Effects of food and predators on the home-range sizes of Arctic ground squirrels (Spermophilus parryii)

Anne H. Hubbs and Rudy Boonstra

Abstract: We used radiotelemetry to study the effects of food addition and predator reduction on the home-range sizes of adult Arctic ground squirrels (Spermophilus parryii) on large-scale experimental grids in the boreal forest of the southwestern Yukon Territory. Home ranges were 2–7 times smaller on food-supplemented grids than on nonsupplemented grids, regardless of whether large mammalian predators were present. Similarly, core areas (where 50% of activities occur) were 8–11 times smaller on food-supplemented grids. Food availability rather than predator presence primarily determined the sizes of home ranges and core areas of Arctic ground squirrels.

Résumé : Nous avons utilisé la radiotélémétrie pour étudier les effets de l’addition de nourriture et de la réduction des prédateurs à une grande échelle sur la taille des domaines vitaux de Spermophiles arctiques (Spermophilus parryii) dans la forêt boréale du sud-ouest du Yukon. Les domaines se sont avérés de deux à sept fois plus petits dans les parcelles à suppléments de nourriture que dans les parcelles sans suppléments, en présence ou en l’absence de grands mammifères prédateurs. De même, les zones d’activité maximale (où les spermophiles procèdent à 50% de leurs activités) étaient de 8 à 11 fois moins grandes dans les parcelles à suppléments de nourriture. Il semble donc que ce soit la disponibilité de la nourriture plutôt que la présence de prédateurs qui soit le facteur déterminant immédiat de la taille des domaines vitaux et des zones d’activité maximale chez le Spermophile arctique.

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Introduction

Few studies have tried to tease apart the various determinants of home-range size (Mares et al. 1982; Meia and Weber 1995). Studies have focussed primarily on food availability (for a review see Boutin 1990), while body size, population density, and predation risk have received only limited attention (e.g., Maza et al. 1973; Harestad and Bunnell 1979; Lima and Dill 1990), often through indirect means. For example, the role of predation risk has been assessed by monitoring foraging...
movements in the presence of predator odours (Jędrzejewski and Jędrzejewska 1990; Parsons and Bondrup-Nielsen 1996) or under different light conditions, amounts of protective cover, or distances from a burrow (Kaufmann and Kaufmann 1982; Holmes 1991; Moreno et al. 1996). Generally, high predation risk restricts movements, but only over the short term (Saarikko 1992).

The Arctic ground squirrel (Spermophilus parryii) is an ideal species with which to examine how predation risk interacts with food availability to affect home-range size. Ground squirrel activity is centred around an underground burrow system; the farther a squirrel is from its burrow system, the greater its risk of predation (Bonenfant and Kramer 1996). Since ground squirrels are an important food source for many predator species (e.g., Elliott and Guetig 1990; Rohner 1995), they should be risk-sensitive and adjust their movements accordingly. However, antipredator behaviours must be balanced against the conflicting demands of foraging. Since food availability may increase with distance from a burrow (Andrusiak and Harestad 1989), ground squirrels may have to accept higher levels of risk in order to improve their foraging efficiency. This is particularly true shortly before hibernation, when squirrels need to accumulate fat stores to enable them to survive winter.

We examined the effects of food availability and predation risk on home-range sizes of adult Arctic ground squirrels in the boreal forest of the southwestern Yukon Territory (61°N, 138°W). This species has seldom been studied in this habitat (Hubbs and Boonstra 1997), where food availability and visibility are low relative to their more typical habitats, alpine meadows and Arctic tundra (Carl 1971; Green 1977; Batzli and Sobaski 1980). In the boreal forest ecosystem, the Arctic ground squirrel is an important alternative food source for mammalian and avian predators such as the coyote (Canis latrans), lynx (Lynx lynx), northern goshawk (Accipiter gentilis), and Harlan’s hawk (Buteo jamaicensis) (Doyle and Smith 1994; O’Donoghue et al. 1998), particularly when numbers of snowshoe hare (Lepus americanus) are in the decline phase of the 10-year cycle. In the summers of 1991 and 1992 we monitored the movements of Arctic ground squirrels during the hare decline (Boutin et al. 1995; Krebs et al. 1995).

We made two predictions: first, that home ranges would be smaller where food was added, because greater food availability should allow squirrels to meet their nutritional needs within a smaller area; and second, that home-range sizes should be similar between areas with and without predators. Though animals may restrict their movements in high-risk situations over the short term (e.g., Parsons and Bondrup-Nielsen 1996), they have to accept the increased risk over the long term in order to obtain adequate food supplies (McNamara and Houston 1992; Hik 1995). Because our study was conducted from May to early August (just prior to hibernation), we measured the long-term response.

**Methods**

We livetrapped squirrels from mid-April to late August in 1990–1992 using Tomahawk live traps (16.5 × 16.5 × 48.0 or 14.0 × 14.0 × 41.0 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, U.S.A.) baited with peanut butter. Food availability and predator presence were manipulated with a 2 × 2 factorial design by adding commercial rabbit chow and (or) excluding predators by placing electric fences (Krebs et al. 1995) on 1 × 1 km areas. Three experimental treatments (“predator exclosure,” “food addition,” and “predator exclosure + food”) were established in 1987 and 1988 and are discussed in Krebs et al. (1995). They were not replicated. One squirrel-trapping grid of approximately 10 ha was nested within each of the experimental treatments (for a description and position of all grids see Hubbs and Boonstra 1997), and in addition, two control grids were established. The squirrel grid on the predator-exclosure treatment was sited so as to exclude both large mammalian predators (it was within the electric fence) and avian predators (it was also underneath the nylon monofilament), whereas that on the predator exclosure + food treatment was protected only from large mammalian predators. Although the electric fences effectively excluded mammalian predators, the nylon monofilament lines on the predator-exclosure grid did not completely exclude avian predators because of periodic breakages. In 1992, 33% of all the squirrels radio-collared on the predator-exclosure grid (24) were killed by avian predators compared with 32–49% on the remaining grids (Table 3 in Hubbs and Boonstra 1997). The food-supplementation treatment consisted of distributing 5 kg of rabbit chow (minimum 16% crude protein) every 5–6 days along four 600 m long transects separated from each other by a distance of 183 m. With the food-addition and predator exclosure + food treatments, the squirrel grids were sited so as to straddle two such transects. All grids were within 5 km of one another, the controls being within 1 km of at least one experimental grid (see Fig. 1 in Hubbs and Boonstra 1997). All grids were dominated by white spruce (Picea glauca) with an understory of bog birch (Betula glandulosa), grey willow (Salix glauca), and grasses (Festuca altuca and Calamagrostis lapponica), and were similar with respect to the five main habitats types of the region (Hubbs and Boonstra 1997).

In 1991, a total of 12 adult males were fitted with 4.1-g radio collars (Model PD-2C, Holohil Systems Ltd., Carp, Ontario; range 150–400 m) on a control grid and the food-addition grid. In 1992, a total of 75 adult females and 21 adult males were collared on all five grids. We focussed on females rather than males in 1992 because we had access to many more radio collars and were particularly interested in how mortality patterns of females (the prime determinant of population growth) varied among treatments as predators shifted from a diet of snowshoe hares during the hare peak to other prey species during the hare decline (Hubbs and Boonstra 1997). The burrow systems of squirrels on the food-addition and predator exclosure + food treatments were 30.9 ± 6.0 (1 SEM) and 35.8 ± 5.0 m from where the food was distributed, respectively, as determined from their locations prior to morning emergence (Hubbs 1994). Males were tracked from May to early August and females from mid-June to early August. They were located on an average of 3 days per week on all grids, with 1–5 checks made per day. We allowed a minimum of 3 h between checks to increase the likelihood of independence of observations (White and Garrott 1990). Home-range sizes of radio-collared squirrels were estimated using the kernel method (Worton 1989), as recommended by Andreason et al. (1993), and are given in hectares. RANGES IV SOFTWARE (Kenward 1990) was used to determine the 50 and 95% utilization polygons (core areas and home-range sizes, respectively). Utilization curves indicated that a minimum of 15 fixes were required for reliable estimates of home-range size, therefore only squirrels with ≥ 21 fixes were included in our analyses. These included 9 males from 1991 and 36 females, but no males, from 1992 (for the exact number per treatment see Table 1). Only three females from each control grid had ≥ 21 fixes. Individual males and females averaged 33 ± 4 fixes over 23 ± 4 days and 26 ± 2 fixes over 18 ± 1 days, respectively.

Population sizes were based on four trapping checks over 2 consecutive days of livetrapping on each grid in July 1991 and 1992. The program capture (Otis et al. 1978) provided an estimate of population size from which densities (squirrels/ha) were calculated. This technique provided very robust estimates of population size, as squirrels are highly trappable (Hubbs and Boonstra 1997).

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Table 1. Sizes of core areas (50% utilization polygon) and home ranges (95% utilization polygon) of adult Arctic ground squirrels (Spermophilus parryii) in the boreal forest of the southwestern Yukon Territory in 1991 (males) and 1992 (females).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Females</th>
<th>Males</th>
<th>Treatment</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50%</td>
<td>95%</td>
<td>Density</td>
<td>50%</td>
<td>95%</td>
</tr>
<tr>
<td>Controls</td>
<td>0.32 (0.19)a</td>
<td>2.97 (1.73)a</td>
<td>6</td>
<td>1.0 (0.2)</td>
<td>0.60 (0.49)a</td>
</tr>
<tr>
<td>Predator exclusion</td>
<td>0.11 (0.03)ab</td>
<td>0.72 (0.13)ab</td>
<td>5</td>
<td>1.4 (0.1)</td>
<td>0.03 (0.01)b</td>
</tr>
<tr>
<td>Food addition</td>
<td>0.02 (0.01)b</td>
<td>0.28 (0.07)b</td>
<td>16</td>
<td>5.4 (0.4)</td>
<td>0.08 (0.08)a</td>
</tr>
</tbody>
</table>

Note: Values given are given as means, with SE in parentheses. Values followed by the same letter are not significantly different; n is the number of squirrels ±15 fixes.

All ANOVAs and post hoc tests (Tukey–Kramer) were performed with superanova (Gignon et al. 1990) and all Spearman’s rank correlations with statsview (Roth et al. 1994). All statistical tests were performed according to procedures in Zar (1984) and Sokal and Rohlf (1981). Means are expressed ±1 standard error. Power analyses were performed according to procedures in Cohen (1988) to determine the probability of correctly rejecting the null hypothesis in cases where effect sizes were large and sample sizes were small, but rejection of the null hypothesis was not indicated below \( P = 0.05 \).

Results

As the sizes of home ranges of females and of core areas did not differ significantly between the two control grids \( F_{[1,34]} = 0.39, P = 0.58 \), and \( F_{[1,4]} = 0.89, P = 0.40 \), respectively; \( n = 3 \) per grid), we pooled data from them. Home ranges and core areas of females differed significantly in size among treatments in 1992 \( F_{[3,32]} = 4.12, P = 0.01 \), and \( F_{[3,32]} = 4.01, P = 0.01 \), respectively), with the ranking as follows: controls > predator exclusion > food addition > predator exclusion + food (Table 1). Home ranges were 7 times smaller on grids where squirrels were fed than on grids where they were not fed \((0.26 ± 0.05 \text{ versus } 1.94 ± 0.97 \text{ ha, respectively}) \), and core areas were 11 times smaller \((0.02 ± 0.01 \text{ ha; nonfed: } 0.22 ± 0.11 \text{ ha}) \). These differences were highly significant \((95\% \text{ polygon: } F_{[1,34]} = 6.96, P = 0.01; 50\% \text{ polygon: } F_{[1,34]} = 8.41, P = 0.007) \).

Home ranges of males on the food-addition grid were half the size of those on the control grids, and core areas were one-eighth the size in 1991 (Table 1). Though these differences were not significant \((F_{[1,7]} = 1.75, P = 0.23 \text{, and } F_{[1,7]} = 0.90, P = 0.38, \text{ respectively}) \), our statistical power was low \((<10 \text{ and } <35\% \text{ for 95 and 50\% polygons, respectively}) \).

Densities of squirrels in 1991 and 1992 were 4–13 times higher on grids where squirrels were fed than on grids where they were not fed (Table 1). Density was negatively correlated with home-range size \((R_s = -0.43, P = 0.003) \); a similar relationship was suggested with core area \((R_s = -0.21, P = 0.07) \).

Discussion

Our results support the hypothesis that food availability rather than predator presence determines the home-range sizes of adult Arctic ground squirrels in the boreal forest, for two reasons. First, home ranges were markedly smaller on the food-addition grid than on the controls for both males and females (Table 1). Second, home ranges were 7- to 11-fold smaller on both food-supplemented grids than on the nonsupplemented grids, irrespective of whether the latter were exposed to predators (controls) or not (predator exclusion) (Table 1). These results are consistent with our predictions and with the results of earlier studies involving food addition in the presence of predators (Boutin 1990).

One caveat that must be borne in mind which may have affected the results is that since our experimental grids were not replicated, the differences among the grids may have been due primarily to differences in site rather than to the experimental manipulations. We do not think this is likely, however, because the habitat on all the grids was similar and demographic parameters (population size, litter size, and growth rate) were similar between the two control grids and between the food-addition and predator exclusion + food grids (Hubbs and Boonstra 1997).

There are two possible ways in which food affects home-range size. First, because animals on food-supplemented areas have ready access to food nearby, they may reduce the distance they travel to get it and hence reduce their home-range size. Alternatively, food addition increases density, which may force animals to move less in order to reduce conflict with neighbours. In our study, food addition increased densities 4- to 13-fold above those on nonsupplemented grids (Table 1). However, we were not able to monitor changes in home-range size when feeding started in 1987 and thus could not decouple the role of density from that of food in affecting home-range size. Mares et al. (1982) manipulated both food and density in the eastern chipmunk (Tamias striatus), another burrowing sciurid living in forests of eastern North America, and found that the reduction in home-range sizes was entirely the result of food addition, not of increases in population density. We suggest that Mares et al.’s results are directly analogous to ours. A test of this conclusion is currently underway in our study area (T. Karels, personal communication), as food addition has ceased after the completion of the long-term experiments, and both densities and home-range sizes are being monitored. We predict that home-range sizes will increase dramatically with the cessation of feeding, irrespective of density. It is difficult to interpret the effects of predator exclusion on home-range size because our samples were small (Table 1) and not all avian predators were excluded from the predator-exclusion grid. Thus, our conclusions must be regarded with caution. Relative to food addition, predator exclusion appeared to have little effect on home-range size. We found that home-range sizes on the predator-exclusion and control grids were similar and that smaller home ranges occurred on both food-supplemented grids (Table 1), despite mammalian predators having been excluded from one. Thus, squirrels did not appear to reduce their home ranges in areas where predators were present, despite evidence that high predator-induced mortality during our study might have constrained their movements (42...
of 45 radio-collared squirrels that died were killed by predators, and summer mortality rates were twice as high in 1992 as in 1990; Hubbs and Boonstra 1997). These results conflict with those of most earlier studies in which predators inhibited prey movement (e.g., Brown et al. 1988; Desy et al. 1990; Saarikko 1992), and may be related to the long-term nature of our study and to the critical need of squirrels to build up fat reserves to ensure successful hibernation. A counterintuitive result which we cannot explain is that despite similar densities on the control and predator-exclusion grids (Table 1), home ranges and core areas were 3–4 times smaller on the predator-exclusion grid than on the control grids. The removal of both of the large electric fences around the predator exclosures at the end of the large-scale experiments should allow us to determine whether this result was a grid effect or some effect of the lack of predators that we do not at present understand.

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**References**


Masculinized females in a population of 

Leptodiaptomus minutus (Copepoda, Calanoida)

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Abstract: In a population of the common freshwater copepod Leptodiaptomus minutus Lilljeborg, 7.3% of adult females exhibited male secondary sexual characteristics. Although these masculinized or intersex females had the internal morphology of normal females, they possessed one or rarely two normal geniculate male antennules, and in a few instances male fifth legs. The sex ratio of normal adult males to females in the population was 1:1. No differences in body size among normal males, normal females, and masculinized females were found. Antennule lengths of males and masculinized females were not significantly different from one another; however, normal females had longer antennules than either males or masculinized females. Mating experiments indicated that masculinized females were functionally female and they were able to mate with normal males to produce offspring that were normal or masculinized. The occurrence of intersex copepods in lakes of North America may be more widespread than we now recognize because they can be easily overlooked or mistaken for normal adults.

Résumé : Nous avons observé que 7,3% des femelles adultes d’une population du copépode d’eau douce commun Leptodiaptomus minutus Lilljeborg avaient des caractères sexuels secondaires mâles. Ces femelles masculinisées ou intersexes possèdent la morphologie interne de femelles normales, mais elles possèdent aussi une ou parfois deux antennules mâles géniculées normales et, dans certains cas, des cinquièmes pattes de mâle. Le rapport mâles:femelles adultes normaux dans la population est de 1:1. Il n’y a pas de différence de taille entre les mâles, les femelles et les femelles masculinisées. La longueur des antennules est la même chez les mâles et chez les femelles masculinisées, mais les femelles normales ont des antennules plus longues que celles des mâles ou des femelles masculinisées. Les résultats d’expériences d’accouplement indiquent que les femelles masculinisées sont fonctionnellement des femelles, qu’elles s’accouplent avec des mâles normaux et donnent une progéniture composée d’individus normaux ou masculinisés. L’existence d’intersexes chez les copépodes dans les lacs nord-américains est peut-être plus répandue qu’on ne le croyait à ce jour parce que ces individus sont faciles à confondre avec des adultes normaux.

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Introduction

Intersexuality describes a broad range of sexual expression in which an individual exhibits both male and female sexual characteristics (Atz 1964). This expression may involve primary and secondary morphological as well as behavioral sexual characteristics. Intersex individuals may be functionally male or female in their ability to reproduce, and yet possess the secondary sexual characteristics of the opposite sex (Howell et al. 1980; Rosa-Molinar and Williams 1984). A distinct form of intersexuality, arrhenoidism, refers specifically to females that exhibit secondary male sexual characteristics (i.e., masculinized, or androgenized females). We describe this form in the copepod Leptodiaptomus minutus. This study presents the first documentation of intersexuality in a freshwater copepod species from North America, including an evaluation of its reproductive capability.

Intersexuality has been reported in dioecious species across many taxa and is especially well documented in crustaceans, including amphipods (Ginsburger-Vogel 1973, 1975; Charniaux-Cotton 1975; Dunn et al. 1990, 1996), isopods (Juchault et al. 1991), and copepods (Cattley 1948; Fleminger 1985; Ianora et al. 1987; Moore and Stevenson 1991, 1994). Sex determination in crustaceans is generally controlled by genetic factors (for review see Legrand et al. 1987), but in some species it may be influenced by environmental cues such as photoperiod and temperature (Naylor et al. 1988; Watt and Adams 1993). Intersexuality has been correlated with environmental factors (Dunn et al. 1990, 1996), skewed sex ratios...