

Behavioral flexibility vs. rules of thumb: how do grey squirrels deal with conflicting risks?

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3 **Lay Summary:** Using ‘rules of thumb’ based on constant environmental cues may be
4
5 2 the best way for squirrels to assess risk when hiding food. When squirrels assess the
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7 3 competing risks of theft and predation, they use fixed cues such as distance from
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9 4 cover, rather than using constantly changing visual cues such as number of other
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11 5 squirrels or predators present. Using fixed cues may save them time that might
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13 6 otherwise be spent constantly updating their risk assessments.
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For Review Only

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3 8 **Title:** Behavioral flexibility vs. rules of thumb: how do grey squirrels deal with
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5 9 conflicting risks?
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8 10 **Abbreviated title:** Behavioral flexibility vs. rules of thumb
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11
12 12 **Abstract:** In order to test how flexibly animals are able to behave when making trade-
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14 13 offs that involve assessing constantly changing risks, we examined whether wild
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16 14 Eastern grey squirrels showed flexibility of behavioral responses in the face of
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18 15 variation in two conflicting risks, cache pilferage and predation. We established that
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20 16 cache pilferage risk decreased with distance from cover, and was thus negatively
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22 17 correlated with long-term predation risk. We then measured changes in foraging and
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24 18 food caching behavior in the face of changes in the risk of predation and food theft
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26 19 over a short time-scale. We found that, overall, squirrels move further away from the
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28 20 safety of cover when they cache, compared to when they forage, as predicted by
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30 21 pilferage risk. However, there was no effect of immediate pilferage or predation risk
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32 22 (i.e. the presence of potential predators or pilferers) on the distance from cover at
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34 23 which they cached, and only a slight increase in forage distance when predation risk
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36 24 increased. These results suggest that ‘rules of thumb’ based on static cues may be
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38 25 more cost-effective for assessing risk than closely tracking changes over time in the
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40 26 way suggested by a number of models of risk assessment.
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48 28 **Key Words:** behavioral flexibility; food caching; pilferage risk; risk assessment; rule
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3 31 **Introduction**
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8 When animals face a conflict between two competing demands, we expect them to
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10 34 make adaptive trade-offs that provide a sensible solution to the problem that they face.
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12 35 Behavior should adjust as a function of the relative intensities of the conflicting
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14 36 demands (e.g. Bouskila 1995). However, this could happen in more than one way.
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16 37 Animals may respond to general cues that are, in the long term, correlated with
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18 38 important risk factors, such as exposure to predators (e.g. Leaver 2004). Recently,
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20 39 however, researchers have become interested in flexibility over a shorter time-scale in
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22 40 the trade-offs made by animal decision makers. This is seen, in some cases, as
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24 41 indicating not just a finer resolution of risk assessment, but a higher level of
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26 42 intelligence than that required by simply following a set of 'rules', implicating the
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28 43 involvement of higher cognitive processes which may be required for more rapid
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30 44 responses to complex trade-offs (Emery and Clayton 2004). If this is the case, we
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32 45 might expect species which are generally considered to possess higher or more
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34 46 complex cognition to excel at adjusting their behavior in response to fine scale
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36 47 changes in various cues of risk. One such group of animals that has been highlighted
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38 48 in this regard are the scatter cachers, animals that hide food in multiple locations for
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40 49 later use.
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45 Examining flexibility of behavior in animals as an assay of intelligence has
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47 51 been suggested as a new and fruitful area of study in comparative cognition (e.g. Roth
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49 52 and Dicke 2005), but in such studies to date, flexibility is usually tested in domain-
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51 53 specific novel situations to see whether animals are capable of innovation (e.g.
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53 54 Thornton and Samson 2012) or by using standard tasks such as reversal learning to
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55 55 quantify flexibility (e.g. Boogert et al. 2010; Leal and Powell 2011, Chow et al.
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3 56 2015), rather than examining how flexible animals are in their everyday lives when
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5 57 faced with commonplace situations involving trade-offs. Flexibility in novel situations
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7 58 is assumed to be associated with flexibility in everyday life (e.g. Sol et al. 2002;
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9 59 Griffin et al. 2014) and ought also to be associated with animal intelligence. A review
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11 60 by Verdolin (2006) brings together papers in which flexibility has been studied by
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13 61 examining the adaptive trade-offs made by animals faced with real-world problems.
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16 62 However these studies are often based on models assuming static environments, or
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18 63 considering only one fluctuating risk factor, namely predation risk, and its effects on
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20 64 foraging and vigilance behaviors (e.g. Lima and Bednekoff 1999; Brown and Kotler
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22 65 2004; Higginson et al. 2012). We do not know as much about how animals respond to
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24 66 small scale changes in *conflicting* risks over time and place, which may require
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26 67 adjustments to the relative values playing into a trade-off on a minute-to-minute basis.
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30 One of the unique problems faced by animals that scatter cache their food into
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32 69 multiple locations is that they must decide how to deal with the conflicting risks of
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34 70 predation and pilferage when deciding where to put their caches. Areas with high risk
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36 71 of predation tend to be the safest from pilferage and vice versa. For example,
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38 72 Merriam's kangaroo rat (*Dipodomys merriami*) caches are at less risk of pilferage
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40 73 when they are in open rather than covered microhabitat, but predation risk is higher in
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42 74 open habitats (Bouskila 1995; Leaver 2004). This dilemma offers an opportunity to
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44 75 study the decisions that animals make in the face of two risk factors that pose
45
46 76 considerable selective pressures. In addition, this decision potentially involves
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48 77 foresight, because consideration of predation risk is important not just during caching,
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50 78 but also during cache recovery at a later point in time when predation risks may have
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52 79 changed, for instance, if leaves have dropped from trees so they provide less cover, or
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54 80 key predators are hibernating.
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3 81 When caching in the presence of potential pilferers, rodents use a number of
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5 82 strategies which may function to reduce loss of caches to pilferers. They may reduce
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7 83 caching, or stop caching entirely (e.g. Preston and Jacobs 2005; Carrascal and Moreno
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9 84 1993) or they may try to conceal the location of caches in various ways (e.g. Leaver et
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11 85 al. 2007; Dally et al. 2005). Additionally, it is possible that they may place caches in
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13 86 areas where they are less likely to be pilfered, for example, choosing to put them in
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15 87 areas further from cover (e.g. Leaver 2004; Steele et al. 2014). In such areas,
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17 88 predation risk is likely to be high, and this is the behavioral choice that we investigate
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19 89 in this study. Pilferage risk is not a constant, rather, it varies with a number of factors,
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21 90 including microhabitat and food value (Leaver 2004; Steele et al. 2014), density of
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23 91 caches (Daly et al. 1992; Leaver 2004) and visual access of potential pilferers (e.g.
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25 92 Bednekoff and Balda 1996; Heinrich and Pepper 1998). Previous research has shown
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27 93 that many caching animals act as though to minimise pilferage by flexibly responding
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29 94 to the presence of conspecifics (e.g. Dally et al. 2005; Leaver et al. 2007), but we
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31 95 know less about how animals modulate these responses to accommodate other
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33 96 simultaneously varying factors, such as predation risk. Predation risk, like pilferage
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35 97 risk, is also highly variable. In the long term, predation risk varies depending on
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37 98 factors such as distance from safety or visibility, but it also varies acutely in the short
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39 99 term when direct predator cues or actual presence are detected by a foraging or
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41 100 caching prey animal.

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47 101 Most small animals are safest when foraging under cover, and they prefer to
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49 102 forage in locations with good overhead cover and close to the base of trees or shrubs
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51 103 particularly when predation risk is high (e.g. Thorsen et al. 1998; Perea et al. 2011).
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53 104 This preference is based on two aspects of protection; ease of escape and restricted
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55 105 visual access for both aerial and ground predators. However, it is likely that the

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3 106 locations where animals feel safest also face the highest risk of cache pilferage since
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5 107 these areas have a higher density of foraging conspecifics, which increases the
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7 108 likelihood that a cache will be discovered and pilfered. As a result, animals are faced
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9 109 with a dilemma about the safest place to make a cache, and they will be forced to
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11 110 make trade-offs between minimising pilferage risk and minimising predation risk. We
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13 111 predict that caching animals will make adaptive and flexible trade-offs in response to
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15 112 cues of pilferage and predation risk. However, these cues are of two types. On the
16
17 113 one hand, there are static cues such as distance from cover. On the other hand, there
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19 114 are dynamic cues such as the number of potential cache pilferers present at the time of
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21 115 caching (since conspecifics might utilise visual access in order to assist them in
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23 116 pilferage) and predation cues such as traffic through the study site during any
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25 117 particular caching bout (Bouskila & Blumstein 1992; Lima & Bednekoff 1999; Steele
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27 118 et al. 2014). We are interested in whether either static or dynamic cues are used by
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29 119 small mammals to assess predation and pilferage risk whilst foraging and caching, and
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31 120 if both are used, what is their relative importance. To the best of our knowledge, these
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33 121 two variables have not been examined within a single study.

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38 122 We used Eastern grey squirrels (*Sciurus carolinensis*) to address this question,
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40 123 since they make numerous long-term scatter caches which they rely on for their
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42 124 survival over winter (Vander Wall 1990). They respond to conspecifics as
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44 125 competitors (Hopewell & Leaver 2008) and they are very sensitive to social cues of
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46 126 pilferage risk when caching food (Leaver et al. 2007; Hopewell & Leaver 2008),
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48 127 which indicates that cache pilferage by conspecifics has been a strong selective
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50 128 pressure in this species, and that they respond to cues of pilferage risk in an adaptive
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3 130 A number of studies show that grey squirrels are also sensitive to predation
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5 131 risk and that they reliably make adaptive trade-offs between predation risk and
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7 132 foraging efficiency in stable environments with unchanging, static, cues of predation
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9 133 risk (e.g. Lima et al. 1995; Newman & Caraco 1987; Newman et al. 1988). All of
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11 134 these changes in foraging behavior under greater risk of predation indicate that
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13 135 squirrels attempt to spend less time in risky areas. One recent study (Steele et al.
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15 136 2014) has also shown that grey squirrels, like kangaroo rats (Leaver 2004), cache
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17 137 more valuable food in areas that are riskier in terms of predation, compared to when
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19 138 they cache less valuable food, which makes it less vulnerable to pilferage. Taken
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21 139 together, these studies show clearly that grey squirrels make adaptive trade-offs when
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23 140 caching food for future use, and that they are sensitive to both predation and pilferage
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25 141 risks.

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29 142 In this study, we investigate the trade-offs made by squirrels foraging and
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31 143 caching food in conditions that naturally vary in both predation and pilferage risk over
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33 144 space and time. In order to ensure that cache placement by squirrels in our study was
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35 145 an adaptive response to pilferage risk, we first sought to replicate Steele et al.'s (2014)
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37 146 findings at our UK study site; namely, to confirm that cache pilferage rates change
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39 147 with predation risk, by burying artificial caches at varying distances from trees and
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41 148 checking pilferage on a daily basis. Subsequently, in order to test whether squirrels
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43 149 added an assessment of pilferage risk to their assessment of predation risk, we
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45 150 observed squirrels caching naturally foraged nuts in the field. We mapped the location
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47 151 of each cache in relation to nearest cover and compared differences in cache
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49 152 placement when pilferage risk varied by recording cache placement decisions when
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51 153 squirrels cached alone versus in the presence of other squirrels. We assessed predation
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53 154 risk by measuring the traffic of potential predators or 'disturbers', mainly humans,
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3 155 through the foraging sites during each observation session, a method that has been
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5 156 shown to stimulate antipredator behaviours in small and medium-sized mammals
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7 157 (Frid & Dill 2002; Weterings et al. 2016). We also measured escape distance of
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9 158 foraging and caching squirrels in response to humans passing through the sites in
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11 159 order to confirm that they were indeed responding to humans as potential predators.
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13 160 We tested the hypothesis that squirrels would behave flexibly by accepting increasing
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15 161 risk of predation with increasing risk of pilferage by tracking small scale changes in
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17 162 these risks over time, rather than by responding inflexibly to unchanging indirect
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19 163 cues.
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25 165 **Methods**

26 166 **Study Site**

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28 167 The study was carried out on the University of Exeter's Streatham Campus, Devon,
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30 168 UK (latitude N50:44:04, longitude W3:32:04). The area used for observations
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32 169 consisted of approximately 69,000m² of parkland dominated by oak and pine trees
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34 170 (*Quercus cerris*, *Q. petraea*, *Q. rober*, *Pinus pinaster*, *P.nigra*, *Picea pungens*, *Picea*
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36 171 *omorika* and *Podocarpus andinus*) and a variety of rhododendron bushes.
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43 173 **1) Artificial caches**

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45 174 Ten sites, spaced at least 100 m apart, where squirrels had regularly been seen
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47 175 foraging and digging, were selected for use in the study. At the centre of each site,
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49 176 there was an oak tree (*Quercus cerris*, *Q. robur* or *Q. petraea*) with shrubs in various
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51 177 locations.
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54 178 Artificial caches were made during May 2004. Eight trios of hazelnuts were
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56 179 buried around the central tree at each site so that trios were either 'near' the base of
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3 180 the tree (within 2m) or 'far' away (between 8 and 10m) and were either 'clustered' (in
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5 181 a triangle of sides 30cm) or 'spaced out' (triangle of sides 150cm), such that 2 trios of
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7 182 each of the 4 possible combinations (near clustered, near spaced out, far clustered, far
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9 183 spaced out) were made around each tree. The direction of caches from the trees was
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11 184 randomly assigned as far as possible but the location of other trees and bushes had to
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13 185 be taken into account.

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16 186 A pinch of brightly coloured fish tank gravel was buried under each hazelnut
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18 187 so that we could easily identify pilfered caches without having to dig up and re-bury
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20 188 each cache each day.

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23 189 Caches were checked for pilferage daily for 60 days. The number of nuts
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25 190 taken from each trio was recorded, and generalized estimating equations were used to
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27 191 examine the totals across the seasons and whether this was affected by distance from
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29 192 the tree and clustering, taking into account the non-independence of the caches at each
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31 193 site by using the site as a random variate with which there were repeated measures on
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33 194 the other variables.

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37 38 196 **2) Cache location**

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41 197 We recorded cache placements made by squirrels in relation to distance to
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43 198 cover at 4 sites, different to those used for the pilferage study, which varied in
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45 199 disturbance rate.

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47 200 Data on cache location were collected in autumn 2010. Before observations of
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49 201 caching behavior took place 20 squirrels were live-trapped and marked for
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51 202 identification purposes. We used 12 collapsible Tomahawk live traps baited with
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53 203 peanut butter, which were placed in sheltered sites by the base of trees or in shrubs
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55 204 sheltered from paths throughout the study area. Trapping was conducted over 17 days,
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3 205 between September 16 – November 19, 2010. The traps were opened in the morning
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5 206 and were subsequently checked every two hours throughout the day. At the end of
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7 207 each day the traps were closed and shelled peanuts were laid at the entrances of the
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9 208 traps to attract squirrels to the trap sites. Upon trapping a squirrel, the animal was
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11 209 moved into a wire mesh handling cone where it was weighed, sexed, measured and
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13 210 individually marked with black hair dye (Boots, Ebony Black) and released at the site
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15 211 of capture (under Natural England permit NNR/2010/0011). Twelve marked squirrels
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17 212 were subsequently seen at the study sites.
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21 213 As in Canadian studies of grey squirrels by Thompson & Thompson (1980),
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23 214 we have found that caching activity in grey squirrels on the University of Exeter
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25 215 campus is highly seasonal, peaking in mid to late autumn, and therefore this period
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27 216 was chosen for observations. Observations were made over 62 days between October
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29 217 1 and December 2, 2010. A typical day involved two observation sessions, one
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31 218 between 0900 and 1200 hrs and one between 1200 and 1630 hrs. Each session
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33 219 consisted of 20 minutes of opportunity sampling at each of 4 observation sites which
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35 220 differed in typical human traffic rate (our measure of predation risk). Each site
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37 221 measured no more than 40 m at its maximum point, with no more than 20 m on either
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39 222 side of any path down which humans passed. Across the 12 marked squirrels, the
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41 223 range of the number of periods during which they were observed visiting their
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43 224 assigned site was 1 to 27 (mean = 18.6, median and mode = 18).
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47 225 Two observers sat at the edge of each site. One recorded times and behaviors,
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49 226 and the other used binoculars and dictated observations to the note-taker. For each
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51 227 foraging and food caching behavior, the individual identity of the focal squirrel was
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53 228 recorded, as well as the distance in meters from the nearest tree, distance to any other
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55 229 form of cover (eg shrubs and ground cover) and the number of other squirrels present,
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3 230 which was our measure of pilferage risk. In addition, we tallied when any human or
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5 231 other potential predator crossed the site, coming within 1-20 meters of the observed
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7 232 squirrels. This measure was used as an assay of predation risk during each 20 minute
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9 233 period. Squirrels on campus are habituated to the presence of humans to some degree,
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11 234 but they do show vigilance and flight in response to humans passing within a few
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13 235 meters of them, so we were confident that this was an accurate measure of predation
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15 236 risk, particularly since there are a number of studies showing that anti-predator
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17 237 responses in prey animals are persistent for generations under relaxed selection
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19 238 (Blumstein 2006; Messler et al. 2007). Squirrels in the UK are culled regularly and as
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21 239 a matter of course on many estates, parkland and farmland, all of which border the
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23 240 University of Exeter campus. Squirrel culling on campus ended in 2007, within the
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25 241 potential lifetime of the squirrels in this study, so it is adaptive for them to be wary of
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27 242 humans.

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32 243 Caching was defined using the series of behaviors outlined by Macdonald
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34 244 (1995), and was only recorded if a nut was seen in the squirrel's mouth at the start of
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36 245 the series of caching behaviors and was no longer there at the end.
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41 247 **3) Response to Humans as Predators**

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43 248 In order to determine whether squirrels responded to humans as predators, we
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45 249 recorded 16 individual squirrels' flight distances in response to natural human traffic
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47 250 across the study sites from November 4-29, 2013 opportunistically during daily 3 hour
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49 251 observation periods 6 days per week. These data were analysed using Generalised
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51 252 Estimating Equations (GEE) with exchangeable correlations, using escape distance as
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53 253 the covariate and escape as a binary response variable. Squirrels were recorded as
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55 254 'escaping' when they stopped ongoing behaviors, mostly foraging and caching, and
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3 255 ran up a tree or into a shrub. Squirrels were recorded as ‘not escaping’ when they
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5 256 failed to change their ongoing behavior in the presence of a human. Flight distance in
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7 257 metres was recorded when squirrels escaped, minimum distance between the squirrel
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9 258 and the human was recorded in metres when they did not escape.
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12 260 **4) Analysis**

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16 261 In order to compare whether squirrels tend to forage and cache at different
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18 262 distances from the safety of cover, we conducted a paired samples t-test across the
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20 263 marked squirrels, on mean distance from the base of the nearest tree while foraging
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22 264 versus caching.

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25 265 To investigate flexibility of caching and foraging behavior in the face of
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27 266 changing pilferage risk, we used paired samples t-tests comparing mean caching or
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29 267 foraging distance when conspecifics were present vs. absent, including only squirrels
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31 268 that were observed to forage, or cache, in both the presence and absence of
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33 269 conspecifics.

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36 270 To investigate flexibility of caching and foraging behavior in the face of
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38 271 changing predation risk we used general estimating equations to predict each variable
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40 272 (caching and foraging distance), using squirrels as subjects, site as a fixed factor, and
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42 273 observed disturbance rate as covariate. Because the distributions of distances were
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44 274 strongly skewed, we specified a Tweedie data distribution with a log link function in
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46 275 the analysis. These analyses were carried out using only data from observations
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48 276 where no conspecifics were present; there were too few cases where other squirrels
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50 277 were present to allow a similar analysis for that situation. Means are presented \pm
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52 278 standard error.
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3 280 **Results**
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7 282 **1) Artificial caches**
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10 283 Of the 240 nuts that were buried, 29 were taken over the 2 month period. No nuts
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12 284 were taken from four of the ten sites, and these sites were dropped from the statistical
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14 285 analysis. All pilfered caches were taken within 10 days, with no pilferage occurring
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16 286 between day 10 and day 60. Of the 29 nuts taken, 25 were within 1 m of a tree trunk
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18 287 (18 clustered, 7 spread more widely), and the remaining 4 were 10 m from a tree
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21 288 trunk, all of them being clustered.

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23 289 The generalized estimating equations analysis showed that the effects of
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25 290 distance from tree and clustering on the number of nuts taken were both significant
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27 291 (distance $\chi^2_1=31.45$, clustering $\chi^2_1=21.14$, $p<0.001$ in both cases). Their interaction
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29 292 could not be tested because too few of the 10m-distant caches were taken, so that the
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31 293 models were unstable.
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36 295 **2) Foraging and Caching**
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41 297 Ten of the 12 marked squirrels were observed both foraging and caching. Compared
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43 298 to when they were foraging, each of the squirrels moved further away from the safety
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45 299 of cover in order to cache. The mean distance from cover when foraging was $2.32 \pm$
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47 300 0.27 m, with a maximum of 10 m; when caching, the mean was 3.14 ± 0.35 m with a
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49 301 maximum of 10 m. The difference of means was significant (paired samples t-test,
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51 302 $df=9$, $t=2.68$, $p=0.025$, Fig. 1).
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54 303 We observed 73 instances of marked squirrels caching, and only 6 of these
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56 304 caches were made in the presence of an observer. We never observed more than one
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3 305 conspecific present while marked squirrels were caching. We observed 158 instances
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5 306 of foraging by marked individuals, 9 of which took place with observers present. The
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7 307 number of observers present during foraging ranged from 0 to 3. The disturbance
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9 308 rate within the 20-minute observation periods varied from 0-28 events when foraging
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11 309 and 0-27 events when caching.

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14 310 Squirrels did not vary their distance from cover for foraging or caching despite
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16 311 variation in pilferage risk. Five of the 12 squirrels cached both in the presence and in
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18 312 the absence of conspecifics, and the distance from cover at which these marked
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20 313 squirrels cached did not differ between the two conditions (mean distance with no
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22 314 other squirrels present = 3.56 ± 0.34 m, mean distance with other squirrels present =
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24 315 3.50 ± 0.67 m; paired samples t-test, $df=4$, $t=0.099$, $p=0.926$, Fig. 2). Similarly, five
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26 316 of the 12 marked squirrels foraged in both the presence and absence of conspecifics,
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28 317 and the distance at which they did so did not differ between conditions (mean distance
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30 318 with no other squirrels present = 2.18 ± 0.17 m, mean distance with other squirrels
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32 319 present = 2.84 ± 1.01 m; paired samples t-test, $df=4$, $t=-0.705$, $p=0.520$). The 7
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34 320 remaining squirrels were observed foraging or caching in the absence of other
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36 321 squirrels, but not in the presence of others.

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39 322 Out of the 58 observed instances of caching used in the analysis above, 6
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41 323 (10%) were made in the presence of other squirrels. Out of the 79 observed instances
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43 324 of foraging used in the analysis above, 9 (12%) were in the presence of observers.
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45 325 This indicates that the squirrels were not actively avoiding conspecifics when caching,
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47 326 in comparison to when they foraged.

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50 327 In the absence of other squirrels, there was a significant effect of disturbance
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52 328 rate on the distance from cover at which marked squirrels foraged (Wald $\chi^2_1 = 6.66$, p
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54 329 = 0.010), in the opposite direction from that predicted by dynamic adjustment to risk:
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3 330 there was a slight increase in distance from cover with increased disturbance rate ($B =$
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5 331 0.029, Fig. 3). There was also a significant effect of site on foraging distance (Wald
6
7 332 $\chi^2_3 = 30.29$, $p < 0.001$). Disturbance rate did not have a significant effect on the
8
9 333 distance from cover at which marked squirrels cached (Wald $\chi^2_1 = 0.98$, $p=0.322$)
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11 334 though there was a significant effect of site (Wald $\chi^2_3 = 12.60$, $p = 0.006$, Fig 3).
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16 336 **3) Response to Humans as Predators**

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18 337 We observed 146 instances of 16 squirrels responding to human traffic; 16 of these
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20 338 instances involved a dog on a lead. GEE analysis showed that distance was a
21
22 339 significant predictor for escape in the squirrels (Wald $\chi^2_1 = 16.19$, $p < 0.001$). Squirrels
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24 340 responded to the presence of humans by rapidly escaping when they came within a
25
26 341 mean of 13.75m (± 0.85 SE) versus continuing ongoing behaviors when humans
27
28 342 passed within a mean distance of 22.75m (± 1.87). This confirms that humans were
29
30 343 indeed responded to as predators by the squirrels in this study, and that human traffic
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32 344 within the confines of each location was close enough to affect the squirrels'
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34 345 behavior.
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40 347 **Discussion**

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42 348 Squirrels responded to the static cue of distance from cover, which affects both
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44 349 predation and pilferage risk. They cached further from safety than they foraged. Our
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46 350 data suggest that this behavior functions to protect caches from pilferage risk, since
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48 351 we found that caches made closer to the base of a tree had a greater likelihood of
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50 352 being pilfered (see also Steele et al. 2014). This indicates that squirrels had a greater
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52 353 encounter rate with caches they had not made themselves when they were buried near
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3 354 the base of trees, which is to be expected given that this is the area in which they
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5 355 preferentially forage.
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7 356 The squirrels moved further from the safety of cover to cache than they did to
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10 357 forage. This may be due to the fact that food is more readily available under the
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12 358 canopy of trees from which it dropped. However, it is notable that they moved away
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14 359 from their foraging radius in order to cache, indicating that they accepted higher
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16 360 predation risk in order to protect caches from pilferage. This finding adds strength to
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18 361 the cache protection hypothesis of food caching (Legg et al. 2016), indicating that
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20 362 squirrels do not just cache where they find food, but that they actively engage in
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22 363 placing caches in locations where they are less likely to be stolen by a conspecific.
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25 364 However, the squirrels did not respond to dynamic cues of either predation or
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27 365 pilferage risk when caching: they did not adjust their distance from the safety of cover
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29 366 in response either to the frequency of human disturbance or the density of
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31 367 conspecifics. While foraging, they did not respond to changing cues of pilferage risk;
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33 368 they did appear to respond to dynamic cues of predation risk, but this response was in
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35 369 the opposite direction to that predicted by foraging models – they tended to forage
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37 370 further away from cover when predation risk was high. It is unclear why they would
38
39 371 do this, as it seems unlikely to be adaptive. This lack of adaptive response to dynamic
40
41 372 risk is despite the fact that they do change their caching behavior qualitatively in the
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43 373 presence of conspecifics, by increasing spacing between caches, taking more time to
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45 374 choose a cache location, and turning their backs on conspecifics (Leaver et al. 2007;
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47 375 Hopewell & Leaver 2008; Hopewell et al. 2008). Similarly, they respond to static
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49 376 cues of predation risk when foraging (e.g. Lima et al. 1985; Newman & Caraco 1987;
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51 377 Newman et al. 1988) and they interrupt foraging when confronted with dynamic
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53 378 auditory cues of predation risk (Jayne et al. 2015). The present results are therefore
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3 379 somewhat surprising. If the scatter hoarding way of life selects for a general flexibility
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5 380 of behavior then, given that the risks of predation and pilferage interact so closely,
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7 381 and are crucially important to foraging and caching squirrels, we would not expect
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10 382 their behavior to be so static in the face of changing risks.

11
12 383 There are a number of studies which show that foraging animals tend to
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14 384 depend more heavily on reliable indirect cues of predation risk such as overhead cover
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16 385 than direct cues of predation left by the predator itself (e.g. Orrock et al. 2004; Fong et
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18 386 al. 2009; Fanson 2010, for a review and meta-analysis, see Verdolin 2006) and that
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20 387 when animals do adjust their behavior in response to more direct cues, such as number
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22 388 of predators encountered, these adjustments are more subtle than might be expected
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24 389 (e.g. St Juliana et al. 2011). It seems that, as in the studies reviewed in Verdolin
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26 390 (2006), in the present study our squirrels were using indirect cues of risk, such as
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28 391 distance from the nearest escape route or overhead cover, rather than actually
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30 392 assessing the current level of human disturbance between sessions. Such behavior is
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32 393 contrary to the predictions made by foraging models, which almost unanimously
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34 394 predict that flexible tracking of predation risk in real time yields the greatest success
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36 395 (e.g. Luttbeg & Schmitz 2000). Bouskila and Blumstein's model (1992) shows that
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38 396 animals are better off tracking changes in predation risk over time than relying on an
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40 397 average hazard assessment, even if they use a simple rule of thumb to assess risk, and
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42 398 in consequence are working with imperfect estimates. If scatter hoarding, with the
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44 399 more complex trade-offs it requires, encouraged a general behavioral flexibility, we
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46 400 might have expected the squirrels to behave in accordance with these models, even if
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48 401 other animals do not; but they did not.

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52 402 If our data show no sign of general adaptive flexibility on the part of the
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54 403 squirrels, however, it remains to be asked why they have no instinctual or readily
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3 404 learned tendency to respond dynamically to dynamic changes in pilferage or predation
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5 405 risk. It is possible that the squirrels we observed were making initial caches in order
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7 406 to rapidly sequester food, and that they came back to redistribute these caches at a
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10 407 later point in time; and that such temporary caches are made in a relatively casual
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12 408 way, without regard to the presence of conspecifics. However our observation
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14 409 techniques were closely similar to those we have used in previous studies, in which
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16 410 we found that squirrels do make adaptive adjustments to conspecifics' presence
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18 411 (Leaver et al. 2007; Hopewell & Leaver 2008). A more plausible possibility is that
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20 412 caching further from cover provides a different kind of protection from pilferage than
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22 413 the behaviors we have observed in our previous studies. Turning away from
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24 414 conspecifics, or waiting to cache until they are otherwise occupied, will protect
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26 415 against conspecifics currently present getting information about the location of a
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28 416 cache, and thus being able to pilfer it more or less immediately. Caching further from
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30 417 cover, on the other hand, reduces the probability that an uninformed conspecific
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32 418 discovers the cache by chance, possibly much later. In addition to this, we found that
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34 419 squirrels only tended to cache when there were very few conspecifics around (none or
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36 420 just one visible), though they foraged with a larger audience of conspecifics (up to
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38 421 three). It may be the case that rather than adjusting their caching decisions in relation
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40 422 to pilferage risk, they chose only to cache when pilferage cues were below an
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42 423 acceptable threshold.

47 Why might the squirrels' caching and foraging distances have shown no
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49 425 adaptive sensitivity to the rates of human disturbance? Clearly they were not so
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51 426 habituated to humans as to just ignore them, since they frequently fled when a human
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53 427 approached. Possibly the entire environment of an urban squirrel is so saturated with
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55 428 humans that distance from cover is always kept at the minimum consistent with
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3 429 current activity, with no scope for trade-off. Once predator density passes a certain
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5 430 point, there may be no advantage in monitoring it, because the arrival of a potential
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7 431 predator is an essentially random event: the fact that three have gone past recently
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9 432 does not make it more, or less, likely that another one will arrive in the next minute.
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11 433 Different locations, or different times of day, will vary in the rate at which dangers
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13 434 appear, and that might be another static cue worth learning about; it may indeed
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15 435 explain the differences in foraging distance between sites that we observed. But the
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17 436 rate of recent predator appearance has no predictive value. Under these conditions,
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19 437 the predictions of models like those of Bouskila and Blumstein's model (1992) or
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21 438 Luttbeg & Schmitz (2000) do not hold. Squirrels necessarily forage close to trees and
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23 439 bushes, and safety probably requires fleeing to cover the moment a predator is
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25 440 detected. Under these conditions, so long as there are any predators at all, the squirrel
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27 441 should not go further from cover than it can run in the time between a predator
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29 442 coming into view and its being able to reach the squirrel. That "escape time" will be
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31 443 known to the squirrel only as a distribution, however, and the overriding need to
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33 444 establish sufficient non-pilfered caches for over-winter survival may still make it
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35 445 worth the squirrel's while to use a somewhat more generous estimate of it, thus
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37 446 running a somewhat higher risk of a fatal encounter with a predator, when caching
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39 447 than when foraging.

448 In summary, therefore, we found that the risk that a cache will be pilfered
449 changes with long-term predation risk, since pilferage from our artificial caches
450 decreased with increasing distance from the safety of a tree; and we found,
451 correspondingly, that squirrels cache further from cover than they forage, thereby
452 incurring increased predation risk when caching (and also when they later recover
453 their caches). But we did not find evidence of flexibility of behavior in response to

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3 454 dynamic changes in pilferage and predation risk. There are plausible reasons why
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5 455 such flexibility might not confer much adaptive advantage, but our prediction that a
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7 456 truly flexible forager would nonetheless be expected to show some dynamic response
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9 457 in terms of the distance from cover at which they foraged and cached was not
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11 458 supported. The case that scatter hoarding, as such, encourages general flexibility of
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13 459 behavior remains unproven.
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3 585 **Figure Legends**
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5 586 **Figure 1.** Mean distance (m) from cover at which each squirrel was observed to cache
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7 587 (black bars) and forage (white bars).
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10 588 **Figure 2.** Mean caching distance (m) by whether or not a conspecific was present
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12 589 during caching.
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14 590 **Figure 3.** Mean foraging (top panel) and caching (bottom panel) distance (m) by
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16 591 number of disturbances per observation session.
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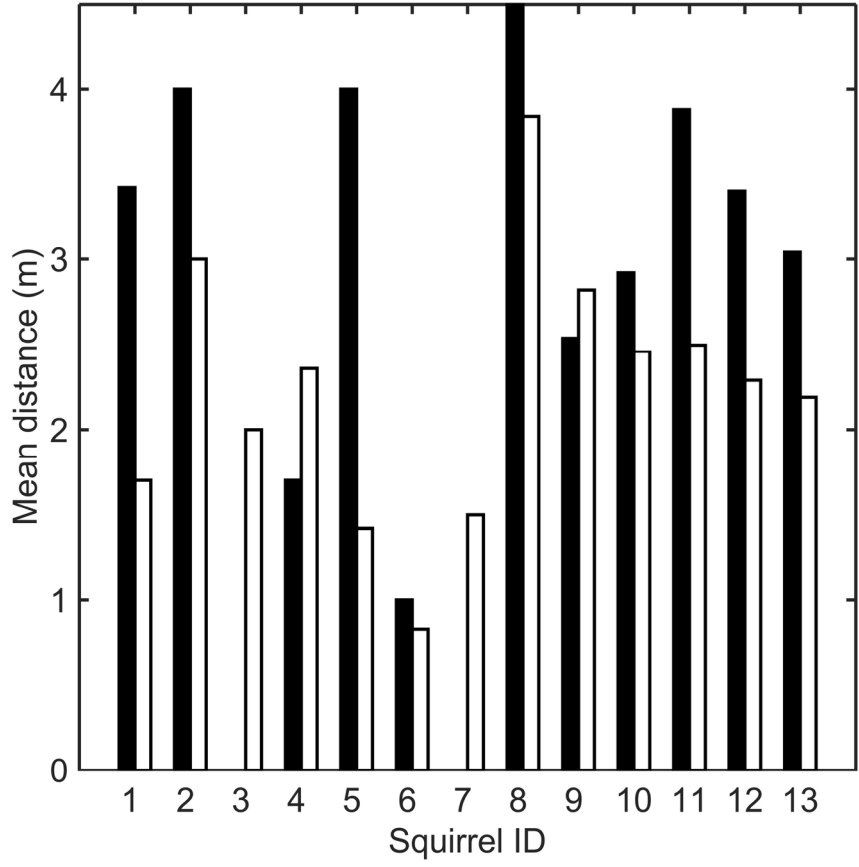


Figure 1. Mean distance (m) from cover at which each squirrel was observed to cache (black bars) and forage (white bars).

158x149mm (300 x 300 DPI)



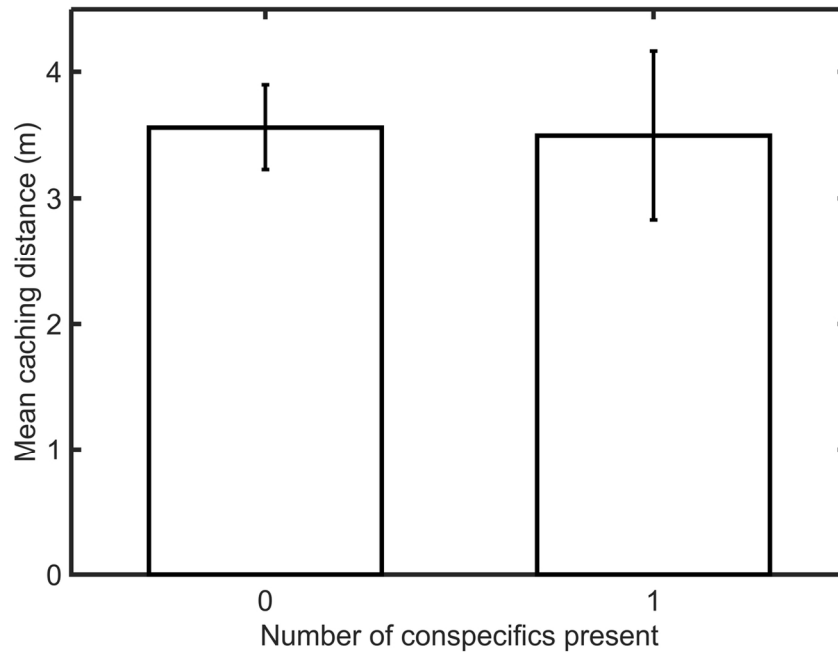


Figure 2. Mean caching distance (m) by whether or not a conspecific was present during caching.

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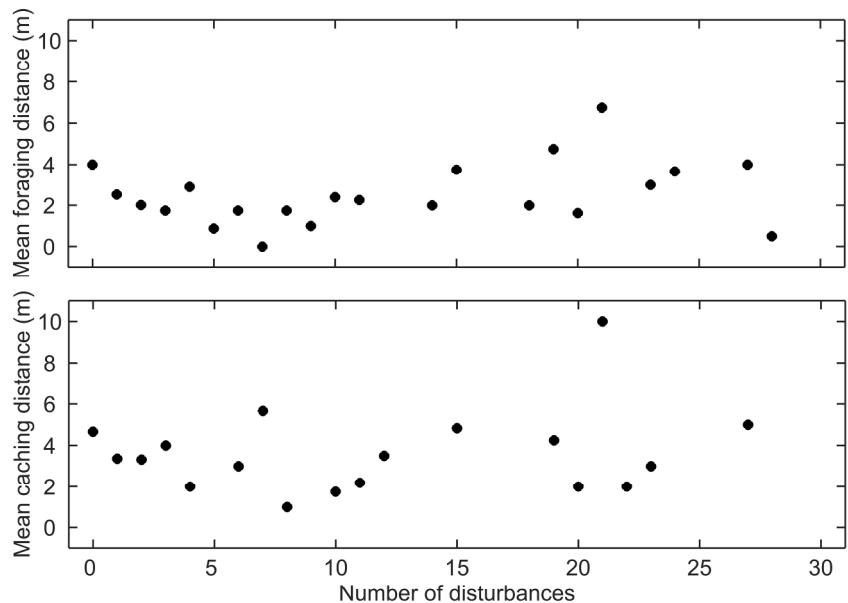


Figure 3. Mean foraging (top panel) and caching (bottom panel) distance (m) by number of disturbances per observation session.

230x167mm (300 x 300 DPI)

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