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Catch the wave: prairie dogs assess neighbours' awareness using contagious displays

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The jump–yip display of black-tailed prairie dogs (*Cynomys ludovicianus*) is contagious, spreading through a prairie dog town as 'the wave' through a stadium. Because contagious communication in primates serves to assess conspecific social awareness, we investigated whether instigators of jump–yip bouts adjusted their behaviour relative to the response of conspecifics recruited to display bouts. Increased responsiveness of neighbouring town members resulted in bout initiators devoting a significantly greater proportion of time to active foraging. Contagious jump–yips thus function to assess neighbours' alertness, soliciting social information to assess effective conspecific group size in real time and reveal active probing of conspecific awareness consistent with theory of mind in these group-living rodents.

1. Introduction

Members of group-living species rely upon collective vigilance to detect predators [1], occasionally synchronizing vigilance so as to enhance the detection of potential threats [2,3]. As the number of individuals residing within a group increases, each individual can devote less time to vigilance and more time to other activities, for example foraging [1,4,5], owing, in part, to the cumulative effect of each individual's finite probability of detecting presumptive threats [6–8]. Where such group-size effects are dependent upon collective detection, however, individual group members must assess the size of the group in which they reside [9], and perhaps more importantly, the vigilance of fellow group members [10,11] to tailor their behaviour to the situation at hand.

Black-tailed prairie dogs (*Cynomys ludovicianus*) are group-living, semi-fossorial rodents that are subject to intense predation by terrestrial and avian predators [12,13]. Classic group-size effects, with diminishing individual allotment of time to vigilance and increasing time devoted to foraging with increasing group size, have been documented observationally [14] and experimentally [15] among black-tailed prairie dogs, though the mechanism via which group size is assessed is unknown. Just as synchrony in the activity of group members promotes social cohesion [16,17] through social facilitation among individuals [18], fine-tuning one's foraging–vigilance trade-off relative to the vigilance of other group members would prove adaptive [11].

We investigated contagious, multimodal 'jump–yip' displays of black-tailed prairie dogs as a potential means of adjusting the instigating individual's foraging–vigilance trade-off relative to the responsiveness, and hence vigilance, of neighbouring group members. In instigating a jump–yip bout, an individual raises its anterior torso above the ground, achieving at least an erect posture, though sometimes propelling itself from the ground. This postural change is coupled with the extension of the signaller's forelimbs and the emission of a vocalization that can be described phonetically as 'wee-oo' [19] as the anterior torso is raised and then lowered, resulting in a multimodal display lasting around a second ([20]; see the electronic supplementary material, movie S1). Unlike other prairie dog vocalizations or displays, the jump–yip is typically contagious, spreading from the initiator through neighbouring colony members as 'the wave' through a stadium ([20]; see the electronic supplementary material, movie S2). To date, the function of the jump–yip has proved elusive.

Initial accounts were purely descriptive [21,22], though subsequent researchers have suggested that the jump–yip serves as a territorial call [12], an 'all-clear' [13,23] or 'end-of-danger' signal [12], a means of promoting social bonding within the group ('contact group cohesion'; [19]), an indicator that the signaller is less likely to show escape behaviour in the face of threat, promoting temporarily heightened vigilance among conspecifics [20], or as Owings & Coss [24] suggested for various animal signals, a means of managing conspecifics. Here, such management would presumably promote reliance on conspecifics for predator detection, thereby allowing the signaller to devote time to activities other than watchfulness.

The acquisition of information from conspecifics proves adaptive in contexts including foraging [25], habitat choice [26], mate choice [27], parenting [28], tool use [29], and both anti-brood parasite [30] and anti-predator responses [31]. Although social learning and public information use are often considered tacitly different concepts [32–34], the effective utilization of socially available information requires that individuals assess the veracity of the information they receive [35–37], and sample available information on an ongoing basis to ensure that information is up-to-date [38]. Such assessment is of particular importance where ignoring information proves costly [39], as would be the case where animals are faced with the risk of predation [8].

We hypothesized that the instigation of a jump–yip bout serves to probe neighbouring individuals for feedback regarding their current vigilance state. If that were the case, we predicted that subsequent time devoted to personal vigilance by bout instigators would be directly proportional to the latency of the first conspecific to respond to the instigator's jump–yip (greater delay in response indicating reduced alertness of neighbours), and inversely proportional to the number of conspecifics joining a jump–yip bout (a smaller number indicating reduced collective vigilance) as well as the overall duration of the bout (reduced length of contagion indicative of lesser collective vigilance). Given the well-documented trade-off between foraging and vigilance in black-tailed prairie dogs [13–15], we also predicted that the allocation of time to foraging by bout instigators would be inversely correlated with the latency of the first conspecific to respond in kind with a jump–yip and positively correlated with the number of individuals recruiting to, and the overall duration of jump–yip bouts.

2. Material and methods

To ascertain whether instigator vigilance and foraging behaviour were affected by subsequent jump–yip bout properties (latency to first response, number of individuals recruited and bout duration), we video recorded a total of 173 jump–yip bouts during November 2003 and from May through September 2004 within 16 distinct prairie dog towns spread across six populations, including 14 naturally occurring towns in South and North Dakota, USA, and two introduced towns in Winnipeg, Manitoba, Canada (see R.L. Senkiw M.Sc. thesis for further details; downloadable at: http://mspace.lib.umanitoba.ca/bitstream/1993/2842/1/MSc%20Thesis.pdf). To ensure our results were unconfounded, we eliminated bouts interrupted by the appearance of predators, prairie dog vocalizations other than those constituting part of the jump–yip bout, humans or vehicles, and those where the behaviour of the bout instigator could not be distinguished because it was out of frame or out of focus in the video recording, or where any ambiguity existed regarding the identity of the bout initiator. Thus, our final dataset included data from 27 independent bout initiators from 14 distinct towns (one to three bouts per town) among the six populations, for which we quantified the proportion of time the bout instigator engaged in vigilance (with its head above the horizontal plane) and the proportion of time spent foraging (head below the horizontal plane, grazing or chewing) in the 1 min subsequent to the second syllable of the bout instigator's 'wee-oo' call. Postures in which the head was below the horizontal plane but where neither active grazing nor chewing occurred were not scored as vigilance or foraging. Limiting estimation of vigilance and foraging to only 1 min maximized the likelihood that the bout instigator's behaviour was attributable solely to properties of the current jump–yip bout. Bouts were considered independent of each other if at least 4 s elapsed without an individual manifesting a jump–yip, based on the 5 s criterion Smith *et al.* [20] employed to delineate unique bouts, and on an obvious discontinuity in the distribution of individuals recruiting to bouts after 4 s in our larger 173-bout sample of videotaped jump–yip bouts. For each bout, we recorded the latency (s) for the first individual to respond with a jump–yip to the bout instigator, the number of jump–yip responses within each bout and the overall duration of each bout (s). We applied linear regressions to test for relationships between those three independent variables, and the proportions of time the bout instigator devoted to either vigilance or foraging in the post-bout period, considering those statistically significant where $p < 0.05$.

3. Results

The proportion of time devoted to vigilance by bout initiators was unaffected by the latency for the initial respondent to recruit to a contagious jump–yip bout ($F_{1,25} = 0.03$, $p = 0.87$; figure 1). Further, although time allocated to vigilance tended to decrease with both an increasing number of respondents and increasing bout duration, those declines fell short of statistical significance ($F_{1,25} = 2.86$, $p = 0.10$ and $F_{1,25} = 2.89$, $p = 0.10$, respectively; figure 1). Similarly, although there was a trend toward decreasing time devoted to foraging with increasing latency of conspecifics to respond to the initial propagation of a jump–yip, that change was not statistically significant ($F_{1,25} = 1.31$, $p = 0.26$; figure 1). Statistically significant relationships were detected for the proportionate allocation of time to active foraging, relative to both the number of respondents recruiting to a given jump–yip bout ($F_{1,25} = 5.87$, $p = 0.02$) and the overall duration of contagious display bouts ($F_{1,25} = 4.50$, $p = 0.04$). Bout instigators increased time allocated to foraging with both an increasing number of individuals recruiting to a jump–yip bout and increasing bout duration (figure 1). That said, bout duration was positively correlated with the number of respondents ($r = 0.82$), though neither bout duration nor the number of respondents recruiting to a jump–yip bout was well correlated with latency to response ($r = 0.32$ and $r = 0.09$, respectively). Significant differences or pronounced trends for bout initiators to alter their allocation of time to foraging and vigilance in accord with our predictions exist for five of the six relationships examined, which in itself, should occur rarely by chance alone (binomial $p = 0.11$).

4. Discussion

Instigators of jump–yip bouts increased their proportionate allocation of time to foraging as the responsiveness of conspecifics increased. The absence of any relationship between

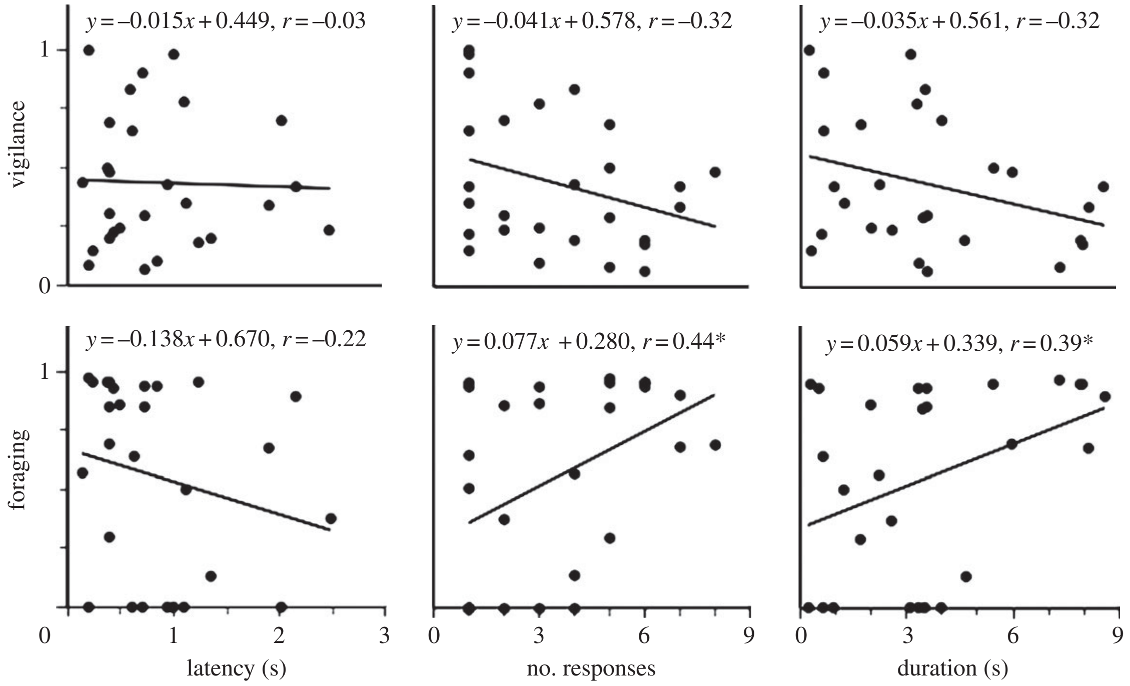

Figure 1. Proportionate allocation of black-tailed prairie dog jump–yip bout instigator time to foraging and vigilance relative to the latency (s) of the first respondent to contribute to a contagious bout of calling, the number of respondents recruiting to the bout and the overall duration (s) of the jump–yip bout evoked (*$p < 0.05$).

bout instigator time allocation to vigilance and latency of initial conspecific response is not attributable to bout instigators consistently manifesting maximal vigilance, in that the proportion of time devoted to vigilance varied considerably across the range of response latencies observed. Moreover, bout instigators are undoubtedly constrained to devote time to vigilance so as to assess bout response characteristics prior to adjusting their foraging–vigilance trade-off accordingly. The effect of conspecific responsiveness on the proportion of time devoted to foraging is not attributable to variation in group size proper, in that treating aboveground group size as a covariate did not alter our findings. Jump–yip displays thus function to promote the accrual of information regarding collective vigilance within the group, clarifying earlier speculation regarding the function of these displays.

While conspecific responsiveness to the instigation of a jump–yip bout significantly affected the time bout initiators allocated to foraging, only an inconsequential change was detected in instigator personal vigilance with variation in conspecific response. How accurately our simple postural assay of the head being held above the horizontal plane reflects an individual's state of vigilance remains an open question, as does consideration of any potential cost associated with the use of this socially acquired information [40].

Our results are consistent with the assertion by Owings & Coss [24] that tonic communication functions to manage conspecifics, in this case providing up-to-date, context-specific information on the vigilance of conspecific group members. Among group-living species, accurate decision-making is facilitated via the use of social information [41,42], particularly where certain group members are less well informed than others [43]. Conspecific neighbours constitute a particularly important source of information where animals are subject to predation risk [44], and reliance on that information may, in and of itself, prompt social contagion [45]. In mimicking the evasive behaviour of neighbours, group-living insects avoid unseen predators (the 'Trafalgar effect'; [46]). Similarly, schooling fish avoid previously un-encountered predators by mimicking their neighbours' behaviour [47].

Based on both previous empirical findings and an individual-based model, Beauchamp *et al.* [11] argued that selection would favour monitoring and copying the vigilance of neighbours, resulting in collective waves of vigilance that would facilitate collective detection of predators. Given the coevolutionary nature of predator–prey relationships, however, predators might be expected to cue-in on, and coordinate their attacks relative to lulls in such waves. Our empirical findings for black-tailed prairie dogs reveal collective waves of coordinated behaviour, presumably optimizing foraging efficiency of individuals reciprocally sharing information regarding collective vigilance. Participants within a bout thus likely benefit via reciprocal altruism [48] among resident town members, with any risk of enhanced detection by presumptive predators owing to the production of this conspicuous display being shared among signallers. Such broadly subscribed patterns of display behaviour may also serve as a potent pronouncement of vigilance [49], thereby reducing predation risk among town members in general.

The wave-like spread of jump–yip displays through towns of black-tailed prairie dogs is consistent with literature implicating the use of public information in social evolution [33,34] and contagious displays in particular, in the evaluation of conspecific social awareness [50]. Yawning in humans and other primates [51,52] and laughter among humans [53] provide familiar examples of contagious displays. Platek *et al.* [51], among others, have reported that such behaviours are associated with self-processing and empathy in humans. Indeed, emotional contagion among humans has been considered at least an important precursor to more advanced 'Theory of mind' abilities [54], wherein contagion represents the first step toward respondent awareness of the emotional state of the instigator by invoking that same state in the respondent [55]. Emotional contagion in humans, however, transcends superficial motor mimicry and represents a means of sharing affect of considerable evolutionary antiquity [56]. Although the existence of a relationship between empathy and social contagion has long been recognized for non-human primates [57], it has more recently been reported for dogs [58]. Applied to our findings, it is evident that in responding to the emergent display properties of neighbours recruited to a jump–yip bout, black-tailed prairie dogs manifest at least a rudimentary awareness of the state of conspecific group members. As Barrett *et al*. [59] aptly point out, communication and mind are intimately intertwined, in that the 'mind' is a form of social participation or process, rather than an entity unto itself, ultimately serving to rationalize the organism's social environment. In this light, it is not surprising that these highly social animals have evolved coordinated social behaviour and commensurate cognitive abilities [60] promoting their success in the face of intense predation pressure. Further study is required to elucidate additional nuances of the mechanism, along with the ultimate implications of this newly discovered, adaptive social contagion in prairie dogs.

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Data accessibility. Bout response characteristic and bout initiator behavioural data file: Dryad doi:10.5061/dryad.g76t8.

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