MORTALITY AND DISPERSAL OF JUVENILE OPOSSUMS, 
*Didelphis Virginiana*

By

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Abstract of Thesis Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Master of Science

MORTALITY AND DISPERSAL OF JUVENILE OPOSSUMS, *DIDELPHIS VIRGINIANA*

By
Debra D. Wright

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Chairman: Dr. John F. Eisenberg
Major Department: Zoology

To determine the times and causes of mortality along with the sex bias, timing, distance and duration of dispersal of juvenile opossums, I conducted a two-year study on the Ordway Preserve in north-central Florida. From nine major trapping sessions, totaling 15,314 trap nights, I toe-clipped 1,062 pouch young from 162 litters. I radio-collared 66 adult female *Didelphis virginiana* to determine the natal range of their offspring and to trap their offspring at weaning age. I radio-collared 68 juveniles at weaning and an additional 67 post-weaning.

Juvenile opossums generally experienced 60-75% mortality within the first 4 weeks post-weaning, after which mortality decreased and leveled off. There was no sex difference in mortality distributions, although there were some cohort differences. Possible resource fluctuations
induced by rainfall variation seemed to greatly affect juvenile survivorship. There was no apparent clumping of survivorship by litter, as would be expected if pre-weaning predation or genotype played a strong role. However, environment or disease (seen through an area effect) may be a factor in unusually high mortality. Most known deaths were attributable to owl predation. Of all pouch young, 10-11% survived until their first breeding season.

Most males dispersed (96%) while most females were philopatric (86%). Some first cohort males dispersed about the time the second cohort was being weaned. Most juvenile dispersal occurred just before or during the mating season.

Dispersal movements were rapid, usually lasting only 1-2 days. This may help avoid increased risk of mortality associated with such movement, as only one death was associated with dispersal. Maximum dispersal distances were 5.6 home range diameters (7.00 km) for males and 6.8 home range diameters (5.75 km) for females. Although the radio-tracking dispersal-distance distribution was basically leptokurtic, there were more-than-expected long distance movements, perhaps due to heterogenous habitat. Adult females will sometimes carry their pouch young to new areas, resulting in their passive dispersal.

These data seem to best support the parent-offspring competition theory for dispersal. Secondarily, opossum dispersal decreases incest, yet may promote beneficial inbreeding.
CHAPTER 1
INTRODUCTION

Mortality

A general survivorship curve for vertebrates shows high early juvenile mortality, then low mortality at mid-ages until senescence, when it rises again (Ricklefs 1973). Juvenile death may occur simultaneously in an entire clutch or litter before young are independent, if for example, a predator comes into the nest or den. Alternatively, death may strike the young individually, either before or after independence, due to selection acting upon some phenotypic character or conversely, through stochastic circumstances. If local environment or genotype affect survivorship, or if early litter-biased mortality has occurred, we may predict greater variance in survivorship between than within litters. Mortality in the pouch is not common in opossums (Tyndale-Biscoe and MacKenzie 1976, Hamilton 1958 as cited in Tyndale-Biscoe and MacKenzie 1976, Reynolds 1952, Gardner 1982). Deaths are more likely when young are left in the den while the mother forages; this should only occur during the 2-3 weeks before weaning (Guillette 1980; "nest phase" of Eisenberg 1975). This type of mortality would be very difficult to discover. I focused on post-weaning mortality in this study, but also looked for clumped survivorship of
litters. Tyndale-Biscoe and MacKenzie (1976) collected a lower proportion of immature opossums (D. marsupialis and D. albiventris) than expected based on average litter sizes, and postulated high mortality in newly independent juveniles as the probable cause.

Generally, long-lived animals with few offspring per year and prolonged parental care experience lower juvenile mortality (K-selected end of continuum) than short-lived animals with many offspring per year and lower levels of parental care (r-selected end) (Pianka 1970, Eisenberg 1981). The former is often associated with unpredictable resources, a consequent increased brain mass, and possibly increased social complexity, while the latter is often associated with predictable (though not necessarily constant) resources, a consequent reduced brain mass and decreased social complexity (Eisenberg 1981). Opossums produce an average of 13-14 young each year and usually live to breed only one year. Shortly after emergence from the pouch, the young are weaned and seem to receive no parental care (pers. obs.). Opossums have relatively small brains (Eisenberg and Wilson 1981, Jerison 1983) and exhibit almost no complex sociality (Eisenberg 1981). Therefore, opossums lie on the r-selected end of the scale and should experience relatively high juvenile mortality. Additionally, we could predict that an unusual fluctuation in the resource base would have dramatic effects on opossum demographics.
Population fluctuations should parallel those of the resource base.

**Dispersal**

Dispersal is an important step in a mammal's life history, having important implications for population biology and population genetics (Chepko-Sade and Haplin, eds. 1987, Anderson 1989). Dispersal is a remarkably widespread phenomenon among organisms; plants, marine organisms, and terrestrial animals all have diverse and often complicated mechanisms for effecting dispersal. Because of this, many hypotheses have been proposed to explain why dispersal has evolved.

Dispersal presents several potential advantages and disadvantages. Dispersing individuals may increase fitness through: better survivorship, higher quality habitat, more matings, wider gene dispersion, beneficial outbreeding, reduced parent-offspring conflict, offspring with better gene combinations, and/or avoidance of competition or disease in crowded areas (Lidicker 1962, Anderson 1989). Conversely, the disperser may show reduced fitness through: increased predation, fewer matings, greater exposure to disease, greater aggression from conspecifics, unbeneificial outbreeding, and/or decreased ability to find food and shelter (Healey 1967, Porter et al. 1981, Shields 1982, Anderson 1989). These various potential costs and benefits of dispersing have been incorporated into a number of
hypotheses explaining the evolution of dispersal. Those most relevant to this study are summarized in Table 1.1 and below. Some of these hypotheses involve proximate causes, while others involve ultimate causes or a combination of the two.

**Proximate Causes for Dispersal**

**Ontogenetic-switch hypothesis.** Holekamp and Sherman (1989) found that male ground squirrels (*Spermophilus beldingi*) waited until they reached a weight or fat level threshold before dispersing. They felt this "fat index" cued a gonadal steroid release, that triggered dispersal. The ultimate cause for dispersal was believed to be the reduction of inbreeding. Barash (1974) also found that marmots (*Marmota* spp.) only dispersed after reaching a certain weight. However, other studies found no mass differences between dispersers and non-dispersers (see Gaines and McClenaghan 1980).

**Pre-natal androgen hypothesis.** This theory also claims that gonadal steroids influence dispersal. Ims (1989) found that female grey-sided voles (*Clethrionomys rufocanus*) born in male-biased litters have a greater tendency to disperse than other females. He postulated that some inflexible physiological mechanism was cued by steroids to cause dispersal and that greater exposure to androgens during prenatal life may cause female dispersal.
Table 1.1. Relevant dispersal theories and their predictions.

<table>
<thead>
<tr>
<th>Theory</th>
<th>Citation</th>
<th>Predictions</th>
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<tbody>
<tr>
<td><strong>Proximal Theories of Dispersal</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ontogenetic -switch</td>
<td>Holekamp and Sherman 1989</td>
<td>dispersers will weigh more or have greater fat reserves than non-dispersers</td>
</tr>
<tr>
<td>pre-natal androgen</td>
<td>Ims 1989</td>
<td>most female dispersers will be from male-biased litters</td>
</tr>
<tr>
<td><strong>Mixtures of Proximal and Ultimate Theories of Dispersal</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>innate vs. environ</td>
<td>Howard 1960</td>
<td>genetic basis for increased disp. tendency in innate dispersers; innate disp. move in 1-2 days; environ. disp. move more slowly</td>
</tr>
<tr>
<td>pre-saturation vs. saturation</td>
<td>Lidicker 1975</td>
<td>genetic basis for increased disp. tendency in pre-sat dispersers; sat dispersers will be inferior animals (e.g. weigh less)</td>
</tr>
<tr>
<td><strong>Ultimate Theories of Dispersal</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>inbeeding avoidance</td>
<td>many (e.g. Pusey 1980)</td>
<td>dispersers do not mate with related individuals</td>
</tr>
<tr>
<td>mate search</td>
<td>King 1983</td>
<td>expect dispersers to achieve more matings than if they had not dispersed</td>
</tr>
<tr>
<td>parent-offspring competition</td>
<td>many (e.g. Murray 1967)</td>
<td>r-selected sp. have greater dispersal than k-selected; peak male dispersal at mating season; juv. female dispersal after mating season, but before last cohort weaned; terminal cohort philopatric; leptocurtic distribution curve</td>
</tr>
<tr>
<td><strong>EFH vs. RFH</strong></td>
<td>Anderson 1989</td>
<td>in EFH, the disperser benefits through his movement; in RFH, the remaining residents benefit; basically summary of above theories</td>
</tr>
</tbody>
</table>

* Emigrant Fitness Hypotheses vs. Resident Fitness Hypotheses
Mixtures of Proximal and Ultimate Causes

**Innate versus environmental dispersal.** Howard's (1960) theory of innate dispersal predicts that individuals have a genetic tendency for dispersal and consequently they may skip over available ranges while dispersing. Conversely, environmental dispersers move for reasons of overcrowding, lack of resources, or parental rejection, and would be philopatric if possible. Howard cited quick dispersal movements of 1-2 days as evidence for innate dispersal, and longer, rambling dispersal movements as support for the environmental hypothesis.

**Pre-saturation Versus Saturation Dispersal.** Lidicker's (1975) pre-saturation and saturation dispersal hypothesis (very similar to Howard's innate versus environmental dispersal) also attempts to explain dispersal when resources are available and there is no apparent reason to move. In pre-saturation dispersal, movements occur before peak density is reached. Dispersers could be any individuals from the population, including healthy ones with a high probability of survival and reproduction. In these animals there is a genetic tendency for dispersal. In contrast, saturation dispersers leave during or after peak density and are physically inferior with a low probability of survival and reproduction. Anderson (1989) points out that this theory assumes a fixed carrying capacity. Additionally, if the area becomes degraded through increased population
density, healthy individuals are equally liable to leave (Anderson 1989).

**Ultimate Causes of Dispersal**

*Inbreeding avoidance.* Inbreeding avoidance has often been postulated as an ultimate reason for dispersal. Many authors have found that inbred litters are smaller than outbred ones (either at birth or through survival) (e.g. Lynch 1977, Ralls et al. 1979). However, small animals that ovulate excess eggs may eliminate inferior embryos in the uterus and still have normal-sized litters (Anderson 1989). Alternatively, smaller litters may actually be advantageous through decreased sibling competition leading to increased survivorship (Dapson 1979, Fuchs 1982). Inbreeding depression may only occur in large breeding populations which allow buildup of deleterious genes (Moore and Ali 1984). Selection should eliminate deleterious genes in small inbreeding units (Bengtsson 1978). Shields (1982) even suggested that beneficial inbreeding may occur in demes of < 1,000 individuals. Additionally, if dispersal evolved for inbreeding avoidance, the sex with the most to lose through inbreeding should have stronger selection to disperse. In polygynous mammals this would be females, but in most cases, the males disperse (Greenwood 1980, Waser et al. 1986, Clutton-Brock and Harvey 1976, Maynard Smith 1978).
Mate search hypothesis. In King's (1983) mate search hypothesis, individuals disperse to find mates because they can not mate (for any of several reasons) in their natal range. Often this results in inbreeding avoidance as well. For example, Hoogland (1982) found that female prairie dogs (*Cynomys ludovicianus*) prefer not to mate with relatives; this seemed to proximately drive male dispersal through mate search. However, the ultimate result was inbreeding avoidance. Dispersers are often subordinate to residents in their new range (through weight, age or resident factors, see Anderson's review 1989) and may not get an opportunity to breed (e.g. Shapiro and Dewsbury 1986). Additionally, often dispersers travel to less-preferred habitats (perhaps with fewer mates) where offspring may fare worse even if mates are found (see Anderson 1989).

Parent-offspring competition. Dominant individuals may cause emigration in subordinates (Christian 1970, see also Anderson 1989). Murray (1967), Armitage (1974) and Hamilton and May (1977) (among others) suggested that parents provoke their young to disperse. The young, if given a choice, would be philopatric. Rodent dispersals are short; their tendency is to be philopatric when possible (Anderson 1989). Males are mate limited. They may maximize their reproductive success (RS) by outcrossing with other females and at the same time, inbreeding with their philopatric daughters. However, they should force their sexually mature sons to emigrate to avoid mate competition with them.
(Anderson 1989). Armitage (1974) found no juvenile male emigration unless an adult male was present. On the other hand, if resources are limited, mothers should oust juveniles during the high energy demands of pregnancy and lactation, especially reproducing daughters who may require more of these resources than sons. Conversely, if resources are plentiful and/or maternal future reproductive value is low, mothers may benefit most by allowing offspring to be philopatric (Anderson 1989). Thus male-induced emigration will occur just before or during the mating season and female-induced emigration will occur from breeding through the weaning of young. This theory predicts that terminal litters will be allowed to be the most philopatric. If the cost of dispersal is great and the parental cost of offspring philopatry is low, parents may allow juveniles to remain (Jones 1986). R-selected species should exhibit more emigration than K-selected species (the former having less parental care and more juveniles for adult conspecifics to compete with) (Anderson 1989). Dispersal distributions should be strongly leptokurtic as juveniles attempt to settle as close as possible to their natal range (Shields 1982, Anderson 1989). Achievement of this leptokurtic curve through parent-offspring competition and expulsion does not require polymorphism in dispersal tendency (Waser 1985). Furthermore, dispersal distances farther than expected through parental-offspring competition could be due to
heterogenous habitat and not to genetically different dispersal tendencies (Waser 1985).

**Emigrant versus resident fitness hypotheses.** Anderson (1989) divided the above theories into "emigrant fitness hypotheses" (EFH) and "resident fitness hypotheses" (RFH). The former involve an emigrant benefit to dispersal and/or an inherited variation in the tendency for dispersal, be it spontaneous or in response to environmental stimuli. Most of the above theories fall under this EFH heading. However, parent-offspring competition is a RFH, assuming the residents remaining benefit from the dispersal of competitors/offspring.

**Problems Associated with Measuring Dispersal**

Dispersal is difficult to study. Juvenile mortality is very high, so many young must be marked in order to have enough marked individuals surviving to dispersal age. Additionally, dispersers usually leave the researcher's study area, and their fate becomes unknown. Although some studies have assumed that animals not recaptured had dispersed and not died, only recaptured animals can be positively identified as dispersers. Further, counting disappearing individuals does not quantify dispersal distance. Reliable and quantifiable results depend on the size of the trapping area, the bigger the better. However, for many mammals an area large enough for an accurate estimate is impossible to run with limited manpower and
funds. Hence, dispersal distributions based on trapping data often lack an accurate representation of the greater dispersal distances, and they obviously lack data on timing and duration of dispersal.

Many individuals must be radio-tagged when young to achieve a realistic measure of dispersal distance. If dispersal timing is known, the chance of premature death and thus the number of individuals collared can be reduced by collaring individuals shortly before dispersal. However, when dispersal timing is in question, large numbers of individuals must be marked at weaning or when newly independent to be certain no dispersal event is missed. Additionally, even radio-tagged individuals can be difficult to find after they have dispersed.

I will give results for trapping and tracking independently. Presenting the results in this fashion allows a comparison of the resulting dispersal distributions.

**Dispersal-Associated Mortality**

There may be an increased risk of mortality associated with dispersal (see Gaines and McClanahan 1980, Anderson 1989). Metzgar (1967) thought that dispersers are more vulnerable to predation through unfamiliarity with hiding places or escape routes, unawareness of danger, or more active wandering and exploring. Ambrose (1972) eliminated the first two causes in owl predation in *Microtus*
*pennsylvanicus*, experimentally concluding that even voles familiar to the area did not detect the birds until it was too late. He concluded that the more extensive movements by transients created the greater risk. If this is true, we would predict higher mortality associated with gradual dispersal movements than with rapid movements (Gaines and McClenaghan 1980).

**Opossums**

In this thesis, natal dispersal refers to movements of one or more home range diameters away from the point of weaning to the place of reproduction or where reproduction would have occurred if the animal had been able to mate (Howard 1960, Greenwood 1980). Natal range refers to the mother's range where the juvenile was weaned. Throughout the thesis the first cohort of 1987 will be referred to as FC87, the second cohort 1987 as SC87, the first cohort 1988 as FC88, and the second cohort 1988 as SC88.

Opossums are ideal for a study of natal dispersal. They are ubiquitous, easily trappable, and, being marsupials, the young can be marked by toe-clipping while they are still in the pouch—leaving no question of maternity or natal range. Thus, when recaptured later, once independent, the distance these marked individuals have traveled can be assessed.

To understand the following chapters, a basic knowledge of opossum biology is necessary. Opossums give birth to as many as 25 young that are one cm long and have well
developed forelimbs with deciduous claws (Reynolds 1952, Farris 1950). The unassisted young must pull themselves 4-5 cm up and into the marsupium located on the mother's abdomen. The mother relaxes the opening of this pouch to allow an easy entry. Once inside, they each attach to a nipple, the nipple tips being only 1.5 mm in diameter even in older females with swollen nipples (Reynolds 1952). All young will not survive as there are only 13 teats, and in many females some of these are apparently not functional (Reynolds 1952). The mouth forms a tight seal for at least 48 days. If the young are forceably removed from their teat between the 3rd and 48th day, they usually can not reattach and will die (Reynolds 1952). By day 17 the young can be sexed. Enough characteristics of opossum development in the pouch are known to age the young accurately to within a few days (Hartman 1928, Petrides 1949, Reynolds 1952, Gardner 1982). The mother continues to carry them in her pouch when she leaves the den, until about day 80, after which she may leave all or some of them behind while she forages ("nest phase" of Eisenberg 1975, Seidensticker et al. 1987). If the mother changes den sites during this late phase, she will carry the young on her back (Guillette 1980). The juveniles are weaned at 96-108 days old (Reynolds 1952, Seidensticker et al. 1987, pers. obs.). One or more of the young may den with the mother or with siblings for up to 1-2 weeks beyond this, after which the young are completely on their own (pers. obs.).
In Florida, a female opossum usually mates in mid-late January or February, gives birth 13 days later (Reynolds 1952), and weans her young in May. The second mating season occurs about two weeks before these young are weaned. Thus her second litter is born about the time her first leaves her. The second litter is weaned in August or early September. The timing of mating and weaning is more synchronous for the first cohort than for the second (Burns and Burns 1957, pers. obs.).

A female opossum in Florida produces on average 13-14 young each year (Burns and Burns 1957, Sunquist et al. in press, this study). Opossums are short-lived, usually living to breed only one year, sometimes two (Reynolds 1952, Sanderson 1961, Seidensticker et al. 1987, Guillette 1980, pers. obs.).

I radio-tracked and trapped juvenile opposums to determine the circumstances of their deaths and to look for mortality differences between first and second cohorts, between sexes, and between years. I also quantified dispersal events and distances, timing and duration of dispersal of juvenile opossums. Additionally, I assessed the mortality risk associated with dispersal in opossums.
CHAPTER 2
MATERIALS AND METHODS

This study was conducted on the 3750 hectare Ordway Preserve 33 km east of Gainesville, Florida (Figure 2.1). A system of one-lane dirt roads winds through the preserve making much of it readily accessible by truck. The preserve is closed to the public and usually only 1-3 researchers are within its boundaries at any time; therefore, disturbance and traffic are minimal. The preserve consists of 47% sandhill (i.e. high pine), 17% other uplands and 36% wetlands. The sandhill is dominated by longleaf pine (Pinus palustris) and turkey oak (Quercus laevis). The remaining uplands include old fields and sand live oak hammocks, the latter dominated by sand live oak (Quercus geminata), laural oak (Quercus laurifolia), some longleaf pine (Pinus palustris), and some palmetto (Sabal palmetto). The wetlands include swamp forest (either mesic hammock, seasonally flooded black water lake fringes, or seasonally flooded bay swamps), wet prairies and open water. Mesic hardwood hammocks are dominated by sand live oak (Quercus geminata), laural oak (Quercus laurifolia), pignut hickory (Carya glabra), sweet magnolia (Magnolia virginiana), loblolly pine (Pinus taeda), and on the lower slopes, saw palmetto (Serenoa palmetto). Seasonally flooded black water
Figure 2.1. Map of the Ordway Preserve showing roads (lines), lakes (blackened areas) and trap sites (stars) used in the major trapping sessions. The black square in the center of the preserve is the lab were opossums were processed.
lake fringes may include black gum (*Nyssa sylvatica*) or pond cypress (*Taxodium ascendens*). Seasonally flooded bay swamps contain swamp bay (*Persea palustris*), loblolly bay (*Gordonia lasianthus*), loblolly pine (*Pinus palustris*), huckleberry (*Gaylussacia dumosa*), and smilaxes (*Smilax auriculata* and *S. laurifolia*). Wet prairies include saw grass (*Cladium jamaicensis*), swamp loosestrife (*Decodon verticillatus*), buttonbush (*Cephalanthus occidentalis*), and primrose willows (*Ludwigia peruviana*). The open water consists of isolated clear water lakes and depression ponds located in the uplands, and dark water lakes which connect through swamps and marshes to become the upper part of the Rice Creek drainage, which empties into the St. Johns River (Richard Franz, pers. comm.).

**Trapping Sessions**

I conducted nine major trapping sessions between March 1987 and February 1989 (Table 2.1). In the first session one large Tomahawk live trap (27 X 32 X 81 cm) was set at each trap site. All following sessions also had one small Tomahawk live trap (17 X 17 X 62 cm) at each site. I trapped at 140 different sites throughout the preserve (Figure 2.1), but with a bias toward mesic areas, where opossum density is greatest (Gardner 1982, Llewellyn and Dale 1964, Sunquist and Daneke, unpublished data). I ran traps in 3-4 lines, each line for 7-8 days, for a total of 15,314 trap nights for all sessions combined (Table 2.1). Traps were anchored by logs or wedged into place to avoid
Table 2.1. Number of trap nights and dates for all major trapping sessions.

<table>
<thead>
<tr>
<th>Beginning date</th>
<th>Ending date</th>
<th>Number of trap nights</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 Mar 1987</td>
<td>23 Apr 1987</td>
<td>1037</td>
</tr>
<tr>
<td>7 Jul 1987</td>
<td>1 Aug 1987</td>
<td>2086</td>
</tr>
<tr>
<td>5 Oct 1987</td>
<td>3 Nov 1987</td>
<td>1906</td>
</tr>
<tr>
<td>13 Dec 1987</td>
<td>26 Feb 1988</td>
<td>2147</td>
</tr>
<tr>
<td>18 Mar 1988</td>
<td>16 Apr 1988</td>
<td>2282</td>
</tr>
<tr>
<td>22 Jan 1989</td>
<td>23 Feb 1989</td>
<td>1952</td>
</tr>
</tbody>
</table>

Total Trap Nights 15,314
raccoon (*Procyon lotor*) or dog interference; floors and roofs were covered with leaves, palmetto fronds, and/or Spanish moss for camouflage, insulation and rain/sun-proofing. I placed one cup of bait (a mixture of 5 lbs dry dog food/ 36 oz. canned sardines) in each trap in the afternoon and checked them the following morning. Traps with opossums were covered with burlap bags and taken to the lab, located in the center of the preserve, for opossum processing (see Figure 2.1). Opossums recaptured in a particular trapping session were released immediately at the trap site.

Opossums were anesthetized using 15-20 mg/kg body mass of ketamine hydrochloride injected intramuscularly in the hip. I ear-tagged all first captures with uniquely numbered tags and assigned each an ID number; if the opossum was already tagged from a previous session, I recorded the old numbers. For each opossum, I took standard measurements and mass, and assessed tooth wear, and physical and reproductive condition. I checked all opossums for wounds and possible toe-clips (see below). This information, along with trap location and date, was recorded on standardized forms. Additionally, I fitted selected opossums with radio-collars. If females had pouch young, I toe-clipped each offspring with a unique pattern, sexed it, aged it, and measured its tail. I did this for 202, 266, 322, and 272 young in the 1st, 2nd, 5th, and 6th trapping sessions, respectively (Table 2.2). If any pouch young were not attached to the
Table 2.2. The number of pouch young and the number of litters that were toe-clipped in 1987 and 1988 on the Ordway Preserve. Pouch young of all females captured were toe-clipped if they were large enough (greater than 10-15 days).

<table>
<thead>
<tr>
<th>Study</th>
<th>Number of toe-clipped young</th>
<th>Number of litters toe-clipped</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>FC87 M</td>
<td>155</td>
</tr>
<tr>
<td></td>
<td>FC87 F</td>
<td>111</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>266</td>
</tr>
<tr>
<td></td>
<td>SC87 M</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td>SC87 F</td>
<td>103</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>202</td>
</tr>
<tr>
<td>87 Total</td>
<td></td>
<td>468</td>
</tr>
<tr>
<td></td>
<td>FC88 M</td>
<td>182</td>
</tr>
<tr>
<td></td>
<td>FC88 F</td>
<td>140</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>322</td>
</tr>
<tr>
<td></td>
<td>SC88 M</td>
<td>127</td>
</tr>
<tr>
<td></td>
<td>SC88 F</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>272</td>
</tr>
<tr>
<td>88 Total</td>
<td></td>
<td>594</td>
</tr>
<tr>
<td>Study</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1062</td>
<td>162</td>
</tr>
</tbody>
</table>
Radio-Tracking

I caught and radio-collared 11 adult female opossums before the first major trapping session and collared an additional 55 adult females during major trapping sessions (Table 2.3). Adult radio-collars weighed 25-35 g and had a range of 1-2 km in forest. They needed battery replacement every 4-6 months. I located the den sites of each adult female about once weekly to determine their home ranges (i.e., natal ranges of their offspring) and to keep track of them for capturing their young at weaning age.

When the offspring of a radio-collared female were estimated to be 90 days old (usually in May/June or August/September), I set traps around her den site to capture the young. I set 4-6 small Tomahawk traps each night at the mother’s, sometimes shifting, den site until (1) most of the young were caught, (2) the young were estimated to be 110 days old and already independent, or (3) the mother was caught and was not lactating, in which case the young were probably either dead or already independent. Sometimes I also set 4-6 Sherman traps or used a funnel trap (a hardware cloth funnel with the small end stuck into the burrow and the baited trap wired into the wide end of the funnel). For some litters in 1988, after catching the
Table 2.3. Number of adult females radio-collared in each trapping session.

<table>
<thead>
<tr>
<th>Trapping Session</th>
<th>Number of females collared</th>
</tr>
</thead>
<tbody>
<tr>
<td>before 1st session (Nov 86-Feb 87)</td>
<td>11</td>
</tr>
<tr>
<td>26 Mar-23 Apr 87</td>
<td>14</td>
</tr>
<tr>
<td>7 Jul-1 Aug 87</td>
<td>5</td>
</tr>
<tr>
<td>13 Dec-26 Feb 88</td>
<td>13</td>
</tr>
<tr>
<td>18 Mar-16 Apr 88</td>
<td>20</td>
</tr>
<tr>
<td>27 Jun-19 Jul 88</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>66</strong></td>
</tr>
</tbody>
</table>
mother in a trap, I dug up or disassembled the den and caught the young by hand. In total, I attempted to catch the young of 20 females in 1987 and 25 in 1988. I did not attempt to trap young of some collared mothers either because I could not locate the mothers or these mothers were in the middle of huge swamps or prairies where finding their young with a transmitter range of 400 meters (once collared, see below) would have been impossible.

I radio-collared most young captured with miniature transmitters weighing 8-10 g. These transmitters had a 300-500 m reception range in forest, and the batteries lasted three months. However, FC88 young collared at weaning received collars with slightly larger batteries (ten months life) which increased the collar weight by 2 g and caused the battery portion to stick out from the collar 13 mm instead of 9 mm; these collars also had a slightly greater range. FC87 and half of SC87 collared at weaning received thin, lightweight antennas on their collars; however, because of problems with antenna breakage, all other juveniles received 1.5 mm thick braided-steel antennas.

For each collared young, I recorded standard measurements, mass, toe-clip number, sex, mother, date, and location. When possible, collaring and measuring were done in the field at the capture site. Occasionally, opossums were kept in the lab overnight while a transmitter was prepared for them. In all cases, newly collared young of weaning age were released into their radio-collared mother’s
Table 2.4. Radio-collared young.

<table>
<thead>
<tr>
<th>Study</th>
<th>Young collared at weaning</th>
<th>Young collared post-weaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>FC87</td>
<td>22</td>
<td>21</td>
</tr>
<tr>
<td>SC87</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>87 Total</td>
<td>39</td>
<td>32</td>
</tr>
<tr>
<td>FC88</td>
<td>18</td>
<td>11</td>
</tr>
<tr>
<td>SC88</td>
<td>11</td>
<td>24</td>
</tr>
<tr>
<td>88 Total</td>
<td>29</td>
<td>35</td>
</tr>
<tr>
<td>Study Total</td>
<td><strong>68</strong></td>
<td><strong>67</strong></td>
</tr>
</tbody>
</table>

Total Young Collared = 135
current den. Once young were collared (Table 2.4), I located their den sites daily for the first one and a half months and at least once weekly thereafter. In trapping sessions, I radio-collared additional young (Table 2.4) and located them at least weekly.

Every 3-5 weeks I recaptured juveniles at their den sites, weighed and measured them, and adjusted their collars to accommodate growth. Every two and a half months I changed the batteries in their radio-collars. Once opossums reached 0.7 kg, I trapped less frequently for collar fitting; once they reached 1.3 kg or more, they received adult-sized collars.

I monitored all collared juveniles until they died, disappeared, or lived past their first mating season. If an opossum disappeared, I searched a 900 km² area, centered on its last known location, using aerial radio-tracking techniques. Many dispersers were located in this fashion. I located dispersers at least 2-5 times each and tried to trap several, to see if they were still alive at least one month after traveling to their new ranges. If an animal remained in its new range for at least one month, I considered it a disperser. When I was finished monitoring an animal, I removed its collar. In addition to the regular trapping sessions, I set 1,543 special traps to initially capture young, change or check collars, check on dispersers, or to remove collars. However, trapping results are based solely on captures during major trapping sessions.
CHAPTER 3

JUVENILE MORTALITY

Results

Radio-Tracking

For FC87 and SC87 combined, 40% of the juvenile opossums collared at weaning (n=30) (excluding those who disappeared) died within 2 weeks, 27% died in the next 2 weeks, 10% in the 2 weeks after that, and 7% in the next two weeks (Figure 3.1). Thus, 84% of the collared juveniles in 1987 died within 2 months post-weaning. There was no difference in the distribution of mortality between the FC87 and SC87 with both sexes pooled (Figure 3.2) (Kolmogorov-Smirnov, P>0.1, D=0.18, n=17, 13). Within each litter, there was no difference in the mortality distributions of males versus females in FC87, SC87 or SC88 (Figure 3.2) (Kolmogorov-Smirnov, P>0.1 for each, FC87: D=0.214, n=10, 7; SC87: D=0.125, n=5, 8; SC88: D=0.321, n=7, 4).

The SC88 (n=11) had lower initial mortality (18%) than the SC87 (46%), but experienced moderate, steady mortality thereafter so that only 9% lived more than 2 months, a comparable figure to SC87 (Figure 3.1). Despite the early difference in mortality, the distributions of SC87 and SC88 do not differ significantly with both sexes pooled (Kolmogorov-Smirnov, P>0.1, D=0.32, n=13, 11).
Additionally, there was no yearly difference in the proportion of young collared at weaning (Fisher's exact test, P>0.48) or collared in later trapping sessions (Fisher's exact test, P>0.26) that lived to dispersal or to mating season (Table 3.1).

All of the FC88 (n=17) radio-collared at weaning died within 2 weeks post-weaning. Eight out of the 17 appear to have died in their dens. There does not appear to be a sex or litter effect in this den mortality (Table 3.2). There is a significant difference in the mortality distributions of FC88 and SC88 with both sexes pooled (Figure 3.2) (Kolmogorov-Smirnov, P<0.001, D=0.82, n=17, 11), and between FC88 and FC87 (Kolmogorov-Smirnov, P<0.005, D=0.65, n=17, 17).

Mortality for juveniles collared in later trapping sessions was much lower—only 21% for all cohorts pooled up to the first mating season (5-8 months post-weaning) (see Table 3.1). These young were at least one month post-weaning, many were older, when collared. This proportion is comparable to the mortality experienced by juveniles collared at weaning after they were 1-2 months old (Figure 3.1).

**Trapping**

Juvenile captures are summarized in Table 3.3. In trapping sessions 1-2 months after weaning, I caught 14.7% FC87, 4.5% SC87, 0.3% FC88 and 9.6% SC88 of the toe-clipped
Table 3.1. Number of radio-collared young dying or disappearing before their first mating season. See Table 4.1 for collared young dispersing or staying in natal area to breed.

<table>
<thead>
<tr>
<th></th>
<th>young and died</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>collared at weaning</td>
<td>and died before mating season</td>
<td>and disappeared</td>
<td>young collared later</td>
<td>and died before mating season</td>
<td>and disappeared</td>
</tr>
<tr>
<td>FC87 M</td>
<td>14</td>
<td>8</td>
<td>4</td>
<td>8</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>FC87 F</td>
<td>8</td>
<td>7</td>
<td>1</td>
<td>13</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>15</td>
<td>5</td>
<td>21</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>SC87 M</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>SC87 F</td>
<td>8</td>
<td>8</td>
<td>0</td>
<td>6</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>13</td>
<td>4</td>
<td>11</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>87 Total</td>
<td>39</td>
<td>28</td>
<td>9</td>
<td>32</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>FC88 M</td>
<td>10</td>
<td>9</td>
<td>1</td>
<td>7</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>FC88 F</td>
<td>8</td>
<td>8</td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>17</td>
<td>1</td>
<td>11</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>SC88 M</td>
<td>7</td>
<td>6</td>
<td>0</td>
<td>10</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>SC88 F</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>10</td>
<td>0</td>
<td>24</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>88 Total</td>
<td>29</td>
<td>27</td>
<td>1</td>
<td>35</td>
<td>10</td>
<td>2</td>
</tr>
</tbody>
</table>

Study Total | 68          | 55          | 10          | 67          | 14          | 4           |

Total Young Collared = 135
Table 3.2. Litter, sex and number of FC88 young dying either by predation or in their dens.

<table>
<thead>
<tr>
<th>Death by Predation</th>
<th>Mother ID Number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>415</td>
</tr>
<tr>
<td>Males</td>
<td>1</td>
</tr>
<tr>
<td>Females</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Died in Den</th>
<th>415</th>
<th>620</th>
<th>687</th>
<th>507</th>
<th>666</th>
<th>662</th>
<th>430</th>
<th>568</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Females</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3.3. All juveniles captured in trapping sessions. The first number in parentheses is the number of individuals in that category that had not been previously caught in another session. The second number in parentheses (below) is the percent of young initially toe-clipped in that category that were caught in that trapping session.

<table>
<thead>
<tr>
<th></th>
<th>1-2 months post-weaning</th>
<th>4-5 months post-weaning</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Toe-Clipped</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>23 (23)</td>
<td>16 (16)</td>
</tr>
<tr>
<td></td>
<td>(14.8)</td>
<td>(14.4)</td>
</tr>
<tr>
<td>FC88</td>
<td>1 (1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>(0.5)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>SC87</td>
<td>6 (6)</td>
<td>3 (3)</td>
</tr>
<tr>
<td></td>
<td>(6.1)</td>
<td>(2.9)</td>
</tr>
<tr>
<td>SC88</td>
<td>12 (12)</td>
<td>14 (14)</td>
</tr>
<tr>
<td></td>
<td>(9.4)</td>
<td>(9.7)</td>
</tr>
<tr>
<td>No Toe-Clip</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>13 (13)</td>
<td>10 (10)</td>
</tr>
<tr>
<td></td>
<td>(5.8)</td>
<td>(7.2)</td>
</tr>
<tr>
<td>FC88</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>SC87</td>
<td>3 (3)</td>
<td>3 (3)</td>
</tr>
<tr>
<td>SC88</td>
<td>7 (7)</td>
<td>6 (6)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>7-8 months post-weaning</th>
<th>9-10 months post-weaning</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Toe-Clipped</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>9 (2)</td>
<td>8 (2)</td>
</tr>
<tr>
<td></td>
<td>(5.8)</td>
<td>(7.2)</td>
</tr>
<tr>
<td>FC88</td>
<td>8 (2)</td>
<td>6 (2)</td>
</tr>
<tr>
<td></td>
<td>(4.4)</td>
<td>(4.3)</td>
</tr>
<tr>
<td>SC87</td>
<td>0 (0)</td>
<td>5 (3)</td>
</tr>
<tr>
<td>No Toe-Clip</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>23 (12)</td>
<td>7 (3)</td>
</tr>
<tr>
<td></td>
<td>(5.8)</td>
<td>(7.2)</td>
</tr>
<tr>
<td>FC88</td>
<td>9 (3)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>SC87</td>
<td>6 (3)</td>
<td>10 (6)</td>
</tr>
</tbody>
</table>

*includes FC87 and FC88 caught in July session and SC87 and SC88 caught in Oct/Nov session
+includes FC87 and FC88 caught in Oct/Nov session and SC87 and SC88 caught in Jan/Feb session
**includes FC87 and FC88 caught in Jan/Feb session and SC87 caught in Mar/Apr session
++includes FC87 caught in Mar/Apr session
Figure 3.1. Percentage of juveniles collared at weaning that died within two week increments post-weaning. These numbers do not include opossums that disappeared (see Table 3.1). Juveniles in the >8 weeks category may have lived past their first mating season or may not have (see Figure 3.2).
Figure 3.2. Number of males and females collared at weaning that died within two week increments post-weaning.
First cohort 1987

- Males: n = 10
- Females: n = 7

Second cohort 1987

- Males: n = 5
- Females: n = 8

First cohort 1988

- Males: n = 9
- Females: n = 8

Second cohort 1988

- Males: n = 7
- Females: n = 4
Figure 3.3. All first cohort juveniles caught in trapping sessions. One to two months post-weaning corresponds to July trapping sessions, 4-5 to Oct/Nov sessions, and 7-8 to Jan/Feb sessions.
Figure 3.4. All second cohort juveniles that were caught in trapping sessions. One to two months post-weaning corresponds to Oct/Nov trapping sessions and 4-5 to Jan/Feb sessions.
Figure 3.5. Frequency of all toe-clipped litters known to have 0-10%, 11-20%, etc. of the litter surviving at least 1-2 months post-weaning.
Proportion of litter surviving at least 1-2 months post-weaning

First cohort 1987

Second cohort 1987

First cohort 1988

Second cohort 1988
Figure 3.6. Toe-clipped juveniles that survived (known by trapping or radio-tracking) at least 1-2 months post-weaning within each area on the preserve (study area). Numerators denote number of toe-clipped survivors and denominators indicate total number of juveniles toe-clipped in that area. Each block is one km². The bold vertical lines delineate the SW portion of the preserve used for analysis.
young. There was no difference between the sexes in capture rates (i.e. presumed survivorship) at 1-2 months post weaning (FC87 $X^2=0$, $P>0.9$; SC87 $X^2=2$, $P>0.1$; SC88 $X^2=0$, $P>0.9$).

FC88 captures are lower than FC87 captures for both sexes in every trapping session with toe-clipped and non-toe-clipped animals combined (Figure 3.3). There were 17% more first cohort juveniles toe-clipped in 1988 than in 1987. If this represents a 17% larger population in that year, the difference between years would be even more dramatic. Proportions of toe-clipped young caught in sessions over total initially toe-clipped young are also much lower for FC88 than for FC87 (Table 3.3).

SC88 captures are higher than SC87 captures for both sexes in every trapping session with toe-clipped and non-toe-clipped animals combined (Figure 3.4). There were 26% more second cohort juveniles toe-clipped in 1988 than in 1987. If this represents a 26% larger population in that year, the difference is smaller, but still dramatic. Proportions of toe-clipped young caught in sessions over total initially toe-clipped young are also consistently higher for SC88 than for SC87 (Table 3.3).

The greater number of male versus female first cohort captures was due to a sex-ratio bias in the pouch (Figure 3.3). Captured mothers with first cohort pouch young had 40% more males than females (in each year independently) (Wright and Kiltie, in prep). Trapping data reflect this
sex-ratio bias as I caught about 40% more first cohort males than females in their initial trapping session and consistently more first cohort males than females in all other sessions. The sex ratio of pouch young was not biased in the second cohort and trapping data do not show consistently greater male over female captures (Figure 3.4).

FC88 does not appear to have exceptional clumping of survivorship by litter when compared to the other three cohorts studied (Figure 3.5).

Fewer toe-clipped FC88 young survived in the SW portion of the preserve (mostly swamp) than in the rest of the preserve (not swamp) \( (X^2=4.8, df=1, P<0.025) \) (Figure 3.6). This differential survivorship did not exist for FC87 \( (X^2=0.098, df=1, P>0.7) \), for SC87 \( (X^2=0.27, df=1, P>0.5) \), or for SC88 \( (X^2=1.24, df=1, P>0.2) \)

Survivorship to Mating Season

The average litter size was 6.7 + 1.2 S.D. \( (n=88) \) for the first cohort and 6.3 + 2.1 S.D. \( (n=74) \) for the second cohort. Most females live to breed only one year, but in this study, at least 29% of the first cohort litters and 15% of the second cohort litters successfully weaned were from females in their second breeding season (based on known history females and females that could be definitely aged on the basis of tooth wear, weight and appearance). For known history females alone, 41% of the first cohort and 36% of
the second cohort litters were from females in their second breeding season.

Radio-tracking data, toe-clipped young survivorship, and non-toe-clipped young survivorship all yield comparable estimates of juvenile survivorship within and between years. With first and second cohorts pooled, 10-11% of the opossums born in any year lived until their first breeding season, but the contribution of each cohort to this 10-11% was not always equal. In 1987 there was about 65% survivorship of the first cohort, 35% of the second. Conversely, in 1988, only 40% of the first cohort survived and 60% of the second did.

Causes of Juvenile Mortality

Most of the radio-collared juveniles that did not survive until breeding season were killed by owls, including Great Horned owls (Bubo virginianus), Barred owls (Strix varia) or, less likely, Barn owls (Tyto alba) (Figure 3.7). I attributed mortality to owls on the basis of: finding remains in pellets (N=2); collar and/or body part caught in vegetation above ground (N=4); nonconspecific mammal fur tufts (fur tufts are bill-sized "pinches" of fur) by collar which had down feathers attached to antenna (N=1); collar, body parts and/or tufts of fur under roost trees, sometimes with owl excreta present (N=17); collar with lower jaw halves and/or tufts of fur or regurgitated fur (N=4).
Figure 3.7. Causes of mortality for all radio-collared juvenile opossums that did not disappear or live past their first mating season.
In 23 cases I could not positively identify the predator. For details of these cases and the owl-slain cases see the Appendix.

The three fox kills were typified by the head and collar being buried together under 1-3 cm of dirt, and being undetectable without the transmitter. Gray (*Urocyon cinereoargenteus*) or red (*Vulpes vulpes*) foxes could have been responsible. Grays are more numerous and regularly hunt at night in mesic habitats, but mammals make up a larger proportion of the diet for red foxes (Sunquist 1989).

The carcass from the bobcat kill (*Felis rufus*) had been completely covered with leaves, and a bobcat scat was located one meter away.

One FC87 male weighing 1.95 kg in October was down to 1.55 kg by December (most juveniles consistently gain weight). When captured at this time he whistled loudly when he breathed. He died shortly afterwards; I attributed this death to illness.

I found one recently weaned juvenile on a small rise of land in the middle of a thick, flooded swamp. She was wet, and her wrist was hooked under her collar although there was plenty of room to remove the paw. When originally caught, this individual weighed 155 g, but when found dead less than one week later she weighed only 120 g. She had no marks upon her, and I attributed this death to starvation, possibly due to the collar.
A recently weaned male was intact except for a broken jaw which was twisted over to the side, and a single puncture wound between his eyes. The puncture appeared to be from the large canine of an adult male opossum; males have much longer canines than females. Fighting between male opossums often results in simple canine punctures to the head, neck or shoulder region (McManus 1970). I have often seen such wounds on captured males. I listed this kill under intra-specific aggression.

Ten opossums probably died in their dens. They remained in their respective dens (in one case, 2 young in one den) for 2 to 8 weeks. Typically, recently weaned juveniles change den sites every 1-4 days (pers. obs.). I tracked them at night and found no activity and set traps many nights for each individual but caught no juvenile opossums. They were never trapped or seen again.

Possibly the most astonishing kill involved an alligator (Alligator mississippiensis). I tracked the transmitter to a lake shore when the signal suddenly became weak. I saw ripples in the water and the signal appeared to move out into the lake. Later, in a canoe, I pinpointed the signal in about 2 meters of water. I quickly pushed my paddle down and hit something. The signal weakened and moved off. I repeated this procedure once more. I presumed this juvenile had been eaten by an alligator!
Discussion

Survivorship

If 10-11% of the young born in a summer survive until their first breeding season, and 13 young are born on average to each breeding female per year, then 1.30-1.43 juveniles per year from each female survive. Given an average female's lifetime reproductive rate of 122% of their yearly output, each female, on average, produces 1.59-1.74 new individuals in her lifetime living at least to their first breeding season. More rapid male than female turnover would bring this even closer to a stable replacement rate.

Even though the first cohort must live about 100 days longer than the second cohort to be alive at breeding season, the FC87 had a higher percentage of survivors at this time than SC87. Llewellyn and Dale (1964) and Fitch and Sandidge (1953 as cited in Llewellyn and Dale 1964) found that about 65% of juveniles captured later in the year were first cohort young. Therefore, 1987 is probably more typical than 1988. Perhaps because first cohort individuals are larger than second cohort individuals they can outcompete them. In contrast, the second cohort did better than the first cohort in 1988, apparently due to the extreme early mortality of FC88.

Influence of Radio-Collars on Mortality Estimates

Although high initial mortality is predicted, the influence of the radio-collars may pose a problem in quantification. The collars were only 5-8% of the animal's
body mass when juveniles were initially collared at 100-150 grams. This is within generally accepted levels for not affecting small mammals adversely (Kenward 1987). Mortality is generally spread out over the first two months (Figure 3.1) and is not confined to the first two weeks as might be expected if the collars were a major source of mortality.

However, FC88 young collared at weaning did die within two weeks. Almost half (8 out of 17) of these individuals appeared to have died in their dens (in one case 2 in 1 den). Possibly they slipped their collars off; however, I never caught them again. If these juveniles had lived, the early radio-tracking FC88 mortality would be much more similar to the other cohorts studied.

The young that died in their dens may have succumbed to disease or parasites, or they may have starved. These juveniles appeared to have died less than two weeks after weaning. The one clear case of starvation I observed occurred less than one week after weaning and this female had her paw through her collar. Three times (2 individuals) I found FC88 juveniles active during the day with their forearms caught in their collars. One of these young had gained some weight since weaning, the other had not. This occurred 1-2 weeks post-weaning and these individuals appear to have died in their dens shortly afterward. These opossums seemed to be foraging during the day as well as at night; perhaps the collars made it more difficult to find food. Additionally, one had maggots on his arm and rear;
perhaps the collars prevented effective grooming. FC88 collars had larger batteries which may have compounded these problems. This is the only evidence I have for these collar influences, but they could have been a factor in these deaths.

Nevertheless, trapping results also suggest unusually high early mortality in FC88. Although I could not expect to catch all toe-clipped offspring that survived, proportions of toe-clipped young caught should indicate population changes. Indeed, trapping data 1-2 months after weaning suggest relatively high survival for the FC87, next highest for the SC88, moderate survival for the SC87 and extremely low survival for the FC88 (Table 3.3). Thus the trapping data mirror the trend observed in the radio-tracking data (Figure 3.1). The radio-tracking data are most likely a correct representation of the population mortality.

First Cohort 1988

The unusually high mortality of FC88 seems to have occurred around the time of weaning. All 17 FC88 young radio-collared at weaning died within 2 weeks (Figure 3.1). In trapping sessions one to two months after weaning, I caught 62 juveniles from the FC87 but only 1 from the FC88 (Table 3.3). Radio-collar mortality does not explain low trapping captures as I collared only 18 out of 322 toe-clipped FC88 young. First cohort captures are consistently lower in all trapping sessions in 1988 compared to 1987,
especially 1-2 months post-weaning (Figure 3.3, Table 3.3). The young have restricted movements 1-2 months after weaning; as their ranges expanded, any survivors would be more likely to encounter a trap, accounting for the increased FC88 captures in subsequent sessions. The high mortality of FC88 is a real phenomenon.

Low rainfall in 1988 may have had a detrimental effect on opossum food resources. Because rainfall is extremely variable locally, I examined data collected on the Ordway Preserve (Bert Charest, unpub. data), at the Gainesville airport, and at the weather station 10 miles WSW of Gainesville (NOAA 1987, 1988) (Figure 3.8). There was an average of 73 mm less rain from March through May in 1988 than in 1987 at the three sites; rainfall in 1988 was 79% of that in 1987 for this period. In the last week of May 1988, there was a tremendous rainstorm. In the period before this week the difference is even more dramatic, with, on average, 103 mm less rain in 1988 at the three sites. For this period, rainfall in 1988 was 70% of that in 1987 (only 62% for the Ordway data alone). Most first cohort young were weaned in the last three weeks of May.

Opossums feed mostly on arthropods (grasshoppers, beetles, larvae, etc.), small vertebrates (many Amphibia), earthworms, mollusks, fruits and mammals (the last group is probably not applicable to newly independent young) (Seidensticker et al. 1987, Hamilton 1951, Lay 1942, Taupe 1947). Perhaps they found fewer of these items at this
Figure 3.8. Rainfall records at three locations from March through June. Rainfall has been divided into 4 roughly equal periods for each month. Ordway data are from B. Charest (unpubl. data), airport and WSW data are from NOAA (1987, 1988).
crucial weaning time due to the lower rainfall. Most fruit is at a low in this area in May and June (Skeate 1987, Wunderlin 1982) so the juveniles may be heavily dependent on the aforementioned food sources.

This is still not a completely satisfactory answer, as the radio-collared young appear to have died in the last week of May and the first week of June after the rain had increased. Perhaps there is a lag between when the rain resumed and any effect on the opossums' food base. Additionally, both 1986 and 1987 were drier than usual (for the last 30 years) (NOAA 1986, 1987) for most of the spring and summer months. Perhaps a cumulative effect of these drought years diminished the food base by 1988 (but see Second Litter 1988). Lake levels were progressively lower from 1986 to 1988 on the preserve (Richard Franz, pers. comm.).

In Virginia, Seidensticker et al. (1987) also found an extreme opossum population drop correlated with a severe drought and probable resultant food supply decreases. However, adults as well as juveniles were affected in that study and only juveniles were in the present study. I would expect newly independent young to be affected well before their parents were.

If there was less food in 1988 than in 1987, increased time spent foraging would increase the risk of predation. Starvation itself would also be a possible cause of death. Evidence for starvation and daytime foraging was discussed
above. As predicted, a slight resource fluctuation may have dramatically influenced this population.

Perhaps the low rainfall affected the food base in the SW portion of the preserve more than in the rest of it, which may help to account for the lack of survivors in this area in 1988. This part of the preserve is swamp, which completely dried up early in the spring; perhaps the possible opossum prey living here were not used to xeric conditions as those typically living in the uplands are and did not survive the drought as well.

Another, nonexclusive, possibility is that the alternative prey base for opossum predators was smaller in May/June 1988 than 1987, thus increasing predation pressure on opossums during this period in 1988. This could also occur as a result of the low rainfall discussed above. Additionally, in 1984-85 we had extreme differential owl predation of adult opossums in the SW portion of the preserve. Perhaps owl density is greater here and with fewer alternative prey, they devoured the juvenile opossum population in the area.

Also a non-exclusive possibility, predators may have entered dens while mothers were foraging and killed the young. Perhaps mothers had to forage for longer periods, exposing their young to this risk, because of the possible rainfall effect. I had an unusually hard time catching FC88 young at weaning, suggesting they had either already died (although timing of SC88 births were not early) or they were
not traveling with their mothers as FC87 and SC87 had. In other cohorts, I would usually catch young along with the mother. In FC88 I had to extract young from their dens after I had caught their mother because trapping success for them was so much lower than for FC87 and SC87. Even then, I found empty dens when young should have been inside. If den predators were the main cause for the increased mortality, I would expect clumped survivorship by litter. There does not appear to be unusual clumping for FC88 compared to the other three cohorts (Figure 3.5), although this may still be a partial cause.

Other possible causes of widespread mortality include heavy parasite load or disease. I would expect to find litter-clumped survivorship and/or clumped survivorship by area if either were responsible. As mentioned above, there is no extraordinary clumping of survivorship by litter (Figure 3.5). However, there was significant clumping of survivors by area for FC88 and not for FC87 (Figure 3.6). Fewer toe-clipped FC88 opossums survived in the SW portion of the preserve. However, disease or parasites in one part of the preserve could not account for the extreme trapping results preserve-wide. Furthermore, adults did not show this increased mortality, which might be expected if disease or parasites were the cause. In 1987 the ratio of adults:juveniles captured was 56:62 whereas in 1988 it was 72:1. The observed area effect is more likely due to
differential effect of the drought in the SW portion as discussed above.

Second Litter 1988

While FC88 survival was low, SC88 survival was high and even better than SC87. Second cohort captures were consistently higher in both trapping sessions in 1988 compared to 1987 (Figure 3.4, Table 3.3). While these trapping data clearly demonstrate higher survival in 1988 over 1987, the radio-tracking data are less conclusive, showing no significant differences between SC87 and SC88 survivorship, although the mortality distribution shows lower initial death rates for SC88 than for SC87 (Figure 3.1). As in the first cohort's low survival, this differentially low survival probably occurred shortly after weaning.

Once more, rainfall probably had an influence. In August and September combined, there was an average of 476 mm (360%) more rain in 1988 than in 1987 (Figure 3.9) at the three locations discussed above (B. Charest, NOAA 1987, 1988). NOAA data (1987, 1988) show that 1987 was drier than the 30 year mean while 1988 had over 300 mm more rain than usual in August and September combined. Most second cohort young weaned in mid-August to early September. Unlike April 1988 (1 month pre-weaning for the first cohort), July 1988 (1 month pre-weaning for the second cohort) was relatively wet, having almost 100 mm of rain compared to less than 25 mm in April (Figures 3.8 and 3.9). Perhaps the July
Figure 3.9. Rainfall records at three locations from July through October. Rainfall has been divided into 4 roughly equal periods for each month. Ordway data are from B. Charest (unpubl. data), airport and WSW data are from NOAA (1987, 1988).
rainfall triggered increases in the opossum food base before the second cohort weaned, preventing the possible lag effect seen for the first cohort. The second cohort should still be fairly dependent on invertebrates and small vertebrates even though fruit levels are somewhat higher at this time of year than in May and June (Skeate 1987).

Additionally, the greater second cohort survival in 1988 over 1987 could be due to the demise of the first cohort in 1988. Perhaps the SC88 experienced less competition for den sites and food than the SC87 because almost all of the FC88 died. Three months after FC87 was weaned, when the SC87 was weaned, 18% of the radio-collared FC87 were alive; 0% of the FC88 were alive when the SC88 was weaned (Figure 3.2). This may have led to less time spent searching for these resources and therefore lower risk of predation. The possible increased food base in 1988 may have multiplied this effect.

Perhaps the alternative food base for predators of juvenile opossums was greater in August/September 1988 than 1987, reducing predation on opossums during this period in 1988. The much greater rainfall at this time in 1988 makes this a distinct possibility.

Causes of Juvenile Mortality

Although other researchers have found human factors such as traffic, hunting and trapping to be the major causes of opossum death (Gardner 1982, Seidensticker et al. 1987), the present study was conducted on a preserve, essentially
removed from these problems. Avian predators were the major cause of death (Figure 3.7). In this study and in previous work on the preserve, I observed that owls, not humans, were probably the major source of mortality for adult and juvenile opossums alike. Gardner (1982) and Hunsaker (1977) both suggest that other than humans, owls are probably the greatest predators. I have assumed these predators were owls and not hawks as the former are nocturnal as are opossums. As slow moving, terrestrial and pale-colored mammals, young opossums should be easily located and killed by large raptors. Young opossums den much more frequently in high tree cavities and nests than adults do (pers. obs.) and when released will soon climb a tree if available (Seidensticker et al. 1987, pers. obs.). Perhaps by staying in the trees when small they are less accessible and less visible to owls. Owls also seem to be the major predator of adult opossums (pers. obs.). I have witnessed a Great Horned Owl eating an opossum carcass and have found three dead adults with talon marks up and down their backs. In two of these cases, the owl ate only the pouch and the young within and left the rest of the carcass. Owls may have a preference for small opossums. Fitch and Shirer (1970) found three of their nine radio-collared juvenile opossums killed by Great Horned Owls. The collars were found amid feathers, tufts of fur and owl excreta. Additionally, owl density is probably greater than the density for most other possible predators of opossums on the Ordway Preserve.
After owls, foxes are probably the most abundant carnivore, with bobcats being the scarcest. Proportions of attributable kills fit this order (Figure 3.7). I probably found few opossums killed by foxes and bobcats because these predators would most likely eat the entire prey, without much left to bury or cover, the only sure signs of their predation. Some of their kills are probably in the unidentified carnivore category, or perhaps in those that disappeared.

Adult males of many species are known to be aggressive towards male juvenile conspecifics, especially if they are unrelated. This may be a mechanism for the reduction of future mate competition. Male immigrants or transients may kill male offspring of the resident male (though especially in social species) (Anderson 1989). The juvenile with the puncture between his eyes may demonstrate this occurring in opossums. When McManus (1970) introduced a young male (100 g) to 5 adult males individually, it was always either defensive or tried to flee, sometimes screeching. The adults were either curious or aggressive; one adult stalked the juvenile as prey. Eisenberg and Leyhausen (1972) found that opossums kill their prey by a rapid series of bites, 40% to the head. Opossums have also been known to cannibalize each other in the wild (Taube 1947).

I had expected to find some snake predation (i.e., transmitters inside snakes), especially by climbing constrictors such as rat snakes (Elaphe obsoleta) and corn
snakes (*Elape guttata*). Shortly after weaning, opossums are roughly the same size as many small rodents (100-300 g), which are food for many snakes (Behler and King 1979). However, because juveniles grow very rapidly, the period during which opossums would be the right prey size for most snakes is restricted. Perhaps because the young are available as prey for only a few weeks in May/June and in August/September, the snakes concentrate on prey that are more plentiful year round. Additionally, snakes feed infrequently and if a snake took an opossum, it may not eat again until the rest of the opossum cohort was too large to be a prey item. On the other hand, owls require roughly 15% of their body mass in prey a night (Johnsgard 1988). Finally, adult opossums are immune to viper venom (Kilmon 1976, Werner and Vick 1977); perhaps the juveniles escape predation by cottonmouths (*Agkistrodon piscivorus*) and rattlesnakes (*Crotalus adamanteus*) (which may be large enough to eat even large opossums) by immunity to their venom.

Openings of juvenile dens, be they up in tree cavities or on the ground, are often much smaller than those of adult opossums (pers. obs.). This may exclude other possible predators such as adult opossums or raccoons.

**General Comments**

Opossums are probably quite vulnerable when first on their own. They must discover food sources, perfect capture
techniques, and find reliable, safe den sites. They must learn to move through the brush unnoticed. Indeed, I have observed small opossums, when released during the day or at night, taking several minutes to raise a leg, hold it in the air motionless and slowly put it down deftly to complete one step, all the while being extremely attentive and silent. Juveniles do this much more frequently and deliberately than adults do.

Newly independent opossums are usually very passive. I could handle most, measuring them and sewing on their radio-collars, without anesthetizing them. Few tried to bite, although they have numerous small, needle-sharp teeth. In contrast, about one month after weaning, most of the juveniles had become belligerent, and would readily bite. Perhaps they are much easier to prey upon in the early passive period before becoming self-defensive.

Additionally, small size alone may lead to greater predation early on. More predators may attempt to subdue and eat a 100-300 g animal than one that is larger, with larger teeth (including long canines) accompanying that larger body size.
CHAPTER 4
JUVENILE DISPERsal

Results

Of the juveniles that did not die or disappear, 100% of the males collared at weaning and 95% of those collared later dispersed; only 7% of the females collared later dispersed (all those collared at weaning either died or disappeared) (Table 4.1, Figures 4.1 and 4.2). Conversely, for all juveniles that did not die or disappear, 93% of the females and only 4% of the males stayed to breed in their natal range (Table 4.1).

Likewise, trapping data show that 29 females stayed to breed in their natal range and only one male did so (based on toe-clips). Trapping data also show that 31 males dispersed but only eight females did so (perhaps only three, see below) (Figures 4.3 and 4.4).

Eleven male dispersers trapped were also radio-collared. Estimated dispersal distances were different in some of these cases. In 5 cases the trapping overestimated distance by 0.25-0.75 km. In one case it underestimated by 3.00 km.

Some juveniles dispersed in the autumn. However, most dispersed just before or during mating season (Figures 4.1,
Additionally, trapping data show more non-toe-clipped males caught during these times, and progressively lower numbers of toe-clipped males caught (Figures 4.6, 4.7). Proportions of first cohort unmarked to total males captured rise from 35% to 60% to 65% in consecutive trapping sessions (Figure 4.6). Proportions of second cohort unmarked to total males captured rise from 36% to 69% (Figure 4.7).

Mean weight of autumn dispersers was the same, or almost the same, as non-dispersers when compared in October (all known weights used) (first cohort males: dispersers=1.9 kg, non-dispersers=1.9 kg; first cohort females: dispersers=1.4 kg, non-dispersers=1.4 kg; second cohort females: dispersers=0.65 kg, non-dispersers=0.98 kg).

Mating season dispersers also weighed almost the same, on average, as non-dispersers when compared in January (first cohort males: dispersers=2.5 kg, non-dispersers= 2.65 kg; second cohort males: dispersers=1.6 kg, non-dispersers=1.5 kg; first cohort females: dispersers=1.85 kg, non-dispersers=1.8 kg; second cohort females: dispersers=1.4 kg, non-dispersers=1.4 kg).

Female dispersers were not differentially from male-biased litters (Binomial test, P>0.8) (Table 4.2). Further, natal-litters of dispersers did not have different sex-ratios than natal-litters of non-dispersers (median test, df=1, P>0.1).
Table 4.1. The fate of all radio-collared juveniles. Juveniles either died, disappeared, dispersed or stayed in their natal area past breeding season.

<table>
<thead>
<tr>
<th>Collared at weaning</th>
<th>total number</th>
<th>died</th>
<th>disappeared</th>
<th>dispersed</th>
<th>stayed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>14</td>
<td>8</td>
<td>4</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>SC87</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>1</td>
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<td>0</td>
</tr>
<tr>
<td>SC88</td>
<td>7</td>
<td>6</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC87</td>
<td>8</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>SC87</td>
<td>8</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>FC88</td>
<td>8</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>SC88</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

| Collared post-weaning |              |      |             |           |        |
| Males                |              |      |             |           |        |
| FC87                | 8            | 1    | 2           | 5         | 0      |
| SC87                | 5            | 1    | 0           | 3         | 1      |
| FC88                | 7            | 2    | 0           | 5         | 0      |
| SC88                | 10           | 3    | 0           | 7         | 0      |
| Females              |              |      |             |           |        |
| FC87                | 13           | 1    | 0           | 0         | 12     |
| SC87                | 6            | 1    | 0           | 0         | 5      |
| FC88                | 4            | 1    | 1           | 0         | 2      |
| SC88                | 14           | 4    | 1           | 2         | 7      |
| Study                | Total        | 135  | 69          | 14        | 25     | 27     |
Table 4.2. Natal-litter sex ratios (male:female) of dispersing females. Two dispersing females had no toe-clip so I can not determine their natal-litter sex ratios.

<table>
<thead>
<tr>
<th>distance dispersed (km)</th>
<th>natal-litter sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.00</td>
<td>5:3</td>
</tr>
<tr>
<td>1.00</td>
<td>5:3</td>
</tr>
<tr>
<td>1.00</td>
<td>2:6</td>
</tr>
<tr>
<td>1.25</td>
<td>6:2</td>
</tr>
<tr>
<td>1.25</td>
<td>6:1</td>
</tr>
<tr>
<td>1.50</td>
<td>1:6</td>
</tr>
<tr>
<td>5.50</td>
<td>2:8</td>
</tr>
<tr>
<td>5.75</td>
<td>5:2</td>
</tr>
</tbody>
</table>
Figure 4.1. Timing and distance of radio-collared male dispersals by cohort.
Figure 4.2. Timing and distance of radio-collared female dispersals. Both dispersals were by SC88 young. Home range diameter was approximated at 0.85 km (see text).
Figure 4.3. Trapping data dispersal distances of male opossums as measured by the number of home range diameters (1.25 km) moved from their previous range.
Figure 4.4. Number of home range diameters (0.85 km) females caught in trapping sessions had dispersed. All were first cohort young except for 2 individuals in the 1-1.9 category. All probably dispersed prior to the breeding season (I can not be certain of 3 in the 1-1.9 category).
at least 3 weeks pre-mating season

less than 3 weeks before or during mating season

n = 24

Figure 4.5. Dispersal distances of radio-collared male opossums as measured by the number of home range diameters (1.25 km) moved from their previous range. One individual moved in September and again at the end of December.
Figure 4.6. Number of marked (toe-clipped) and unmarked first cohort young captured during three trapping sessions in 1987 and 1988.
Figure 4.7. Number of marked (toe-clipped) and unmarked second cohort young captured during two trapping sessions in 1987 and 1988.
Figure 4.8. Timing of dispersal by first and second cohort males based on trapping data, both years combined.
Figure 4.9. Timing of male dispersals in 1987 and 1988 based on trapping data, first and second cohorts combined.
Discussion

Dispersal Timing

Some radio-tracked first cohort young dispersed in September when the second cohort was being weaned (Figure 4.1). Perhaps the first cohort young are crowded out by the increased number of opossums, although they would be much larger than the second cohort, or perhaps the mothers push them out to make room for the second cohort. Young pikas, Ochotona princeps, disperse in midsummer, apparently due to juvenile crowding (Smith 1974). Additionally, in Wisconsin Guillete (1980) found at least 4, possibly 7, of his monitored first cohort opossums dispersed between late August and mid October. None of his second cohort young dispersed until mid-April. Likewise, only first cohort young dispersed before the end of December in my trapping data (Figure 4.8). Note that almost all of these movements (both tracking and trapping), were in 1987 (Figures 4.1 and 4.9). The lack of early dispersers in 1988 is most likely due to the increased mortality of FC88; there were fewer FC88 left to disperse. The lack of early dispersers was probably not due to lower opossum density, because more second cohort young survived in 1988, so opossum density may have been comparable to 1987 despite the high mortality in FC88. Adult densities in the autumn are the same in 1987 and 1988 (roughly equal number of individuals
captured/trapping effort), so density differences would have to be due to juveniles.

Dispersal peaks during the first mating season. Most male dispersals occurred just before or in the first half of this mating season (late December-late January, Figures 4.1 and 4.3). Most of these mating season dispersals were initial movements away from the natal area (I can not be sure of 7 opossums without toe-clips, data combined). The one exception dispersed 2.75 km from his natal area (in good opossum habitat based on trapping opossum density, mesic hammock) before November, returned to that natal area only for the mating season, then returned back to the new area (in marginal opossum habitat based on trapping opossum density, xeric uplands). Opossum densities (including females) in his new area were very low. Perhaps he was looking for mates, although he passed through some excellent opossum habitat (very high opossum density, mesic hammock) on his return to his natal range. Incidentally, this was the only FC88 male that dispersed prior to the breeding season. In contrast, five males dispersed solely for the mating season; they returned to their original ranges afterward. Four of these had toe-clips so I know they were shifting away from their natal range. These dispersals were all equal to or under 2.5 km, and could have been expansions or shifts to find mates. Alternatively, they may have been pushed out by adult males (whose ranges increase at this time), only being able to return after the mating season’s
completion and their neighbors' return to normal ranges. Male home ranges are large; however, opossums have a keen sense of smell and it may take only one violent encounter to impress a juvenile. Finally, a disproportionate number of males were last caught in the sessions just before or during the mating season; these males probably also dispersed. Guillete (1980) found no juvenile dispersal in Wisconsin during the winter (including mating season), and concluded this was due to freezing temperatures. He expected a different temporal pattern of dispersal in more southern localities.

Even though most males dispersed at mating time, it is doubtful any would procure a mate unless they were larger than the other males in the area. Ryser (1989) found that males regularly check on females around their range (expanding their home range 2.3 times, n=42) and arrive at a female's den on the night she is receptive. Matings take place late at night so that many males can congregate at the den and compete (e.g. fight) for the female. Ryser (1989) found male body size is the only factor that appears to influence the outcome of this battle. Age (independent of size) and residence do not play a role. Therefore, if a dispersing male finds a receptive female, he must be the largest active male vying for mating privileges to be successful. This would not usually be the case. To some degree, his victory may depend on female synchrony.
Trapping data also indicate that most juvenile dispersal is by males, that the first cohort moves more before the breeding season than the second cohort, and that there is much dispersal around the mating season. Numbers of unmarked and marked females remain fairly constant through time. Meanwhile, the number of unmarked males rises sharply with each session while the number of marked males decreases (Figures 4.6 and 4.7). Unmarked males are probably moving into the preserve from outside and marked males are dispersing out of it. The higher initial number of marked first cohort males over females (Figure 4.6) is a result of the sex ratio bias discussed in Chapter 3. Initial numbers of second cohort marked males and females are similar (Figure 4.7). Second cohort sex ratios were not biased (Chapter 3).

Distance versus Home Range

An average non-breeding, adult male's home range is 1.26 + 1.12 S.D. km in diameter if the area is transformed to a circle. This is based on minimum convex polygon area corrected for lakes or wet prairies (unused portions) (n=33) (Ryser, in prep.). However, during the breeding season, this range increases to 2.3 times its original size on average (Ryser, 1989). Normally there is some overlap between ranges, but this overlap increases dramatically during the breeding season (Ryser, 1989). I have used the
typical range diameter of 1.25 km for the Figures as this is probably the typical living area for a male opossum.

An average adult female’s home range is 0.83 + 0.70 S.D. km in diameter if the area is transformed to a circle. Again, this is based on corrected minimum convex polygon area (n=33) (Ryser, 1989).

I did not count movements as dispersals unless they were greater than or equal to 1.25 km for males and 0.85 km for females.

Using a circle for home range diameter may either overestimate or underestimate actual diameter as some of the ranges are rather long and narrow, bordering on lakes.

Dispersal Distributions

The large number of males and females dispersing 1-1.9 home range diameters in the trapping data might be an overestimate (Figures 4.3 and 4.4). Traps were not set deep within the large prairies and swamps of the preserve, only on their edges (Figure 2.1). Therefore, when an opossum was retrapped on the other side of this expanse of land, he or she may have been living mostly inside this area and only shifted a short distance, although the measured distance in some cases was 1.00-1.75 km. This may have occurred for 6 males and for 5 females. This problem did not occur with radio-collared opossums as exact ranges were known.

In general, the radio-tracking and trapping dispersal distributions look quite similar (Figures 4.3 and 4.5).
However, as predicted, most of the longer dispersal distances were not obtained by trapping.

**Passive Juvenile Dispersal**

Mothers may occasionally actively disperse the young. Although most females, juveniles and adults, stayed in the same range throughout their lifetime, evidence suggests that one mother took her first litter 4.5 km away from her normal range when they were 1-2 months from weaning. She returned almost all the way to her initial range to wean her second litter. Stenseth (1978) reviews similar data on pregnant microtine rodent females giving birth in one area and traveling to another for their second parturition. My data show that six other females weaned their first and second litters in different ranges. Guillete (1980) found that most adult female opossums that did disperse had pouch young at the time and suggests this as a mechanism for rapid species range expansion.

**Disappearing Juveniles**

I was unable to find animals that are listed under disappeared in Table 4.1 through ground searches and aerial radio-tracking (I spent 1 1/2 hours in the air per individual searching a 900 km² area; I found opossums 76 times using this method and failed to find only 14). I may have either missed them somehow (see below), or they may have dispersed outside my search area—which would mean a
distance of over 15 km from their last known location, over twice the greatest known dispersal.

Alternatively, their transmitters may have failed due to technical failure, predation damage or faulty batteries. Another possibility is antenna breakage, which would have reduced the reception range to only 50 m, making them difficult to find, even from the air. In 1987 I had a distinct problem with antenna breakage (see Methods). I found 5 FC87 and 1 SC87 young with broken antennas. This may partially account for the increased number of disappearing juveniles collared at weaning in 1987 (Table 4.1). Timing of disappearance might provide some insight into a probable explanation.

Eight disappearances are probably transmitter-related; the individuals were lost 1-3 days after collaring. The four FC87 males collared at weaning and lost may have had broken antennas or failed batteries; three disappeared 4 weeks and one 9 weeks after collaring. Two of the disappearances are probable dispersals. A FC87 male collared after weaning and a FC88 female collared at weaning were lost in late Jan, the peak dispersal season (Figure 4.1).

Dispersal Duration

Jan Ryser tracked three of my juvenile males into the night for his study of male mating success (Ryser, 1989). In all 3 cases, the males moved to their new locations
within 1-2 nights and the paths were fairly direct. My daytime locations for the rest of the dispersers also indicate relatively rapid, more or less unidirectional dispersal movements. Guillete (1980) also found that juvenile opossums have punctuated dispersals, moving 1.7 km in the first night.

Dispersal Mortality

There was only one death associated with dispersal. One month after weaning, a male moved 1 km and was killed by an owl. The rest of the radio-collared dispersers experienced no mortality either in their travels or for at least the first month in their new ranges. All collars from dead juveniles were found well within their normal ranges. By moving and settling quickly opossums may decrease their chance of mortality by reducing the active transient portion most associated with this mortality (Ambrose 1972). Additionally, opossums are very adaptable, being generalists in den site and food choice (Allen 1985). This may also enable them to safely colonize without increased mortality.

Dispersal Theories

In comparing my results to the dispersal theories discussed in the introduction (Table 4.1), I find that these data do not support the ontogenetic-switch hypothesis (Holekamp and Sherman 1989). Dispersers are not heavier
than non-dispersers either in the autumn or at mating season.

These data do not seem to support the prenatal androgen theory (Ims 1989), as female dispersers were not differentially from male-biased litters and their natal-litter sex ratios were not different from those of non-dispersers. However, being marsupials, opossums spend relatively little time in the uterus and this should decrease their exposure to this steroid from siblings. Therefore, a steroid-affected physiological cue cannot be ruled out.

Dispersal movements were quick as Howard (1960) predicted in his innate versus environmental theory. However, this is probably a result of selection acting to decrease the risk of mortality associated with dispersal rather than a result of any innate tendency to disperse. Dispersals appear to be consistently rapid, not fast for innate and slower for environmental as may be expected from this theory.

Lidicker (1975) predicted that during peak density periods, dispersers will be in poorer condition than non-dispersers. Densities are highest in the fall when the second cohort is weaned (Seidensticker et al. 1987, pers. obs.), but dispersers did not weigh less than non-dispersers at this time.

Inbreeding may not be a major problem in opossum populations. Opossums have extremely high population
turnover rates (Hunsaker 1977, Gardner 1982). With low survivorship of close relatives and with fast population turnover there is less of a chance for inbreeding (Anderson 1989, Jones 1984, Patton 1985). Likewise, breeding units are probably small in opossums (given dispersal distances) and inbreeding depression should not exist (Shields 1982). Additionally, observed dispersal movements are not long enough to eliminate all inbreeding, but should exclude most parental or sibling mating. This may lead to beneficial inbreeding as discussed by Shields (1982).

Because juvenile opossums are smaller than adults, they probably can not improve their chances of mating through dispersal. Therefore dispersal probably did not evolve explicitly for mate procurement.

Finally, these data do seem to support the parent-offspring competition hypothesis (i.e. resident fitness hypothesis). If juveniles benefit most from philopatry and do not have a genetic disposition to travel far, we would expect shorter dispersal distances in opossums than in animals with lower turnover rates (Waser 1985). In many other mammals dispersal distances exceed ten home range diameters (Shields 1982); in this population the maximum was less than six home range diameters. Dispersal distributions are partially leptokurtic as predicted (Figures 4.3 and 4.5). The greater-than-expected number of long distance dispersals may be due in part to heterogenous habitat (Waser 1985). Opossums have high dispersal rates as predicted for
r-selected species. Emigration peaks in the mating season as predicted if males are expelling sexually mature sons (all monitored males showed signs of sexual maturity by this time; Ryser, 1989).

Females do not appear to be ousting daughters when pregnant and lactating and requiring excess resources as the parent-offspring theory predicts. Perhaps the mothers do not expel the first cohort to save resources for themselves, but to give the second cohort a better chance of survival. Alternatively, perhaps the increased density itself drives the first cohort away. Again, opossums have high turnover rates and mothers may benefit by allowing their daughters to be philopatric. The second (terminal) cohort is the most philopatric as predicted, at least before mating season when adult males become aggressive.

I agree with Dopson and Jones (1985) that many factors may work in concert to promote dispersal, and that there probably is no single answer for its cause or evolution. Dispersal of *Didelphis virginiana* in Florida seems to be driven by male adult expulsion of male juveniles and perhaps to some extent by either maternal or density-related pressures. A secondary effect of this is to decrease incest, yet perhaps maintain beneficial inbreeding.
Juvenile opossums experience very high early mortality (generally 60-75% within the first 4 weeks post-weaning) which quickly levels off to much lower levels similar to adult mortality rates. There was no sex difference in mortality distributions, although there were some cohort differences. Possible resource fluctuations induced by rainfall variation seem to greatly affect juvenile survivorship. There also is no litter-biased clumping of survivorship, as may be expected if pre-weaning predation or genotype played a strong role. However, with unusually high mortality, environment or disease (seen through an area effect) may be factors. Most mortality is due to owl predation. Of all pouch young, 10-11% survive until their first breeding season.

Almost all juvenile males disperse (96%) and almost all juvenile females remain in their natal range (86%). Some first cohort males disperse about the time the second cohort is being weaned. This may be due to maternal pressuring or to increasing juvenile opossum density. Most juvenile dispersal occurs just before or during the mating season. This is probably due to adult male expulsion of juvenile males.
Dispersal movements are rapid, usually occurring in 1-2 nights. This may help avoid the increased risk of predation associated with such movement. There appears to be very little mortality associated with dispersal in this population. Maximum dispersal distances were 5.6 home range diameters (7.00 km) for males and 6.8 home range diameters (5.75 km) for females. Dispersal distributions are partially leptokurtic, with more-than-expected long distance movements revealed by radio-tracking, perhaps due to heterogenous habitat. As expected, trapping distributions lack the long-distance movements radio-tracking revealed. Adult females may often carry their litters to new areas before weaning, resulting in their passive dispersal.

Many factors may affect dispersers. These data seem to best support the parent-offspring competition theory for dispersal. Dispersal may benefit the parents more than the dispersing juveniles as Anderson (1989) suggested. A secondary effect may be to decrease incest, yet promote beneficial inbreeding.
APPENDIX
DETAILS OF DEATHS ATTRIBUTED TO OWL OR UNKNOWN CARNIVORE PREDATION

Owl Predation

1. collar, two lower jaw halves, head with neck still attached to it and owl pellet (2.5 cm X 9 cm) with opossum fur and small bones in it; sandhill

2. collar, owl pellet (1.5 cm round ball of opossum fur), lower jaw, and skull with weaker parts gone; all under roost tree; mesic hammock

3. head and collar in fork of vegetation 0.7 m above ground; other remains 0.5 m from base of plant; mesic hammock within 5 m of prairie

4. collars two m apart under oak; three lower jaw halves with some meat still on them; nose (fur and all) still attached to upper palate found hanging in vegetation 15 cm above ground; mesic hammock, near prairie

5. see number 4

6. collar under roost caught in branches below; boundary of sandhill and xeric hammock

7. collar with down feathers attached to antenna and nonconspecific fur tufts under oak; head with lower jaw two m away; xeric hammock

8. collar and lower jaw (the anterior point sticking in the
pinestraw and the coronoid processes pointing straight up into the air) at base of pine; sandhill
9. collar only under pine roost; mesic hammock, near prairie
10. collar and undamaged ear at base of large snag; collar antenna partially stripped; mesic hammock
11. collar at base of pine; owl excreta present; sandhill
12. found with number 11, same description
13. tufts of fur scattered around base of oak; also lower jaw half and collar; 30 m into mesic hammock
14. collar under oak, sharp punctures in tape (all collars are wrapped with electrical tape before collaring animals); 50 m into mesic hammock from sandhill
15. piece of fur and tufts of fur under pine (collar up in tree?); mesic hammock
16. collar under oak roost; swamp, mesic hammock boundary
17. collars found 5 m apart on pinestraw under pine; swamp, mesic hammock boundary
18. see number 17
19. collar and two lower jaw halves under snag; snadhill
20. collar with pieces of tape with punctures scattered under tree; 10 m from field into mesic hammock
21. collar at base of pine; owl excreta present; mesic hammock
22. collar under oak roost; xeric hammock
23. collar under roost; mesic hammock
24. collar under oak; mesic hammock, sandhill boundary
25. collar, fur tufts and some skin by side of log; xeric hammock

26. collar, lower jaw half and 20-30 tufts or "pinches" of fur; strip of mesic hammock between field and lake

27. collar and regurgitated fur; sandhill

28. collar and tufts of fur; field

**Unidentified Carnivore Predation**

1. found bitten through chest at 0830; died shortly afterwards (less than one hour); xeric hammock

2. collar on top of leaves; some loose vertebrae and limb bones under leaves (bobcat?); mesic hammock ten m from dark lake edge

3. collar on ground; 25 cm X 3-10 cm strip of skin draped over log 40 cm off ground, skin side up; xeric hammock

4. collar under one m of water by or under cypress knee in dark lake (gator? dropped by bird? drowned in den when water rose with terrific rain storm evening before?); swamp edge

5. collar, broken upper jaw, body whole except for a large piece of fur five m away in a dried-up pond; mesic hammock on edge of field

6. collar; lower jaw; skull with jaws gone; vertebrate column intact with some meat attached, ribs and limb bones missing; all lying close together; mesic hammock near field

7. collar next to body; head attached to vertebrate column
with column bent back to form top part of an S; ribs and upper limb bones missing; 2 1/2 months old when killed; mesic hammock on swamp edge

8. skull with upper jaw intact and still attached to vertebrate column which was bent back to form the upper part of an S; collar still on neck; ribs and upper limb bones missing; lower jaw two m away; three months old when killed; sandhill

9. collar with head in pieces; broken lower jaw; swamp near prairie edge

10. collar, lower jaw; upper jaw and skull in pieces; tooth marks on collar tape; xeric hammock

11. collar, lower 2/3 of lower jaw half, and some fur under vine mass; mesic hammock five m from field

12. collar under thick vegetation 100 m out into prairie

13. collar under brambles with some fur attached; mesic hammock on prairie edge

14. collar under dense vine mass; border of field and mesic hammock

15. collar in palmetto clump; mesic hammock near field, dark lake

16. collar only; mesic hammock

17. collar only, trees above; near dark lake edge in mesic hammock

18. collar, lower jaw; head with neck two m away; tufts of fur around; no roost; sandhill

19. collar and matted fur tufts; by big cypress stump; 2 1/2
months old when killed; one m from dark lake in swamp
20. collar and some fur; mesic hammock
21. collar, piece of lower jaw; mesic hammock
22. collar and jaw bone fragments; xeric hammock
23. collar one m from clear lake edge; ten m from xeric hammock
LITERATURE CITED


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BIOGRAPHICAL SKETCH

Debra D. Wright was born in Frederick, Maryland, in 1958. She grew up in Florida. At 19 she left to travel through the U.S. and returned 6 years later, having visited or lived in all 50. She received her B.S. in zoology from the University of Florida in 1986. In 1989 she was granted her M.S., also from the Zoology Department of the University of Florida. She is currently enrolled as a PhD student in the Tropical Biology Program at the University of Miami. Her dissertation topic will be the foraging ecology of Dwarf Cassowaries (Casuarius benneti) in Papua New Guinea.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

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This thesis was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Master of Science.

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