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The impact of thermoregulatory costs on foraging behaviour: a test with American Crows (*Corvus brachyrhynchos*) and eastern grey squirrels (*Sciurus carolinensis*)

A. Marm Kilpatrick*

Department of Zoology, University of Wisconsin, Madison,
1117 W. Johnson Street, Madison, WI 53706, USA

ABSTRACT

I attempted to test for the effects of thermoregulatory costs on the foraging behaviour of eastern grey squirrels (*Sciurus carolinensis*) and American Crows (*Corvus brachyrhynchos*). I examined the foraging of these two animals in paired trays filled with sand and sunflower seeds under cold winter conditions. One tray was exposed to direct solar radiation that reduced the thermoregulatory costs of the animal foraging in that tray. Both crows and squirrels foraged more in trays exposed to the sun, resulting in reduced giving-up densities (the mass of seeds remaining) in those trays. I also examined the foraging behaviour of American Crows under warmer conditions within their thermal-neutral-zone, and found no significant difference in giving-up densities between trays in the sun and the shade. This verified that the differences in giving-up densities (sun *vs* shade) found in cold conditions were a result of thermoregulatory costs and not something else (e.g. predation risk due to differences in lighting). As a result, this study provides the first direct evidence that thermoregulatory costs can play a significant role in the patch-leaving decisions of foragers. Solar radiation and temperature can cause differences in thermoregulatory costs and lead to changes in foraging pressure that may have important consequences for the distribution of seeds and other prey items.

Keywords: foraging costs, giving-up density, temperature.

INTRODUCTION

When an animal forages in a depletable patch, the rate of energy the animal gains from that patch declines with the amount of time spent in the patch. Previous theory (Charnov, 1976; Brown, 1988) argues that to maximize fitness, foragers should leave patches when the quantity of food they are harvesting per unit time declines to a value – the quitting harvest rate – that matches the sum of the costs they incur while foraging. These costs include the risk of predation, the energetic or metabolic costs of foraging, and the missed opportunity

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* e-mail: kilpatrick@conservationmedicine.org

costs [the costs of not engaging in other activities such as foraging elsewhere, defending a territory, looking for a mate, grooming (Brown, 1988)]. Brown (1988) showed that these three costs can be translated into a common unit of currency by expressing all three costs in terms of their fitness value to the animal. One surrogate for measuring the quitting harvest rate of animals is to measure the quantity of prey left in a patch after a foraging bout; this is termed the giving-up density (Brown, 1988). A large body of research has examined the effects of temperature on foraging behaviour (Caraco, 1979; Belovsky, 1981; Huey, 1991; Bozinovic and Vasquez, 1999; Bozinovic *et al.*, 2000), including several previous attempts to examine the effect of temperature or thermoregulatory costs on the quitting harvest rates or patch-leaving decisions of animals (Bowers *et al.*, 1993; Kotler *et al.*, 1993; Brown *et al.*, 1994; Meyer and Valone, 1999). Researchers have measured the giving-up densities of animals over a number of days or months and have concurrently measured minimum, maximum or average temperatures. Most of these studies have found support for theoretical predictions, in that hot or cold temperatures resulted in fewer resources being harvested from a patch. Generally, the quantity of seeds remaining in a patch after a foraging bout increased with the thermoregulatory costs of the forager in the patch, but the magnitude of this effect varied between small and substantial, especially when compared with the predation costs of the forager (Brown *et al.*, 1994; Meyer and Valone, 1999).

The shortcoming of these studies is that none of them separated the effects of differences in predation risk and missed opportunity costs on giving-up densities occurring on different days or seasons from the effects of differences in temperature. Differences in giving-up densities that are correlated with differences in temperature could also be due to differences in predation risk or missed opportunity costs on the different days examined. Missed opportunity costs differ between non-breeding and breeding seasons, and may differ depending on the background level of resources outside the experimental patch and the availability of mates (see Brown *et al.*, 1994, for a more thorough discussion of missed opportunity costs). For animals foraging in non-breeding seasons and following a time-minimizing strategy, giving-up densities in experimental patches on different nights might differ due to differences in ambient resources. Perceived predation risk would be expected to vary through changes in the density, activity and behaviour of predators, as well as the marginal fitness value of energy. As a result of day-to-day variation in missed opportunity and predation costs, a proper test for the independent effect of thermoregulatory costs on foraging decisions requires holding all other foraging costs constant.

I attempted a direct examination of the role of thermoregulatory costs on foraging by examining the patch-leaving decisions of eastern grey squirrels (*Sciurus carolinensis*; hereafter squirrels) and American Crows (*Corvus brachyrhynchos*) in paired trays in cold winter conditions. In conditions below an animal's thermal-neutral-zone (which has a lower limit called the lower critical temperature), an animal must expend additional metabolic energy above its basal rate to maintain its core body temperature. However, an animal can use solar radiation to reduce these thermoregulatory costs in cold conditions. To take advantage of this, I placed one tray in the sun and one in the shade on the ground on either side of a large tree. Animals foraging in the sun should have lower thermoregulatory costs than animals foraging in the shade. For American Crows, I also examined foraging in similarly paired trays under thermally benign conditions to verify that differences in foraging in cold conditions were due to thermoregulatory costs and not other differences between the trays.

METHODS

This study was carried out in Madison, Wisconsin at two residential locations in the fall and winter (October–March) of 2000 and 2001. Both sites were mowed grassy areas with large trees. Both sites were within 100 m of semi-natural patches of deciduous forest. Pairs of aluminium trays, each 24 × 30 × 7 cm, were placed on the ground, 10 cm from either side of the base of a tree on clear days when solar radiation was unimpeded by clouds or haze. I placed one tray in full sunlight and the other completely in the shade; in all other aspects, the trays were the same. In addition, because I sampled in the morning and the afternoon an approximately equal number of times, the shaded tray was on the east and west side of each tree roughly an equal number of times. This should have eliminated a bias associated with a squirrel's or crow's preferred side of the tree, or which tray was closer to a building or woodlot where a predator might perch.

I filled each tray with ~1.2 litres (40 oz) of finely sifted sand thoroughly mixed with 15.4 g of husked sunflower seeds. I placed trays out between 08.00 and 16.00 h and checked them every 2 h for signs of foraging. I recorded temperatures at the beginning and end of each 2 h period and averaged them. If both trays showed signs of foraging activity, I collected them and sifted them for remaining seeds. I weighed the seeds remaining in each tray (the giving-up density) to the nearest 0.01 g using a Sartorius 1212 MP electronic balance.

I studied squirrel foraging near 116 E. Gilman Street during the winter (February–March) of 2000 on days when the high temperature was 1–8°C. This temperature range is substantially below the lower critical temperature of winter-acclimatized eastern grey squirrels (~25°C; Ducharme *et al.*, 1989). I studied American Crow foraging in the Eagle Heights housing area during the winter (October–January) of 2001 over a range of temperatures, from −11 to +15°C. Although the energy expenditure of American Crows has not been studied in a metabolic chamber to measure their lower critical temperature, measurements on other birds in the family Corvidae (Prinzinger, 1976) of larger and smaller size suggest that their lower critical temperature is approximately 9–10°C. As a result, I separated the crow foraging data into trials done below (<8°C) and within their thermal-neutral-zone (11–15°C).

Statistical analyses

I collected data from pairs of trays at the same station/tree multiple times. As a result, if the same squirrel foraged in the paired trays on multiple occasions, these differences in giving-up density would not represent independent data points. I did not mark individual animals, so I could not determine which animal was foraging in each set of trays in a given foraging trial. I dealt with this issue by analysing the data in two ways. First, I used each foraging trial (a set of paired trays) as an independent data point. In the second, more conservative analysis, I grouped all the data collected at each station/tree and considered the mean difference in giving-up densities at each tree as an independent data point. The trees were separated by ~100 m, and most squirrels foraged within 50–80 m of their nest tree, so data at each station should represent different foragers. There were 8–10 squirrels foraging at the four trees/stations in 2000 and at least 10 different crows foraging at the three stations in 2001. Because the results remain the same regardless of which way the data are analysed, the pattern does not appear to be caused by one or two animals skewing the data.

I analysed the difference in giving-up densities for crows foraging in sunny and shaded trays using an analysis of variance (ANOVA) with the effect of temperature (cold *vs* warm) included as a factor. For squirrels, I did not collect data for thermally benign conditions, so I used a *t*-test and tested the hypothesis that the observed difference in giving-up densities between sunny and shaded trays was less than zero. Because this was an *a priori* hypothesis, I used a one-tailed test.

RESULTS

The giving-up density, or mass of seeds remaining in the tray, of squirrels was significantly lower in trays in sunlight than in shade. This was true regardless of whether the foraging trial (set of paired trays) or station (tree) was used as the unit of analysis (Table 1). This supported the prediction that foraging in sunlight would lower thermoregulatory costs and lead to lower giving-up densities if the ambient temperatures were below an animal's lower critical temperature.

Similarly, the giving-up density of American Crows was lower in sunlight than in shade under cold conditions for both units of analysis (Table 1). However, at temperatures within the estimated thermal-neutral-zone for American Crows, the giving-up density was lower in the shaded trays, but not significantly so (Table 1). A significant effect of temperature in the ANOVA on the difference in giving-up densities showed that crows foraged more intensely in sun-exposed trays under cold conditions than in thermal-neutral conditions (Table 1). These results supported the prediction that giving-up densities in the sun-exposed trays would be lower only under cold conditions.

DISCUSSION

The energetic costs of foraging can have important cascading impacts on many aspects of ecosystems. The results presented here suggest that granivores reduce the density of seeds

Table 1. Differences in giving-up density (GUD) between shaded and sun-exposed trays after foraging by eastern grey squirrels and American Crows (mean ± 1 standard deviation)

Species	Mean difference in GUDs between trays[1] (g)	# of foraging trials (# stations)	Comparison
Eastern grey squirrel	−1.317 ± 0.80	15 (4)	[4]$t = 2.25$, d.f. = 14, $P = 0.021$ [5]$t = 3.30$, d.f. = 3, $P = 0.023$
American Crow			
cold	−1.18 ± 0.18[2]	14[2] (3)	[4,6]$F_{1,21} = 8.70$, $P = 0.008$
warm	+1.16 ± 0.96[3]	5[3] (3)	[5,6]$F_{1,4} = 17.29$, $P = 0.014$

[1] GUD or mass of the seeds remaining in the tray in the sun – GUD from the shaded tray.

[2] GUDs from periods where the temperature was between −11°C and 8°C.

[3] GUDs from periods where the temperature was between 11°C and 15°C.

[4] Comparison using the foraging trial as the unit of analysis. See Methods for explanation.

[5] Comparison using the station or tree as the unit of analysis. See Methods for explanation.

[6] The results of an ANOVA with temperature as an effect comparing the difference in GUDs between warm and cold conditions.

in patches to a greater extent in areas where foraging is less energetically costly. As a result, in cold climates, seeds will be more likely to be eaten (rather than survive and possibly germinate) in sunny areas than in shade. This effect is only likely to occur during cold months, but seed predation by squirrels, crows and other granivores during the winter months represents a significant impact on the seed bank (Marino *et al.*, 1997; McCormick and Meiners, 2000; Schreiner *et al.*, 2000; Howe and Brown, 2001) and, as a result, many systems are likely to be impacted by this phenomenon.

Thermoregulatory and other energetic costs of foraging are overlaid on the spatial distribution of predation costs. Previous work has shown that predation risk is often higher in the open than under cover (Brown, 1988; Bowers *et al.*, 1993; Brown *et al.*, 1994; Pusenius *et al.*, 2000; Smith and Litvaitis, 2000; Vasquez *et al.*, 2002, and references therein) and increases with distance from a 'safe' area. For squirrels, chipmunks and other rodents, this safe area might be their burrow or a tree they can climb (Bowers *et al.*, 1993). As a result of differences in the energetic cost of foraging and variation in perceived predation risk, we can imagine a spatial map of quitting harvest rates (measurable as different giving-up densities) that animals will use to forage for resources. Whether food densities in the environment reflect the foraging decisions of animals or the inputs from the suppliers (e.g. seeds produced by plants) remains to be tested. Nevertheless, the results from this study and previous work suggest that seeds and other prey items are more likely to be consumed in less costly microhabitats.

Several issues warrant discussion. First, the sample sizes in this study were quite small, especially for crows foraging on thermally benign days. However, even with low sample sizes, significant effects of the costs of foraging are evident under cold conditions. This strongly contrasts with differences in giving-up densities on warmer days (Table 1). Second, using the technique of measuring the remaining density of seeds in a tray has recently come under attack for some of the assumptions inherent in the technique. Price and Correll (2001) suggested that animals may be following different patch-leaving rules than are assumed when using giving-up densities as indicators of the costs of foraging (Brown, 1988). However, I was able to watch approximately half of the foraging trials in this study and I observed both squirrels and crows visiting both sunny and shaded trays in a single foraging bout. I subsequently collected the trays and measured the giving-up densities. Systematic differences between the paired trays thus represent differences in foragers' decisions of when to leave each of the two patches. Finally, if animals consistently foraged first in sun-exposed trays and then in shaded trays, the reduced foraging in shaded trays could simply be a result of satiation rather than differences in energetic costs. However, of the 20 foraging trials I observed (13 of crows foraging, 7 of squirrels foraging), the shaded tray was visited first in half of them, suggesting that the observed differences were not due to satiation.

The shaded trays (and by extension shaded or cooler areas) represent substantially poorer patches in terms of the net energy gained by a forager. Foragers left shaded patches after harvesting fewer seeds compared with the trays in the sun, and also paid higher thermoregulatory costs while foraging in the shade. This study not only provides valuable evidence for the role of thermoregulatory costs in animals' foraging decisions, but also suggests that these costs can have important implications for animals' energy balance and for the survival of seeds or other prey items that animals forage for in a heterogeneous environment.

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