCTION

Animals living in urban environments continuously face anthropogenic disturbances through increased noise, light pollution, or the presence of humans and their pets (Atwell et al. 2012; Weston and Stankowich 2013; Swaddle et al. 2015; Weaver et al. 2019; Beltran et al. 2021; Łopucki et al. 2021). In many areas, humans and their

dogs are some of the most common causes of disturbances (Butler et al. 2004; Antos et al. 2007; Underhill-Day and Liley 2007; Weston and Stankowich 2013) and both can have negative effects on local wildlife (Boyle and Samson 1985; Fernández-Juricic and Schroeder 2003; Gompfer 2014; Weston and Stankowich 2013; Larson et al. 2016; Mikula et al. 2018). These effects include changes in reproductive success (Finney et al. 2005; Gingold et al. 2009), movement (Stillfried et al. 2015; Tucker et al. 2018), habitat use (Tolon et al. 2009; Rogala et al. 2011), social behavior (Sime 1999; Gingold et al. 2009), and physiology (Müllner et al. 2004; Smith et al. 2015; Hammond et al. 2020).

Address correspondence to Gabriella Gall, Bücklestrasse 5, 78467 Konstanz, Germany. E-mail: gabriella.gall@uni-konstanz.de; Jennifer Smith, 5000 MacArthur Blvd, Oakland, CA 94613, USA. E-mail: smith.jennifer.elaine@gmail.com.

In many instances, humans have replaced natural apex predators leading to cascading effects across multiple trophic levels (Clinchy et al. 2016; Suraci et al. 2019). Specifically, large carnivores have been shown to adjust their circadian rhythms (George and Crooks 2006; Podgorski et al. 2013; Gaynor et al. 2018), and avoid areas with humans (Suraci et al. 2019). Medium-sized animals similarly adjust their circadian rhythm and also reduce the amount of time spent foraging, increase vigilance, and generally show a greater fear response to humans compared with natural predators (George and Crooks 2006; Ciuti et al. 2012; Podgorski et al. 2013; Clinchy et al. 2016; Gaynor et al. 2018). Small animals such as birds or rodents with a diurnal activity pattern often avoid human presence by changing their spatial location and maintaining a safe distance from humans (Atwell et al. 2012; Bateman and Fleming 2014; Cavalli et al. 2018; Mikula et al. 2018; Uchida et al. 2019). Nonetheless, small animals can also benefit from human presence, as the absence of large and medium-sized carnivores in the presence of humans translates to an increase in available foraging time (Muhly et al. 2011; Suraci et al. 2019).

Given the diverse ways humans can influence the lives of animals, it is important to examine the effects of humans and their pets on behavioral responses, compared to those of natural predators. For example, animals could potentially assess the risk associated with a disturbance type, that is, distinguishing between threatening and non-threatening disturbances (Bateman and Fleming 2014). We would then expect animals that are not directly persecuted by humans to react less strongly to and recover faster from disturbances caused by human presence than from disturbances by natural predators. If disturbances by humans are frequent, animals might also habituate to human presence over time, showing no or slight responses and thus reducing the negative impact of such disturbances (Lafferty 2001; Baudains and Lloyd 2007; Madsen and Boertmann 2008; Rankin et al. 2009; Blumstein 2016; Pellitteri-rosa et al. 2017). Although animals may habituate to human activity, wild animals are unlikely to habituate to the presence of dogs, even if disturbances by these are frequent. This is because dogs often move unpredictably, roaming freely and chasing small animals they come across (Glover et al. 2011; Weston and Stankowich 2013). The roaming behavior of dogs likely makes them more threatening for small terrestrial animals who are limited in their modes of escape (Stankowich and Blumstein 2005; Weston and Stankowich 2013). Even leashed dogs can strongly affect activity patterns and habitat use, especially of smaller animals (Lenth et al. 2008). In this case individuals might actually respond more strongly to an increased frequency of disturbances by dogs, thus becoming sensitized (Glover et al. 2011; Weston and Stankowich 2013). However, whether animals respond more strongly to humans, dogs, or humans accompanied by dogs remains unclear. Although some studies have reported a stronger response (e.g., an increase in vigilance or fleeing) by prey animals in response to humans with dogs than to humans without dogs (Mainini et al. 1993; Sime 1999), other studies find animals to be less likely to flee when encountering humans accompanied by dogs (Cooper et al. 2008). However, the relative effects of humans and/or their dogs and natural predators on social interactions have been largely overlooked.

In social species, anthropogenic disturbances have the potential to not only affect an individual's physiology, survival, and reproduction, but also their group's social cohesion and functioning (Frid and Dill 2002; Banks and Bryant 2007; Naylor et al. 2009; Shannon et al. 2013; Goldenberg and Wittemyer 2017; Gaynor et al. 2018; Jones et al. 2019). For example, direct removal of members from a

social group through hunting leads to increased levels of stress attributed to partner loss (Engh et al. 2006), unstable spatial and social patterns (Davidson et al. 2011), and changes in the social structure of groups (Whitman et al. 2004; Davidson et al. 2011; Shannon et al. 2013; Goldenberg et al. 2016; Goldenberg and Wittemyer 2017). Even non-lethal anthropogenic disturbances, such as traffic noise or human presence, can be harmful by promoting increased social aggression (Bruitjies and Radford 2013; Marty et al. 2019) or disrupting communication (Putland et al. 2018), parental care (Pandit et al. 2021), and mate choice decisions (Bent et al. 2021).

Despite anthropogenic disturbances having the potential to greatly affect social dynamics (Sterl et al. 2008; Rodrigues 2017), their immediate, short-term effects on social behavior have been largely overlooked, particularly in natural populations of mammals (Wilson et al. 2020). Whereas some affiliative interactions might increase after a disturbance, others may decrease. For example, affiliative behaviors such as sitting within body contact or foraging together can reduce physiological stress caused by disturbances (Müllner et al. 2004; Kern and Radford 2021). These aggregations might also be driven by individuals acting to reduce their own risk of predation, as predicted by the dilution hypothesis (Hamilton 1971; Pulliam 1973; Bertram 1978). Similarly, the “many eyes hypothesis” (Pulliam 1973; Powell 1974) predicts that disruptions might lead to increases in group vigilance. Disruptions can also drive animals apart and increase the need for animals to re-establish relations, thereby increasing greetings (Smith et al. 2015) but reducing social foraging (Maldonado-Chaparro et al. 2018). Moreover, there is emerging evidence in mammals from social carnivores (Belton et al. 2018) to primates (Morrow et al. 2019) that non-lethal disturbances can also reduce the strength of social relationships. Social network analysis offers a powerful tool to quantify such changes in animal social behavior and can offer new insights into the various effects of disturbances (Wey et al. 2008; Sih et al. 2009; Smith and Pinter-Wollman 2021).

Here we examine the impact of short duration perturbations by humans, domestic dogs, and a natural predator (the coyote, *Canis latrans*) on the social interactions in a human-tolerant population of California ground squirrels (*Otospermophilus beecheyi*). Specifically, using social network analysis, we asked whether and how natural and anthropogenic disturbances affected squirrels' social behavior depending on the age category of the individuals involved. California ground squirrels feed primarily on seeds and herbaceous vegetation (Grinnell and Dixon 1918; Smith et al. 2016) and occur in open habitats, including California grasslands, oak woodlands, and agricultural environments (Grinnell and Dixon 1918; Smith et al. 2016). They are facultatively social rodents in which juveniles and adults of both sexes engage in repeated social interactions with each other in multiple contexts, including those occurring above- and below-ground (Smith et al. 2018). As such, residential social units are characterized by individual-based fission–fusion dynamics (Aureli et al. 2008; Smith et al. 2008). Specifically, the subgroup size and composition of squirrels in close proximity are regularly changing as individuals move apart and come back together, balancing time spent socializing and foraging aboveground with that spent safely in belowground burrow complexes either alone or with group-mates (Ortiz et al. 2019; Smith et al. 2018). As a major prey item for many avian, reptilian, and mammalian predators (Owings et al. 1977; Owings and Leger 1980), California ground squirrels engage in a suite of anti-predator behaviors to reduce predation risk and increase survival, including vigilance (Loughry and McDonough 1988; Ortiz et al. 2019), alarm calling

(Leger and Owings 1978), and collective mobbing (Owings et al. 1977). We also know that members of this species possess individual differences in terms of their risk-sensitive foraging in close proximity to natural predators (Holding et al. 2020), tendency to call in a trap (Hammond et al. 2019), or flee (Ortiz-Jimenez et al. 2022) when approached by a human, and in their social network position across contexts (Smith et al. 2018). These traits are also repeatable over time (Hammond et al. 2019).

Although historically considered a pest species, California ground squirrels are not directly killed for sport in our study area and the population size has never been actively reduced. Thus, when animals are confronted with human presence, the risk of death is usually limited compared with disturbances caused by natural predators or domestic dogs. Importantly, however, both domestic dogs and coyotes have been documented to directly kill our study subjects during daytime observations at the study site (unpublished data). On detecting a coyote, ground squirrels usually hold their ground, producing alarm calls (Owings and Leger 1980) and increasing their vigilance (Owings et al. 1986). Due to the similarity in the threat levels posed by dogs off-leash (e.g., chasing squirrels) and coyotes (e.g., stalking squirrels), we expected squirrels to respond in a similar way to these two disturbance types. When directly approached by a human, squirrels at our site generally run away (with an average flight initiation distance of 9 m), and most (70%), but not all, subjects remain active aboveground in response to these assays; the 30% that seek shelter in burrows resumed aboveground activity, on average \pm SE, in 18 ± 2 min. (Ortiz-Jimenez et al. 2022). Squirrels may be more habituated to human-only disturbances, showing no or little change in social behavior after these and in contrast to coyotes and off-leash dogs, humans with dogs on a leash might be perceived as comparatively less threatening.

As a response to high-risk disturbances (e.g., a predator) we thus expected squirrels to either seek safety belowground (Ortiz-Jimenez et al. 2022) or to increase the number of affiliative interactions with conspecifics compared with low-risk disturbances (e.g., a human alone). In the first case, individuals might alarm call prior to seeking safety, thereby alerting other individuals. Accordingly, we would expect a reduction in aboveground affiliative interactions and, on subsequent reunions aboveground, increasing greetings. In the latter case, following the many eyes hypothesis, we would expect an increase in behaviors that allow individuals to aggregate to dilute risk while simultaneously maintaining high vigilance, such as sitting in close proximity or foraging socially (Fernández-Juricic and Schroeder 2003). Furthermore, social behaviors which reduce the ability for individual vigilance, such as play or greetings, may decrease (Harcourt 1991; Blumstein 1998). Consistent with the dilution effect, California ground squirrels have been shown to decrease vigilance intensity the more squirrels are grouped together (Ortiz et al. 2019). However, they also detect threats sooner and flee more readily from an approaching human when more conspecifics were present than when alone (Ortiz-Jimenez et al. 2022). Moreover, given that adults are generally more responsive to threats than juveniles (Ortiz et al. 2019), we expected adults to be consistent in their responses to disturbances than juveniles.

METHODS

Data collection

Since 2013, California ground squirrels have been live-trapped, marked, and released at Briones Regional Park in Contra Costa

Country, California (39.956769 N, 122.124304 W) (Smith et al. 2018). That is, on its first capture, each individual received a Monel metal ear tag (National Band and Tag Co., Newport, Kentucky, USA) attached to one pinna, a unique Nyanzol cattle dye mark (Greenville colorants: New Jersey) applied to its back for visual identification during social observations, and a unique passive integrated transponder (PIT) tag (Biomark, Inc., Boise Idaho) inserted beneath the skin as a reliable “lifetime” barcode. Fur marks were updated every 1–2 weeks to ensure all individuals were easily observed from a distance with binoculars. Located in the San Francisco Bay area, this 6117-acre regional park is primarily a wilderness area; although vehicular traffic is prohibited, the park is frequently visited by humans and their dogs.

Trapping and observations occur primarily from late May to early August, the time of year when squirrels of all ages are most active aboveground, and park visitors are most frequent (Hammond et al. 2019). Young of the year are fully weaned when they emerge from burrows in May and remain juveniles until about one year of age (Grinnell and Dixon 1918; Hanson and Coss 2001). We assigned age, sex, and reproductive status with high accuracy; adults were rarely reproductively active during the summer months of this long-term study (Smith et al. 2018). Specifically, for each first capture of the week, we weighed each squirrel and visually inspected its external genitalia, and, for females, examined their teats for evidence of milk production. This reproductive information in combination with each individual’s body mass and our demographic records was used to identify animals as juveniles (weaned young of the year) or adults (at least one-year-old; Hanson and Coss 1997).

In the current study, we focused on observational data collected from 2013 to 2019 (Table 1) at our moderately-disturbed study site (Figure S1). Their diurnal lifestyle (Owings et al. 1977) and preference for socializing on open substrates (e.g., short grass, dirt) (Ortiz et al. 2019) make the aboveground behavior of California ground squirrels particularly straightforward to observe (Smith et al. 2016). Trained observers monitored aboveground affiliative exchanges and disturbances within the study area using 10 X 42 Eagle Optics Ranger ED Binoculars (Middleton, Wisconsin, USA). These were recorded primarily in the mornings (0800 to 1200 h) and some afternoons (1200 to 1400 h) from multiple locations within the study site (Figure S1). Marked individuals belonging to all age and sex categories interact across the study site, although the strength of pairwise direct ties varies among dyads across the site (Smith et al. 2018). Our daily observations coincided with periods of high human foot traffic in the park.

Pairs or trios of observers sat quietly together at a total of three distinct locations, each at a distance of ≥ 20 m from subjects to avoid influencing their behavior (see Smith et al. 2018 and Figure S1 for details). The observers simultaneously watched study subjects to capture site-level changes in social behavior and disturbance events (Figure S1). Using all-occurrence sampling (Altmann 1974), we recorded all aboveground greetings (two individuals touching nose to nose, touching nose to cheek, or otherwise sniffing each other), proximity maintenance (in body contact or within less than 1 m), social foraging (consuming seeds or fresh vegetation within less than 1 m), play (Smith et al. 2016), and alarm calls (Owings and Virginia 1978).

Greetings involved two individuals meeting head-on and touching noses, one individual rubbing his or her cheek on that of another squirrel, or one individual approaching a second head-on and rubbing its nose near the corner of the receiver’s mouth (Owings et al. 1977; Smith et al. 2016). We also included other aspects of

Table 1

The size and structure of the observed colony per year as given in the final dataset used, as well as the number of disturbance events during each period

Year	Number of data collection days	Number of observed individuals in final network data				Number of disturbance events			
		Total	Juveniles	Adults	Females	Males	Total	Single	Multiple
2013	28	28	12	16	14	14	31	24	7
2014	30	36	9	27	15	21	36	34	2
2015	22	69	46	23	37	32	54	43	11
2016	29	97	59	38	60	37	72	61	11
2017	23	105	55	50	64	41	53	49	4
2018	38	115	56	59	75	40	82	54	28
2019	20	110	57	53	71	39	39	22	17
Total	190	Total number of unique individuals observed 366	–	–	193	173	367	287	80

Note that disturbance events here only include disturbances imposed by humans, dogs (on and off-leash) and coyotes. Disturbances where the 10 min after the event would overlap with the 10 min of the following disturbance were merged to one event here marked as “Multiple” whereas “Single” stands for events that were composed of only a single disturbance. For the final analysis, we only included merged disturbance events where the last disturbance was within 10 min of the first.

olfactory investigation such as when one individual sniffed the side or anogenital area of another conspecific in this category of behavior. Proximity maintenance occurred when one individual approached a second and sat in direct body contact or within less than 1 m of the second individual (Smith et al. 2016). Individuals foraged socially when they consumed seeds, grass, or other forage within less than 1 m (Smith et al. 2016). Each unique play bout started with one individual initiating play slapping, boxing, chasing, mounting, pouncing, or wrestling with a second individual and ended when one of the two individuals moved apart from the other (Smith et al. 2016); play was distinctive from agonistic interactions in that roles often changed within a bout, it did not involve actual aggression (e.g., biting) (Blumstein et al. 2013), and play was largely limited to juvenile–juvenile interactions.

As the observations took place in a public park, squirrels were frequently disturbed, both through human activities, which included humans exercising dogs both on- and off-leash, and natural predators (e.g., coyotes, snakes, birds of prey; Hammond et al. 2019). Disturbances were defined as a specific disturber (human, dog, coyote, etc.) getting within 15 m of a landmark within the squirrel field site. Landmarks included natural and anthropogenic features (see Figure S1) and were used to approximate the location of squirrels during social interactions at the study site. They also made it easier for observers to accurately follow squirrels during observations. The distance of 15 m was chosen as some of the landmarks are quite far apart from each other, though in most instances disturbers were closer than 15 m to a landmark. For each disturbance, the type, and the number of disturbers were recorded. We also noted the start time, duration, and the number of calls produced in response to these stimuli during our observations. Alarm vocalizations produced by California ground squirrels involve the caller(s) producing a single, discrete (non-repetitive) acoustic signal (call), or a series of repetitive discrete signals (calls) over time in response to a perceived threat (Leger et al. 1979; Owings et al. 1986; Loughry and McDonough 1988). Each calling bout therefore contained from one to multiple calls produced in short succession by an animal in response to an environmental threat; only repetitive calls tend to elicit an extended period of vigilance by receivers (Schleidt 1973). Each bout of repetitive calls was counted by observers using a 4-digit hand tally counter (KRTIO). Note that the response of

squirrels was not recorded unless an alarm call occurred, or squirrels interacted with each other. We focused on disturbances caused by humans, humans with dogs on leash, off-leash dogs, and coyotes in this analysis.

Data analysis

Network construction

To test whether disturbances affected squirrels’ social behavior, for each disturbance event, we calculated two social networks: a “pre-disturbance” network and a “post-disturbance” network. In these networks, nodes represented individuals and edges the number of interactions between individuals. The pre-disturbance network was comprised of the social interactions observed in the period 10 min before the disturbance event, whereas the post-disturbance network was built using all interactions occurring in the period 10 min after the disturbance event. Each pair of “pre-disturbance” and “post-disturbance” networks were separated by a one-minute (or greater for merged disturbances, see below) time interval during which the subjects experienced one (or more) disturbance(s). Determining the exact duration of disturbances experienced by our subjects was generally difficult for human observers to ascertain because this would assume that we share the same risk perception as our study subjects. Instead, we assumed each disturbance event lasted roughly one minute because this is the typical duration of alarm calling in response to a disturbance, a reliable measure of behavioral arousal to threats at Briones (mean \pm Standard Error (SE) call duration is 1.48 ± 0.08 min, $n = 1839$ alarm calls; unpublished data).

We limited pre- and post-disturbance intervals to 10 min as we expected to see the strongest change in behavior immediately after a disturbance. Previous studies on other social rodents have used similar or even shorter time frames and showed that individuals are alert for only a short period after an alarm call or a disturbance and resume foraging very quickly (Eastern grey squirrels: Jayne et al. 2015; gerbils: Randall et al. 2000, Randall and Rogovin 2002). If two disturbances occurred within 10 min of each other, we included them as a single “merged” disturbance event (Table 1). Disturbances were excluded from the analysis if they occurred within 20 min of each other, as this would lead to an overlap between the post-disturbance period of one with the pre-disturbance period of the other (Table 1).

For merged events, we defined the disturbance type as “multiple” in the analysis if a merged event was comprised of disturbances caused by different disturber types. In these cases, the pre-disturbance network for merged events was calculated before the first disturbance and the post-disturbance network after the last disturbance. Because we did not have detailed information on the location of disturbers, we focused on the effects of disturbances on social interactions collected from the whole study site (~9596 m²; Ortiz et al. 2019) rather than on localized effects at the area first disturbed. Squirrels alarm called in 114 of the 367 disturbances analysed here, making information on the threat available across the whole site.

To calculate networks, we only included instances where at least five squirrels had been observed in affiliative interactions from the start of the day until the end of a specific disturbance event across the whole study area. To gain general insights into the extent to which disturbances disrupt versus increase affiliative behaviors, we examined the effects of disturbances on networks in which edges were comprised of: 1) all affiliative behavioral categories combined and separately from each of the following behavioral categories on their own: 2) proximity, 3) foraging, 4) greetings, and 5) play. In all networks, edges were generated as a count of pairwise interactions between squirrels and were thus weighted and undirected. All networks were constructed and analyzed in R version 4.0.3 (R core team 2020) using the package “igraph” version 1.2.6 (Csardi and Nepusz 2006).

Behavioral responses to disturbances

To evaluate whether juveniles and adults responded differently to disturbances, we calculated the sum of weighted degrees of all individuals in an age category within each pre- and post-disturbance event network and for each network type, where the weighted degree is the sum of all edge weights connected to a node. Note that because adult squirrels very rarely play, we did not include them in the play network and analysed it for juveniles only. Due to the low interaction rate of squirrels across the population within small snapshots of time (e.g., 10 min.), we tested for possible zero inflation and over/under dispersion using the package “DHARMA” (Hartig 2020). We found no evidence for either in any network type and accordingly fitted generalized linear mixed effects models (GLMMs) with a Poisson distribution (Bates et al. 2015). In each model, we included the sum of the weighted degree by age category as a response variable. As explanatory variables, we included the main effects of age category (juvenile, adult) and disturbance type (pre-disturbance, coyote, dog, human and dog, human, multiple) as well as their interaction. We did this to investigate whether young individuals respond to the different disturbance types more strongly than more experienced adults. There were no significant associations between the two categorical predictor variables (Pearson’s Chi-squared test $\chi^2 = 0$, $df = 5$, $P = 1$). As individuals were observed multiple times across different years, we included “year” as a random effect. Similarly, we included a “unique identifier for each disturbance event” as a random effect to control for baseline variation across disturbance events and to pair each pre- and post-disturbance network. Finally, we controlled for the difference in the number of juveniles and adults seen during different disturbances by including the “percent of juveniles in each network” as a random term (number of categories = 63 with mean = 23.3 (range = 4–84) observations per category). For the model using the play network data, we only included “disturbance type” as a fixed effect (an explanatory variable) as well as “year” and “the

unique identified for each disturbance event” as random terms. As models did not converge with the default lme4 optimizer, we used the “bobyqa” (short for “bound optimization by quadratic approximation”) optimizer instead (Bates et al. 2015). It is one of many different optimizers that can be used in the lme4 package; glmer uses a combination of bobyqa (nAGQ = 0 stage) and Nelder_Mead by default. Different optimizers have different numbers (and probably types of) convergence checks and can accordingly perform slightly differently.

Individual consistency in disturbance response

To test whether individuals showed consistency in their response across disturbance events, we calculated the change in individual weighted degree for each disturbance event by subtracting an individual’s ‘pre-disturbance’ weighted degree from their ‘post-disturbance’ weighted degree. Because the relationship between network size and the weighted degree was non-linear (Figure S2), we focused on the direction of a change rather than its magnitude (the value would be strongly affected by network size, which varied among disturbance events, range 5–62 mean \pm SD = 24.2 \pm 14.4). Specifically, the direction of a change was one if weighted degree increased after a disturbance event, zero when weighted degree remained consistent over time, and negative one when weighted degree decreased after a disturbance event. We then calculated the mean and SD of directional change for each individual. The mean indicates the overall direction of change for each individual whereas the standard deviation reflects how consistent an individual is. Thus, more consistent individuals had smaller standard deviations than less consistent individuals. Our approach is similar to that used by (Wilson et al. 2013), but adapted to account for the large number of zeros in the dataset, to which our approach is more robust.

As we were interested in investigating whether individual repeatability depended on an individual’s ontogenetic stage, we calculated the mean and standard deviation for each individual and each life stage separately. Given the longitudinal nature of the study, we calculated two separate means/standard deviations if an individual was observed as both a juvenile and an adult. In addition, as many squirrels did not interact at all during our short observation periods, we also calculated the means and standard deviation excluding instances where individuals did not interact at all, neither pre- nor post-disturbance. To quantify the proportion of individuals that had non-random mean and standard deviation weighted degrees (i.e., whether their behavior was non-random across different disturbances), we performed node permutations. Node permutations break down the relationship between node-identity and edge structure (Farine and Whitehead 2015; Weiss et al. 2021). Specifically, we randomized node labels within each post-disturbance network, thus retaining network topology but leaving individual traits unchanged. We then calculated the same measures (means/standard deviations of the direction of change in behavior) and compared these to the empirical results. The mean and standard deviation of an individual were considered non-random if 97.5% of the permuted values were either below or above the empirical values. We then used a two-sided Kolmogorov-Smirnov test to compare the distribution of means and standard deviations between adults and juveniles for the individuals with a non-random change (Marsaglia et al. 2003). We used a Bonferroni correction (Benjamini and Yekutieli 2001) to correct for multiple testing thus adjusting alpha to 0.025.

RESULTS

Network structure

In total, we calculated 367 pre- and post-disturbance networks over 147 days (Table 2). Each observed squirrel ($N = 366$, Table 1) had up to 22 (median = 2) affiliative interactions during each of the 10-minute periods before or after a disturbance. Of these, individuals sat in close proximity of each other on up to 8 (median = 1) occasions,

Table 2
Number of disturbances for each of the different disturbance types (e.g., natural predator)

Year	Number of disturbance events for each disturbance type					Total
	Human	Dog on-leash	Dog off-leash	Coyote	Multiple	
2013	15	5	4	0	7	31
2014	–	7	22	5	2	36
2015	–	17	25	1	11	54
2016	–	26	35	0	11	72
2017	–	21	28	0	4	53
2018	8	16	28	2	28	82
2019	11	0	9	2	17	39
Total	34	92	151	10	80	367

For merged events, we here only present the disturber of the first disturbance in the event. Human disturbances were caused by 1–30 individuals (median = 2). Disturbances by dogs on-leash by 1–6 individuals (median = 2) disturbances by dogs off-leash were caused by 1 to 6 individuals (median = 2) and all disturbances by coyotes by a single individual. Multiple combined disturbances ranged from 2 to 15 individuals (median = 4).

foraged socially up to 6 (median = 0) times, greeted each other up to 6 (median = 0) times and had up to 6 (median = 0) play interactions per day. Network sizes included ranged from 5 to 62 individuals (median = 21, mean \pm standard deviation (SD) = 32.74 ± 14.06 , Figure S2). See Table S1 for more details on the number of interactions of juveniles versus adults and males versus females.

All population-level social networks considered in the 10-minute windows were sparse with low edge densities across all different network types (Full affiliative network: median density = 0.01, range: 0.00–0.40; proximity network: median density = 0, range: 0–0.36; foraging network: median density = 0, range: 0–0.30; greeting network: median density = 0, range: 0–0.25; play network median density = 0, range 0–0.27). Across networks of all types, maximum density increased by up to 0.07 from the pre- to the post-disturbance networks, but median density did not change (Figures 1 and 2, Supplementary Figures 3–4). Further, we found an increase in the number of networks with no interactions among squirrels and thus a density of zero in the post-disturbance networks across all network types. Specifically, “zero” networks increased by 26% from 92 out of 367 pre-disturbance networks to 116 out of 367 post-disturbance networks for the affiliative networks, by 16% from 140 to 162 for the proximity networks, by 22% from 180 to 219 for the foraging networks, by 14% from 168 to 191 for the greeting networks and by 4% from 240 to 250 for the play networks.

Behavioral responses to disturbances

Overall, observed disturbances by humans, dogs, and coyotes were associated with a total of 689 unique calling bouts containing 27

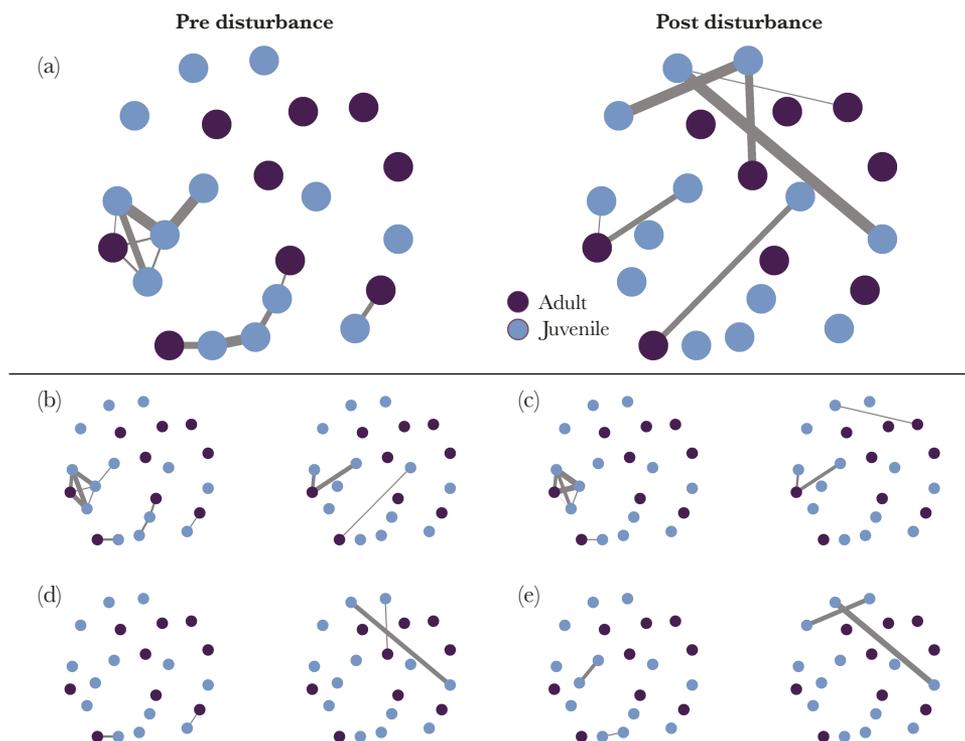


Figure 1

Example networks for a disturbance caused by dogs off-leash. Shown are pre- (left) and post- (right) disturbance networks including (a) all network types combined, (b) sitting in proximity, (c) social foraging, (d) greeting, and (e) play. Darker nodes indicate adults and lighter nodes juvenile individuals. Edge thickness represents edge weights.

683 alarm calls at the disturbed site from 2013 to 2019 (Table 3). Whereas only 1118 calls (range: 96–202 calls per bout, $n = 17$ calling bouts) were associated with humans (without dogs), 19 050 calls (range: 2–3120 calls per bout, $n = 635$ calling bouts) were associated with dogs. Squirrels also generally called more in response to off-leash ($n = 15\ 254$ calls, 489 bouts) than on-leash dogs ($n = 3796$ calls, 146 bouts). Although coyotes were rarely detected during our daytime observations (e.g., Table 2), each coyote disturbance to the study site triggered a comparatively large number of calls (range: 618–1710 calls per bout, $n = 7515$ calls, 37 bouts). When checking the vocal responses of squirrels to the disturbances analysed here, we found that squirrels alarm called in 114 of the 367 disturbances and emitted a total of 5896 calls. More specifically, individuals emitted a total of 311 calls (median = 40.5, range: 1–117) in response to 60% of coyote disturbances analysed here, 2092 calls

(median = 3, range: 1–473) in response to 35% of disturbances by off-leash dogs, 376 calls (median = 6, range: 1–82) in response to 23% of disturbances by on-leash dogs, 178 alarm calls (median = 89, range: 69–109) in response to 5% of disturbances by humans and 2939 alarm calls (median = 25, range: 1–986) in response to 40% of multiple merged events.

With respect to changes in aboveground affiliative behaviors, we found a statistically significant difference in the response of juveniles and adults to different disturbance types (P -value < 0.001 across all network types). Juveniles interacted more than adults across all network types (Figures 3 and 4, Tables 4–8). The response to the different disturbance types varied among the behaviors. When including all behaviors in one full affiliative network, we found a stronger decrease in the interactions of juveniles in response to coyotes, on-leash dogs, and humans compared with adults (Figure 3,

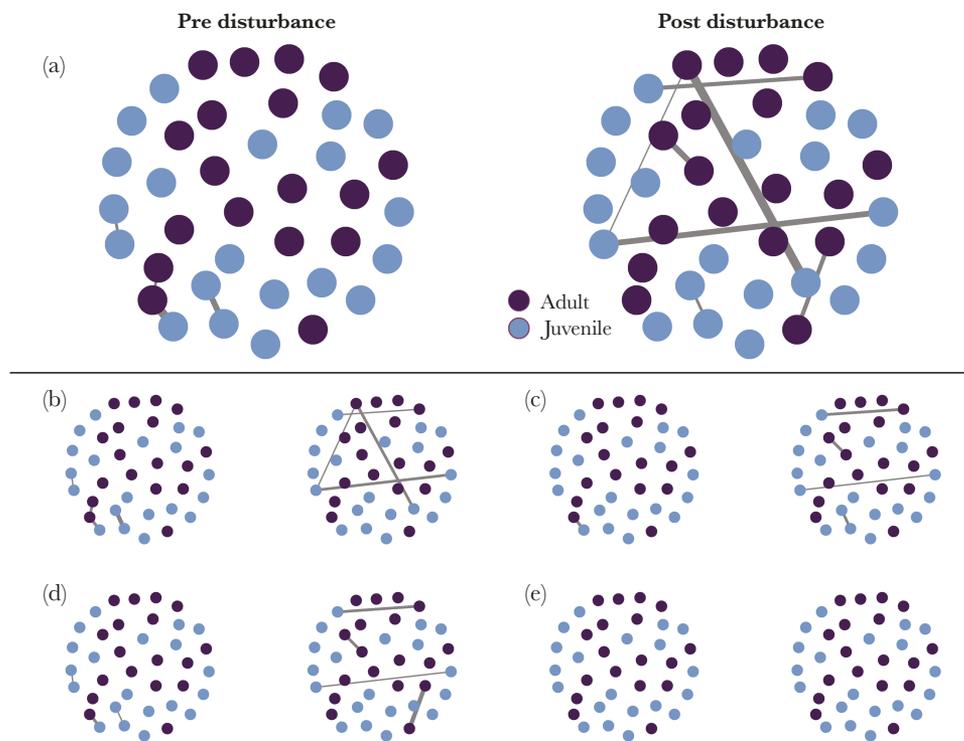


Figure 2

Example networks for a disturbance caused by a coyote. Shown are pre- (left) and post- (right) disturbance networks including (a) all network types combined, (b) sitting in proximity, (c) social foraging, (d) greeting and sniffing behaviors, and (e) play behaviors. Darker nodes indicate adults and lighter nodes juvenile individuals. Edge thickness represents edge weights.

Table 3

Number of calls observed for each of the disturbance types (e.g., natural predator)

Year	Number of calls produced by ground squirrels for each disturbance type				
	Human	Dog on-leash	Dog off-leash	Coyote	Total
2013					
2014	–	2 calls (1 bout)	3120 calls (23 bouts)	662 calls (10 bouts)	3784 calls (34 bouts)
2015	–	798 calls (44 bouts)	2750 calls (104 bouts)	1710 calls (4 bouts)	5258 calls (152 bouts)
2016	200 calls (7 bouts)	869 calls (53 bouts)	2732 calls (136 bouts)	1576 calls (9 bouts)	5377 calls (205 bouts)
2017	196 calls (2 bouts)	571 calls (14 bouts)	1871 calls (41 bouts)	–	2638 calls (57 bouts)
2018	424 calls (1 bout)	285 calls (16 bouts)	1434 calls (80 bouts)	1745 calls (7 bouts)	3888 calls (104 bouts)
2019	96 calls (5 bouts)	1017 calls (15 bouts)	2429 calls (92 bouts)	681 calls (4 bouts)	4223 calls (116 bouts)
Total	1118 calls (17 bouts)	3796 calls (146 bouts)	15 254 calls (489 bouts)	7515 calls (37 bouts)	27 683 calls (689 bouts)

Table 4). We found no statistically significant change in behavior after disturbances by off-leash dogs or multiple disturbances in this network for either adults or juveniles.

For the networks including only one type of behavior, we found adults responding to coyotes by greeting more, whereas juveniles greeted less often but maintained similar levels of play (Figure 4C,D, Tables 7 and 8). Squirrels of all ages responded to off-leash dogs and humans with dogs on a leash by reducing their social foraging (Figure 4B, Table 6). Furthermore, individuals generally reduced their tendency to sit in close proximity after disturbances by humans with dogs on a leash, with juveniles showing a greater reduction in this behavior than adults (Figure 4A, Table 5). Juvenile squirrels also reduced play behavior after disturbances by dogs on a leash (Figure 4D, Table 8). In response to disturbances by humans (without dogs), squirrels reduced sitting in close proximity and greeting behaviors (Figure 4, Table 5 and 7). Finally, we found no overall directional response to multiple disturbances when all age classes were considered together, but juveniles reduced play behavior (Figure 4D, Table 8).

Individual consistency in disturbance response

When we analysed the mean (indicating direction of change) and standard deviation (indicating consistency of change) of the direction of change in weighted degree, we found only weak evidence that the aboveground social interactions of squirrels changed consistently in response to disturbances. Results that included only squirrels observed interacting before or after a disturbance did not agree with those including all squirrels. When we only included individuals that were recorded interacting before or after a disturbance,

we found no difference between individuals by age in any network type ($\text{mean}_{\text{Affiliative}} \pm \text{SD} = -0.07 \pm 0.54$; $\text{mean}_{\text{Proximity}} \pm \text{SD} = -0.05 \pm 0.53$; $\text{mean}_{\text{Foraging}} \pm \text{SD} = -0.01 \pm 0.56$; $\text{mean}_{\text{Greeting}} \pm \text{SD} = -0.09 \pm 0.61$; $\text{mean}_{\text{Play}} \pm \text{SD} = 0.00 \pm 0.61$; Figure 5c). Including individuals that were not observed interacting, the mean response of squirrels to disturbances was close to zero ($\text{mean}_{\text{Affiliative}} \pm \text{SD} = -0.04 \pm 0.19$; $\text{mean}_{\text{Proximity}} \pm \text{SD} = -0.02 \pm 0.15$; $\text{mean}_{\text{Foraging}} \pm \text{SD} = -0.02 \pm 0.12$; $\text{mean}_{\text{Greeting}} \pm \text{SD} = -0.02 \pm 0.13$; $\text{mean}_{\text{Play}} \pm \text{SD} = 0.00 \pm 0.09$; Figure 5a) indicating most individuals did not change their number of social interactions. However, individual squirrels did show a great spread with the mean direction of change in weighted degree of different individuals ranging from -1 to 0.67 (Figure 5a), such that individuals responded quite differently to disturbances, with most not responding and others decreasing or increasing the number of social interactions after disturbances. For juveniles, standard deviations of change in weighted degree were the smallest in the play networks (Figure 5b), meaning that juveniles showed the most consistent behavior in the play networks compared with the other networks. When including “zero-interaction” squirrels, most individuals did behave consistently: between 70% and 98% of individuals had a mean and standard deviation in directional change in weighted degree after disturbance events significantly different from random (Table S2). Squirrels were even more likely to behave more consistently in the observed rather than permuted networks when the non-interacting squirrels were excluded, as between 85% and 100% of individuals had a non-random mean and standard deviation in directional change in weighted degree after disturbance events. We also found a statistically significant difference in the standard deviation of directional change in weighted

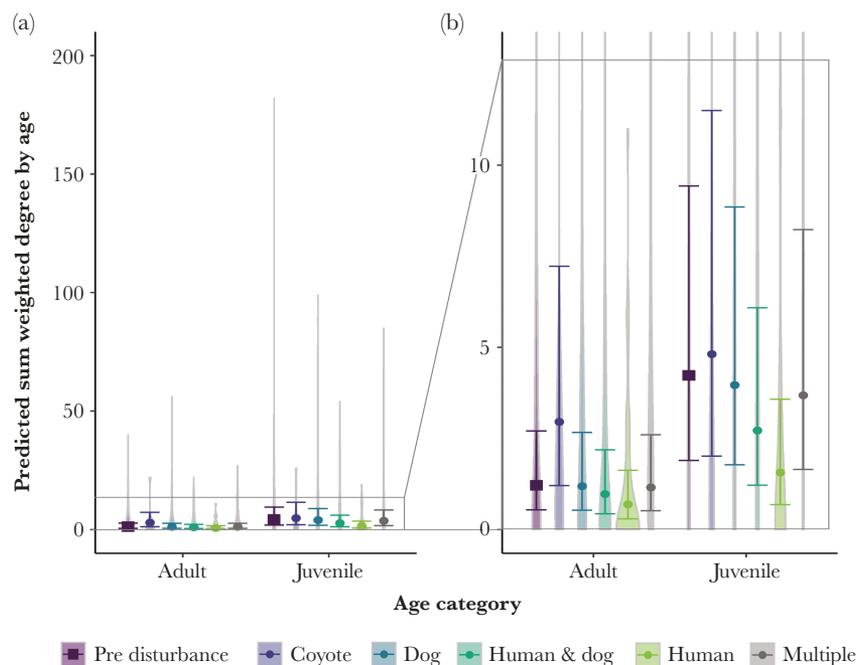


Figure 3

Predicted sum weighted degree against age category and disturbance type for the full affiliative network (a) shows the total range of the raw data and (b) the zoomed-in version to better see the estimates and confidence intervals from the model predictions. Given are the back transformed estimate and 95% confidence intervals of a generalized linear mixed effects model with the sum of weighted degree by age category as the response variable, age category as well as the disturbance category (predisturbance, coyote, dog, human(s) plus a dog(s) [i.e., human with a dog on-leash], human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. The violin plots underneath the mean and confidence intervals indicate the raw data.

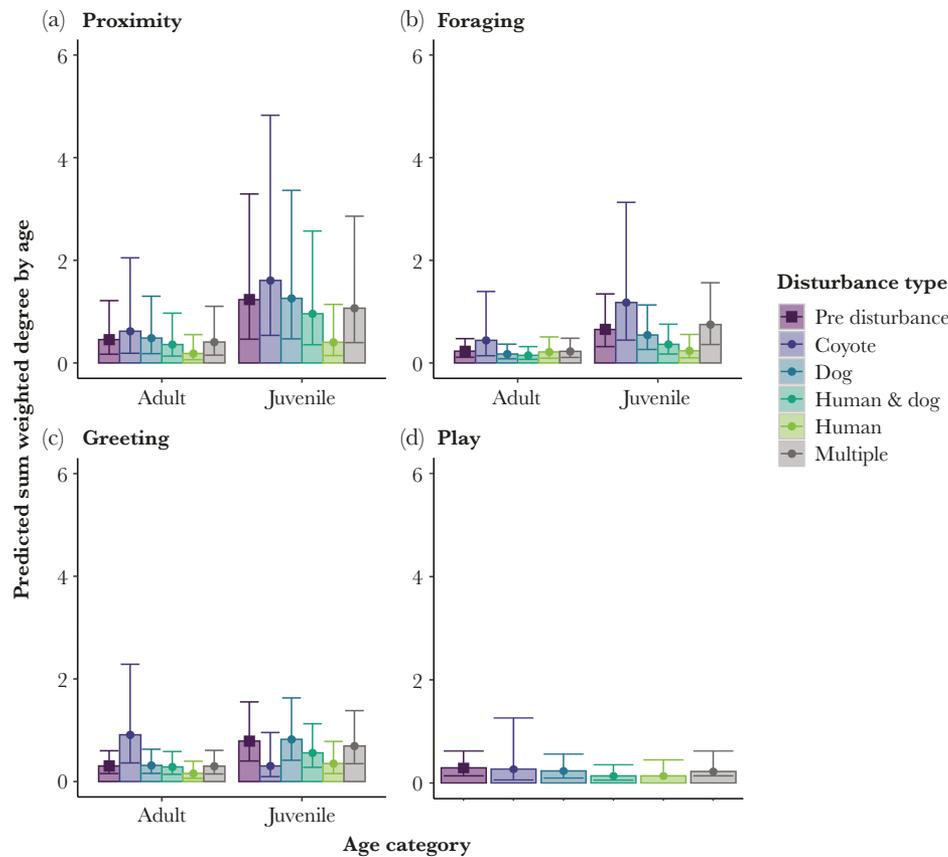


Figure 4

Predicted sum weighted degree against age category and disturbance type for the (a) proximity network, (b) the foraging network, and (c) the greeting network, (d) the sum weighted degree against disturbance type in the play network, which only included juvenile squirrels. Given are the back transformed estimate and 95% confidence intervals of a generalized linear mixed effects model with the sum of weighted degree by age category as response variable, age category as well as the disturbance category (pre-disturbance, coyote, dog(s), human(s) plus a dog(s) [i.e., human with a dog on a leash], human(s), or multiple) as the explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. See Figure S5 for a more detailed plot including the raw data.

Table 4

Model summary statistics for the combined affiliative network from a generalized linear mixed effects model with the sum of weighted degree by age category as the response variable, age category as well as the disturbance category (pre-disturbance, coyote, off-leash dog(s), on-leash dog(s) plus a human(s), human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. Data from 376 pre- and post-disturbance networks. Individual squirrels had up to eight (median = 1) proximity interactions before a disturbance and up to eight (median = 1) after disturbance events

Explanatory variables	Estimate	l-95% CI	u-95% CI	Std. Error	z value	P value
Intercept	0.141	-0.655	0.937	0.406	0.347	0.728
Age (juvenile)	1.250	1.192	1.307	0.029	42.686	>0.001
Disturbance type (coyote)	0.887	0.483	1.291	0.206	4.304	>0.001
Disturbance type (dog)	-0.018	-0.116	0.080	0.050	-0.355	0.722
Disturbance type (dog + human)	-0.221	-0.353	-0.089	0.067	-3.279	0.001
Disturbance type (human)	-0.562	-0.867	-0.257	0.156	-3.610	>0.001
Disturbance type (multiple)	-0.045	-0.162	0.072	0.060	-0.751	0.453
Age (juvenile) * Disturbance type (coyote)	-0.762	-1.181	-0.342	0.214	-3.560	>0.001
Age (juvenile) * Disturbance type (dog)	-0.046	-0.153	0.061	0.054	-0.843	0.399
Age (juvenile) * Disturbance type (dog + human)	-0.221	-0.366	-0.075	0.074	-2.972	0.003
Age (juvenile) * Disturbance type (human)	-0.434	-0.781	-0.087	0.177	-2.450	0.014
Age (juvenile) * Disturbance type (multiple)	-0.093	-0.220	0.034	0.065	-1.438	0.150

Significant results are highlighted in bold.

degree by age for the foraging network (Figure 5f, Table S3), with adults showing a narrower distribution of change than juveniles, though this result did not remain when excluding non-interacting squirrels (Figure 5h, Table S3). By contrast, we found no difference in the mean direction of change in weighted degree by age for any network type (Figure 5e,g; Table S3) suggesting that these results are driven by adults not being recorded interacting before or after a disturbance in the foraging network.

DISCUSSION

In this study, we examined whether and how natural and anthropogenic disturbances affected the affiliative behavior of California ground squirrels. We expected that if squirrels were more habituated to human disturbances we would detect no significant differences in their affiliative behaviors between the pre- and

post-disturbance networks. Accordingly, we predicted individuals would only increase the social behaviors which simultaneously allow them to maintain high levels of vigilance after disturbances by coyotes and dogs (i.e., social foraging and sitting in proximity). In contrast to these predictions, we found an increase in greeting behaviours by adults in response to coyotes and a reduction in social foraging in response to dogs and humans by all individuals. Furthermore, we found that median network densities were similar after disturbances by all disturbers across any of the network types, though we found more variability in the number of social interactions (network density) as well as more occasions with no aboveground interactions after all types of disturbances. Squirrels mostly did not alter their social interactions to disturbances, and there were no clear directional changes when they did, that is, after some disturbances, squirrels engaged in more affiliative behaviors whereas after other disturbances squirrels engaged in fewer

Table 5

Model summary statistics for the proximity network from a generalized linear mixed effects model with the sum of weighted degree by age category as the response variable, age category as well as the disturbance category (pre-disturbance, coyote, off-leash dog(s), on-leash dog(s) plus a human, human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. Data from 376 pre- and post-disturbance networks. Individual squirrels had up to eight (median = 1) proximity interactions before a disturbance and up to eight (median = 1) after disturbance events

Explanatory variables	Estimate	l-95% CI	u-95% CI	Std. Error	z value	P value
Intercept	-0.848	-1.824	0.128	0.498	-1.704	0.088
Age (juvenile)	0.999	0.912	1.085	0.044	22.627	<0.001
Disturbance type (coyote)	0.297	-0.399	0.993	0.355	0.837	0.402
Disturbance type (dog)	0.064	-0.076	0.204	0.072	0.892	0.372
Disturbance type (dog + human)	-0.239	-0.440	-0.039	0.102	-2.337	0.019
Disturbance type (human)	-0.913	-1.431	-0.394	0.265	-3.448	0.001
Disturbance type (multiple)	-0.107	-0.281	0.067	0.089	-1.203	0.229
Age (juvenile) * Disturbance type (coyote)	-0.043	-0.759	0.673	0.365	-0.119	0.906
Age (juvenile) * Disturbance type (dog)	-0.044	-0.200	0.113	0.080	-0.549	0.583
Age (juvenile) * Disturbance type (dog + human)	-0.015	-0.236	0.206	0.113	-0.133	0.895
Age (juvenile) * Disturbance type (human)	-0.210	-0.809	0.388	0.305	-0.689	0.491
Age (juvenile) * Disturbance type (multiple)	-0.039	-0.232	0.154	0.098	-0.396	0.692

Significant results are highlighted in bold.

Table 6

Model summary statistics for the foraging network from a generalized linear mixed effects model with the sum of weighted degree by age category as the response variable, age category as well as the disturbance category (pre-disturbance, coyote, off-leash dog(s), on-leash dog(s) plus a human(s), human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. Data from 376 pre- and post-disturbance networks. Squirrels had up to six (median = 0) social foraging interactions before a disturbance and up to five (median = 0) after disturbance events

Explanatory variables	Estimate	l-95% CI	u-95% CI	Std. Error	z value	P value
Intercept	-1.482	-2.210	-0.753	0.372	-3.985	<0.001
Age (juvenile)	1.050	0.927	1.173	0.063	16.749	<0.001
Disturbance type (coyote)	0.659	-0.252	1.570	0.465	1.418	0.156
Disturbance type (dog)	-0.279	-0.513	-0.045	0.119	-2.339	0.019
Disturbance type (dog + human)	-0.427	-0.691	-0.164	0.134	-3.178	0.001
Disturbance type (human)	-0.068	-0.562	0.425	0.252	-0.272	0.786
Disturbance type (multiple)	-0.017	-0.283	0.249	0.136	-0.126	0.900
Age (juvenile) * Disturbance type (coyote)	-0.068	-0.974	0.835	0.461	-0.150	0.881
Age (juvenile) * Disturbance type (dog)	0.098	-0.160	0.356	0.132	0.745	0.456
Age (juvenile) * Disturbance type (dog + human)	-0.166	-0.465	0.133	0.153	-1.088	0.277
Age (juvenile) * Disturbance type (human)	-0.945	-1.562	-0.327	0.315	-3.000	0.003
Age (juvenile) * Disturbance type (multiple)	0.154	-0.130	0.438	0.145	1.061	0.289

Significant results are highlighted in bold.

Table 7

Model summary statistics for the *greeting-sniffing network* from a generalized linear mixed effects model with the sum of weighted degree by age category as response variable, age category as well as the disturbance category (pre-disturbance, coyote, off-leash dog(s), on-leash dog(s) plus a human(s), human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. Data from 376 pre- and post-disturbance networks. Greeting interactions ranged from zero to six (median = 0) before a disturbance and from zero to five (median = 0) after a disturbance event

Explanatory variables	Estimate	l-95% CI	u-95% CI	Std. Error	z value	P value
Intercept	-1.243	-1.923	-0.563	0.347	-3.584	<0.001
Age (juvenile)	0.954	0.837	1.070	0.059	16.044	<0.001
Disturbance type (coyote)	1.095	0.456	1.733	0.326	3.362	0.001
Disturbance type (dog)	0.036	-0.150	0.223	0.095	0.383	0.702
Disturbance type (dog + human)	-0.062	-0.320	0.196	0.132	-0.472	0.637
Disturbance type (human)	-0.644	-1.275	-0.014	0.322	-2.003	0.045
Disturbance type (multiple)	-0.011	-0.238	0.216	0.116	-0.093	0.926
Age (juvenile) * Disturbance type (coyote)	-2.052	-3.031	-1.074	0.499	-4.112	<0.001
Age (juvenile) * Disturbance type (dog)	0.009	-0.200	0.218	0.107	0.084	0.933
Age (juvenile) * Disturbance type (dog + human)	-0.281	-0.574	0.012	0.15	-1.877	0.060
Age (juvenile) * Disturbance type (human)	-0.165	-0.884	0.554	0.367	-0.451	0.652
Age (juvenile) * Disturbance type (multiple)	-0.118	-0.371	0.136	0.129	-0.910	0.363

Significant results are highlighted in bold.

Table 8

Model summary statistics for the *play network* from a generalized linear mixed effects model with the sum of weighted degree by age category as response variable, age category as well as the disturbance category (pre-disturbance, coyote, off-leash dog(s), on-leash dog(s) plus a human, human(s), or multiple) as explanatory variable and year of data collection, the unique disturbance identifier and the percentage of juveniles seen during the disturbance as random effects. Data from 376 pre- and post-disturbance networks. Juvenile squirrels interacted up to six times (median = 0) before a disturbance and up to five times (median = 0) after a disturbance event

Explanatory variables	Estimate	l-95% CI	u-95% CI	Std. Error	z value	P value
Intercept	-1.229	-1.982	-0.475	0.385	-3.196	0.001
Disturbance type (coyote)	-0.081	-0.869	0.707	0.402	-0.202	0.840
Disturbance type (dog)	-0.217	-0.331	-0.103	0.058	-3.732	<0.001
Disturbance type (dog + human)	-0.740	-0.922	-0.559	0.093	-7.993	<0.001
Disturbance type (human)	-0.741	-1.155	-0.327	0.211	-3.509	0.001
Disturbance type (multiple)	-0.259	-0.404	-0.113	0.074	-3.486	0.001

Significant results are highlighted in bold.

affiliative interactions. We did, however, regularly detect alarm calls in response to disturbances, particularly in response to the presence of domestic dogs and coyotes, suggesting that individuals alert each other and then seek safety below ground.

In response to disturbances by coyotes, adults greeted more, whereas juveniles greeted less and maintained levels of play similar to those before a coyote arrived. This contrasts with our predictions, as we expected squirrels to increase behaviors that allow for increased vigilance (i.e., sitting in proximity and social foraging) in response to this natural predator. We expected this response as we have witnessed direct predation by both dogs and coyotes at the study site. Despite our limited number of disturbance events by coyotes, we detected a difference in response according to age whereby adults greeted more but juveniles greeted less after disturbances by coyotes. An increase in greetings by adults might be caused by adults initially hiding belowground in response to coyotes and then re-emerging to join groupmates or some individuals shifting from solitary to group behaviors; both forms of re-joining groupmates following temporary separations could trigger greeting events. Juveniles might not respond to a threat and thus never leave their group, resulting in fewer greeting interactions. Alternatively, juveniles might also initially flee (Hanson and Coss 1997), but might start

to play upon re-emergence rather than greeting each other. This is supported by our finding of juveniles maintaining high levels of play after coyote disturbances, indicating that they might be more naïve about the threat posed. Squirrels may therefore show a spatial behavioral adjustment, forming small subgroups when predation risk is moderate (i.e., a coyote is present though far away) and increasing individual spacing (leading to fewer social interactions) when predation risk is low. Similar patterns of individual aggregation in order to decrease predation risk have been found on a larger spatial scale across different taxonomic groups (Krause and Ruxton 2002; Aureli et al. 2008; Edwards and Waterman 2011; Creel et al. 2014; Gil et al. 2017). Moreover, several species use greetings to promote social cohesion prior to risky collective behavior. For example, spotted hyenas greet coalition partners before mobbing lions (Smith et al. 2011) and wild dogs greet before setting off on group hunts (Robbins 2000; Rütten and Fleissner 2004). The function of greetings in social rodents is relatively poorly understood and our results highlight the need for additional inquiry into its role in promoting social cohesion.

Our findings of reduced network connectivity across all network types (i.e. more completely unconnected networks) suggest that temporary disturbances caused by humans can reduce some

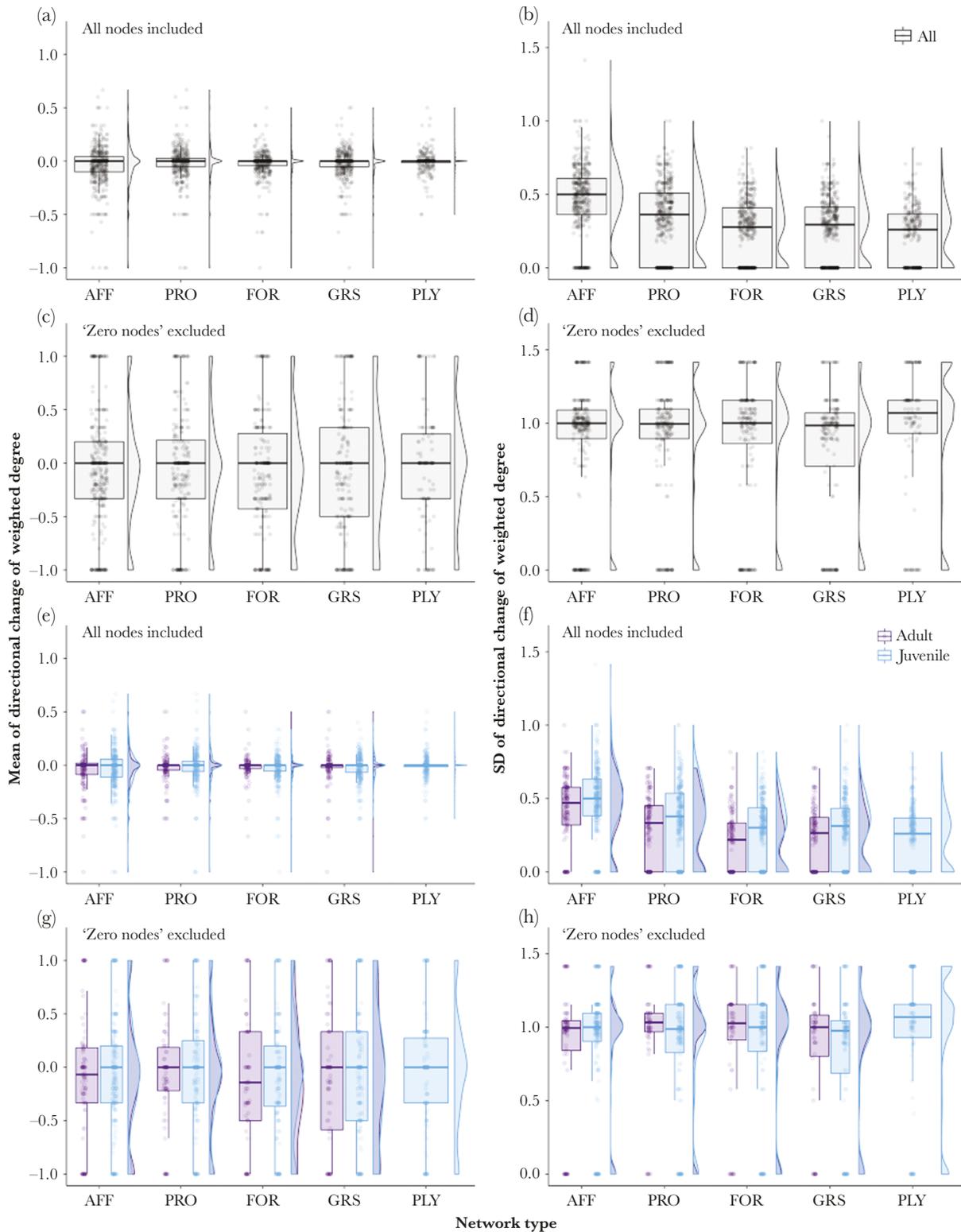


Figure 5

Vertical raincloud plot of the (a) mean and (b) standard deviation (SD) of directional change in weighted degree for each of the full affiliative networks (AFF), proximity networks (PRO), foraging networks (FOR), greeting networks (GRT), and play networks (PLY) including all individuals (black), (c) mean, and (d) SD of directional change in weighted degree for each network type but excluding “zero nodes”, that is individuals which did not interact both before and after a disturbance. (e) mean and (f) SD of directional change in weighted degree by age (adults in dark and juveniles in light) for each network type including all individuals and (g) mean and (h) SD of directional change in weighted degree by age excluding zero nodes. Note that we did not include adults in the play network for plots (e)–(h). The direction of a change was 1 if weighted degree increased after a disturbance event, 0 when weighted degree remained consistent over time, and -1 when weighted degree decreased after a disturbance event. The mean indicates the overall direction of change for each individual whereas the SD shows how consistent an individual is (e.g., a small SD reflects a consistent individual).

activities while promoting others even in a human tolerant species. Thus, overall, disturbances appear to disrupt social connections in aboveground affiliative networks, although animals may remain in vocal contact with conspecifics. For example, these animals likely pay a cost for social instability prompted by responding to dogs off-leash as reflected by their reduced social foraging (despite maintaining consistent levels of proximity, greetings, and play). We found a similar response for humans with a dog on a leash (i.e., reduced social foraging), as well as reduced sitting in proximity. In addition, contrary to our expectations of habituation to humans, squirrels reduced the number of observed affiliative interactions in response to humans across all behavioral categories. However, a similar reduction in social foraging when animals were disturbed was detected, as shown for other species (Pirotta et al. 2015; Maldonado-Chaparro et al. 2018).

A reduction in social foraging in response to dogs and humans might indicate that squirrels perceive these disturbances as more threatening than coyotes, thus moving belowground, rather than staying within proximity of each other aboveground after disturbances. Although we lack precise data on the effect of disturbances on the tendency for squirrels to seek belowground shelter, we know that 70% of California ground squirrels remain aboveground even after being closely approached by a human (during flight initiation distance assays; Ortiz-Jimenez et al. 2022) and typically remain vigilant aboveground when they encounter coyotes or dogs (Owings and Leger 1980; Owings et al. 1986). Individuals that seek shelter belowground or remain vigilant aboveground may suffer an opportunity cost by allocating less time to valuable social foraging activities aboveground. Our interpretation of the social foraging data is also consistent with experimental evidence from captive zebra finch groups that were split from a single socially stable group into two smaller ones for a short amount of time. This disturbance decreased both the strength of social relationships and group foraging efficiency, suggesting that temporary changes in (sub)group size and composition triggered by an outside stressor can negatively affect social structure and group efficiency (Maldonado-Chaparro et al. 2018). Alternatively, because we lack parallel data on all occurrences of solitary foraging, it is also possible that human presence, by providing a “safety cue” from predation, allows individuals to focus on solitary foraging (Luttbeg et al. 2020), and, thus, interact less with each other after disturbances caused by humans. With human activity likely being more global (across the whole study site) than the other disturbance types and lasting longer than other disturbances (though we lack detailed data), the safety effect might be further increased. Coyotes usually stay farther away and remain mostly at one location (Wells and Bekoff 1982; Breck et al. 2019). In contrast, disturbances by dogs can vary widely, with some remaining mostly at one location and others, especially off-leash dogs, traversing the entire study area. Humans going to the park, on the other hand, tend to move around and might also make continuously more noise, for instance when having a picnic or listening to music which might lead to prolonged disturbances not accounted for in this study (pers. obs.).

Due to their relative naïvety, we predicted juvenile squirrels to be less consistent in their social responses than adults. Nonetheless, we found that directional changes in social centrality (weighted degree) of individuals displayed some consistency in responses to short-term perturbations of any type. Adults’ responses were only more consistent than those of juveniles within the social foraging network when all individuals were included. However, this effect is likely due to the individuals that were present before and after

the disturbance, but not interacting with other individuals, that is, “zero nodes”, rather than by adults being more socially selective in their affiliative networks as has been shown for other social mammals (Berman 1982; Holekamp et al. 2012; Smith et al. 2013; Murphy et al. 2020).

To date, few studies have quantified the effects of short-term disturbances on social behavior (but see: Maldonado-Chaparro et al. 2018). Our current study focuses on the effects of various disturbances on aboveground affiliative behaviors as measured across a whole population. Whereas our results extend knowledge by demonstrating the short-term effects of disturbances, including those imposed by humans and domestic dogs, on the social behavior of free-living animals, there are some limitations. Although we assumed all squirrels to be equally affected by and aware of disruptions, this does not have to be the case. For example, it is possible that not all individuals across the landscape perceived threats similarly based on their spatial location relative to the disturbance. Similarly, although our networks were proximity based it is unclear to what extent individuals can use auditory signals such as alarm calls to order to stay connected with further away group members. Moreover, as this species may also socialize belowground, further research is required to understand the effects of disturbance types on belowground activities.

To conclude, our findings suggest that even animals residing in public parks continuously alter their behavior to anthropogenic disturbances multiple times within a day. Human and dog presence reduced social interactions whereas disturbances by coyotes mostly promoted social interactions. We interpret these results as indicating that humans disrupt immediate social interactions for squirrels, and that human presence can lead to an opportunity cost. However, this interpretation requires confirmation through targeted experiments and further analysis of alarm call production by context. More broadly, our findings demonstrate the underappreciated sensitivity of animal social interactions to short-term ecological disturbances, raising key questions about their long-term consequences for animal social cohesion. By documenting that human-induced changes in social interactions vary from those triggered by natural predators, our findings provide a deeper understanding of possibly divergent forces that natural threats – encountered over evolutionary time scales – and relatively recent anthropogenic factors impose on the social lives of animals. Such divergent social responses may indeed have important downstream effects on behaviorally-mediated ecological processes in a rapidly changing world.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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AUTHOR CONTRIBUTIONS

The observational data was collected by J.E.S. and C.O.J. with additional help from other members of the field crew who contributed to this long-term study. This specific project was conceived by J.E.S. and G.E.C.G. and the data were analyzed by G.E.C.G. with support by J.C.E. and M.J.S. G.E.C.G. wrote the first draft of the manuscript with support from J.E.S.; all authors helped to revise it and gave final approval for publication.

Ethics Statement: All field methods were approved by the Animal Care and Use Committee of Mills College, U.S.A., and are consistent with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon 2011). Research permits were obtained from the California Department of Fish and Wildlife, U.S.A. and the East Bay Regional Park District, U.S.A.

Data Availability: Analyses reported in this article can be reproduced using the data provided by the authors (Gall et al. 2022).

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