Differential Reproduction Among Female Richardson’s Ground Squirrels and Its Relation to Sex Ratio

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Summary. The reproductive success of ten female Richardson’s ground squirrels resident on a grassland pasture in southern Alberta in 1975 was determined by noting the number of their descendants present in 1976, 1977, and 1978.

The two most successful females were the progenitors of 67% of the females resident in 1977 and of 57% of the females resident in 1978. None of the other eight females had descendants in the population in 1978. The two most successful females produced more daughters than did the other females and they did so, not by rearing larger litters, but by producing female-biased litters. The daughters of the two most successful females lived slightly longer than did the daughters of other females.

Although the adult sex ratio was strongly female biased each breeding season, ranging between 0.26 and 0.42 males per female, typically all females became pregnant.

Adult female offspring inherited their mother’s home range and, if the mother or any female sibs were present, shared this area with them. Sons rarely remained resident in or near the natal area and adult males rarely remained resident in the same area for two consecutive years. Thus, post-weaning investments were greater in daughters than in sons.

There were no conclusive correlations between sex ratio of litters and size of litters, age of the mother, previous reproductive success of the mother, population density, or the length of the overwinter period. More studies spanning several generations are required to elucidate the effects of the sex ratio of litters on the likelihood of an animal being represented by descendants in subsequent generations.

Introduction

Although Dawkins (1978) has suggested that the concepts of individual and inclusive fitness should be abandoned in favour of the concept of replicator survival, assessing replicator survival is even less feasible in field studies than assessing fitness in the Darwinian or in the Hamiltonian sense. The individual fitness of an animal is measured by the number of descendants it produces and this typically involves noting the number of its offspring that survive to reproductive age (e.g. Duvall et al. 1976; Downhower and Armitage 1971). However, if these adult offspring fail to reproduce, then the effective individual fitness of the parent is zero. As Alexander (1974) and West-Eberhard (1975) have pointed out, there is no consensus on how many generations should be considered when calculating an animal’s fitness, and few studies have attempted to look at fitness over several generations. McCarley (1970) followed the reproductive success of female thirteen-lined ground squirrels over several years and found that 80% of the original residents failed to leave descendants in the population four years later. The aims of this study were to follow the reproductive success of female Richardson’s ground squirrels by noting the number of their descendants in the population over the ensuing three years, and to determine whether the most successful females followed a reproductive strategy different from that of the least successful ones.

Materials and Methods

The study area and methods of trapping, marking, and determining range size of squirrels are described in Michener (1979a, b). In brief, Richardson’s ground squirrels (Spermophilus richardsonii) resident on a 0.66-ha portion of grassland near Longview, Alberta, were trapped and identified at frequent intervals during the spring and summer in 1975, 1976, and 1977, and during the spring only...
in 1978 and 1979. At first capture, all squirrels were individually
marked for permanent identification with a numbered metal tag
in each ear. In 1975, 1976, and 1977, juveniles were captured 1–7
days after their first emergence from the natal burrow and could
be assigned unambiguously to a litter of known maternity. The
paternity of litters was not known.

In 1976, 15 pregnant females captured adjacent to the study
area were held in captivity, and the sex ratios of their litters at
birth noted. Details on housing and feeding are reported in Miche-
ner (1977).

During a four- to five-week period in the spring of 1975 and
of 1976, when females were pregnant and lactating, squirrels were
observed for 48 h and 28 h, respectively, and their locations on
the area were recorded every 12 min during each hour of observa-
tion. The home range of each adult female resident in both 1975
and 1976 and of each yearling female resident in 1976 was calcu-
lated as the area of the minimum convex polygon enclosing the
most clustered 95% of all locations at which the animal was seen
(see Michener 1979a for details). The amount of overlap between
the home ranges of different squirrels or of the same squirrel
in different years was calculated from the polygons by using a
compensating polar planimeter. On average, the ranges were based
on 150 sightings per female in 1975 (n=8, SE=12) and 93 sightings
per female in 1976 (n=12, SE=6).

A resident squirrel was defined as an animal that remained
for at least two continuous weeks on the area, used a burrow
system on the area, and spent the majority of its above-ground

Averages are given with ± one standard error of the mean.

Results

In 1976, 100% of the population of adult females, and in 1977, 92% of the population of adult females
was composed of squirrels originally resident in 1975
and their descendants (Table 1). By 1978, there were
no surviving original residents, but there were four
descendants. Although three other original resident
in 1978 had not originated on the study area, they
had all been captured as adults within 50 m of the
boundary of the area at least once prior to their year
of immigration and so were long-term local residents.
Of the nine adult males that resided on the area from
1975 to 1978, only one had been born on the area and
only one remained resident for two consecutive years.

Figure 1 shows the contribution made by each of
the ten females originally resident in 1975 to the
population of females in the succeeding years. Three
of the original residents (B, D, and E) plus their
five yearling daughters accounted for 57% (8 of 14)
of the females resident in the spring of 1976. In 1977,
original resident C and her three yearling daughters
were present and original resident D was represented
by two 2-year-old daughters and two yearling grand-
daughters. Thus, maternal lines C and D accounted
for 67% (8 of 12) of the females resident in 1977.
In 1978, only the C and D matrilines were represent-
ed; by two 2-year-old daughters, and by one 3-year-
old daughter plus one 2-year-old granddaughter,
respectively. Therefore, of the ten females originally
resident in 1975, two were the progenitors of 57%
of the females resident in the spring of 1978. The
remaining eight original residents were not represent-
ted by female descendants three years later. There
were no sons, either of the original females or of
their daughters, on the study area in 1978.

The two females, C and D, that were represented
by female progeny in 1978 had, respectively, produced
15 and 10 daughters plus granddaughters over the
three-year period, whereas the average for the other
seven original females that reared at least one litter
to weaning was 2.1 ±0.6 female descendants. The ave-
range size of the eight litters weaned by females C
and D and their daughters (4.3 ±0.4) was not signifi-
cantly larger (one-tailed t=1.07, P>0.10) than that
of the 15 litters produced by the other females and
their daughters (3.5 ±0.4). However, there were pro-

<table>
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<th>Origin</th>
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<th>Origin</th>
<th>Number resident each year</th>
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<tr>
<td></td>
<td>Females</td>
<td></td>
<td>Males</td>
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<td>Resident in 1975</td>
<td>10 (A–J)</td>
<td>9 (A–I)</td>
<td>3 (A–C)</td>
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<td>2&lt;sup&gt;b&lt;/sup&gt;</td>
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</tr>
<tr>
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<tr>
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<tr>
<td>Immigrant in 1976</td>
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<td>Total residents</td>
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</tr>
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<sup>a</sup> Letters in parentheses identify the females shown in Fig. 1
<sup>b</sup> A third 2 year old was recovered, but she established residency adjacent to the study area.