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METHODS AND TOOLS FOR ESTIMATION OF THE EXPOSURE OF TERRESTRIAL WILDLIFE TO CONTAMINANTS

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EXECUTIVE SUMMARY

A critical component in ecological risk assessment is the evaluation of exposure experienced by endpoint receptors. Exposure can be defined as the coincidence in both space and time of a receptor and a stressor, such that the receptor and stressor come into contact and interact. Without sufficient exposure of the receptor to the contaminants, there is no ecological risk.

Unlike some other endpoints considered in ecological risk assessments, terrestrial wildlife are significantly exposed to contaminants in multiple media. They may drink or swim in contaminated water, ingest contaminated food and soil, and breathe contaminated air. Exposure models for terrestrial wildlife must therefore include multiple media. In addition, because most wildlife are mobile, moving among and within habitats, exposure is not restricted to a single location. They may integrate contamination from several spatially discrete sources. As a consequence, the accurate estimation of wildlife exposure requires the consideration of habitat requirements and spatial movements.

This report presents methods for estimating exposure of terrestrial wildlife to both chemical (Sect. 2.1) and radionuclide (Sect. 2.2) contaminants. Approaches for probabilistic exposure estimation (Sect. 2.3) and extrapolation from individual-level exposures to population-level effects (Sect. 2.4) are reviewed. Finally, methods and models to estimate contaminant concentrations in selected food types consumed by wildlife (Sect. 3.2) and life history parameters (Sect. 3.3) needed to accurately estimate exposure are presented.

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1. INTRODUCTION

Exposure can be defined as the coincidence in both space and time of a receptor and a stressor such that the receptor and stressor come into contact and interact (Risk Assessment Forum 1992). In the context of ecological risk assessment, receptors include all endpoint species or communities identified for a site [see Suter (1989) and Suter et al. (1995) for discussions of ecological endpoints for waste sites]. In the context of hazardous waste site assessments, stressors are chemical contaminants and the contact and interaction are represented by the uptake of the contaminant by the receptor. Without sufficient exposure of the receptor to the contaminants, there is no ecological risk.

Unlike some other endpoint assemblages, terrestrial wildlife are significantly exposed to contaminants in multiple media. They may drink or swim in contaminated water, ingest contaminated food and soil, and breathe contaminated air. Exposure models for terrestrial wildlife must therefore include multiple media. In addition, because most wildlife are mobile, moving among and within habitats, exposure is not restricted to a single location. They may integrate contamination from several spatially discrete sources. As a consequence, the accurate estimation of wildlife exposure requires the consideration of habitat requirements and spatial movements.

The purpose of this report is to present generalized methods for the estimation of exposure of terrestrial wildlife, focusing primarily on methods and models for birds and mammals. Reptiles and amphibians are not considered because few data exist with which to assess exposure to these organisms. In addition, because toxicological data are scarce for both classes, evaluation of the significance of exposure estimates is problematic. The general exposure estimation procedure developed for birds and mammals, however, is applicable to reptiles and amphibians (EPA 1993).

Methods are presented for estimating exposure to both chemical (Sect. 2.1) and radionuclide (Sect. 2.2) contaminants. Approaches for probabilistic exposure estimation (Sect. 2.3) and extrapolation from individual-level exposures to population-level effects (Sect. 2.4) are reviewed. In addition to exposure models, methods and models to estimate contaminant concentrations in selected food types consumed by wildlife (Sect. 3.2) and life history parameters (Sect. 3.3) needed to accurately estimate exposure are presented.

2. METHODS FOR ESTIMATION OF EXPOSURE

Contaminants to which terrestrial wildlife may be exposed may be grouped into two broad classes: chemical (e.g., heavy metals, organics) and radionuclide. Because the mode of action differs greatly between these two general classes of contaminants, methods for estimation of exposure also differ. Methods for estimation of exposure to both chemical and radionuclide contaminants are presented below.

2.1 ESTIMATION OF EXPOSURE TO CHEMICAL CONTAMINANTS

As terrestrial wildlife move through the environment, they may be exposed to contamination via three pathways: oral, dermal, and inhalational. Oral exposure occurs through the consumption of contaminated food, water, or soil. Dermal exposure occurs when contaminants are absorbed directly through the skin. Inhalational exposure occurs when volatile compounds or fine particulates are respired into the lungs. The total exposure experienced by an individual is the sum of exposure from all three pathways or

$$E_{\text{total}} = E_{\text{oral}} + E_{\text{dermal}} + E_{\text{inhal}} \quad (1)$$

where

E_{total}	=	total exposure from all pathways,
E_{oral}	=	oral exposure,
E_{dermal}	=	dermal exposure,
E_{inhal}	=	exposure through inhalation.

Dermal exposure is assumed to be negligible for birds and mammals on most U.S. Department of Energy (DOE) hazardous waste sites. While methods are available to assess dermal exposure to humans (EPA 1992), data necessary to estimate dermal exposure are generally not available for wildlife (EPA 1993). Additionally, many contaminants found at DOE facilities (e.g., metals and radionuclides) are unlikely to be absorbed through skin (Camner et al. 1979; Watters et al. 1980). Feathers and fur of birds and mammals further reduce the likelihood of significant dermal exposure by limiting the contact of skin with contaminated media. Therefore, dermal exposure is expected to be negligible relative to other routes in most cases. If contaminants that have a high affinity for dermal uptake are present (e.g., organic solvents and pesticides) and an exposure scenario for an endpoint species is likely to result in significant dermal exposure (e.g., burrowing mammals or swimming amphibians), dermal exposure may be estimated using the model for terrestrial wildlife presented by Hope (1995).

Inhalation of contaminants is also assumed to be negligible at most DOE facilities. This is for two reasons. First, because most contaminated sites are either capped or vegetated, exposure of contaminated surface soils to winds and resulting aerial suspension of contaminated dust particulates are minimized. Second, most volatile organic compounds (VOCs), the contaminants most likely to present a risk through inhalation exposure, rapidly volatilize from soil and surface water to air, where they are rapidly diluted and dispersed. Paterson et al. (1990) suggest that organic compounds with soil half-lives of <10 days are generally lost from soil before significant exposure can occur. As a consequence, significant exposure to VOCs through inhalation is unlikely. In situations where inhalation exposure of endpoint species is believed to be occurring or is expected to occur, models for vapor or particulate inhalation (Hope 1995) may be employed. In these cases, EPA (1993) recommends consulting an inhalation toxicologist.

Because contaminant exposure experienced by wildlife through both the dermal and inhalation pathways is negligible, the majority of exposure must be attributed to the oral exposure pathway. Equation 1 can therefore be simplified to

$$E_{\text{total}} \approx E_{\text{oral}} \quad (2)$$

2.1.1 Estimation of Oral Exposure

Oral exposure experienced by wildlife may come from multiple sources. They may consume contaminated food (either plant or animal), drink contaminated water, or ingest soil. Soil ingestion may be incidental while foraging or grooming or purposeful to meet nutrient needs. The total oral exposure experienced by an individual is the sum of the exposures attributable to each source and may be described as

$$E_{\text{oral}} \approx E_{\text{food}} + E_{\text{water}} + E_{\text{soil}} \quad (3)$$

where

E_{food}	=	exposure from food consumption,
E_{water}	=	exposure from water consumption,
E_{soil}	=	exposure from soil consumption.

For exposure estimates to be useful in the assessment of risk to wildlife, they must be expressed in terms of a body weight-normalized daily dose or milligrams of contaminant per kilograms body weight per day (mg/kg/d). Exposure estimates expressed in this manner may then be compared to toxicological benchmarks for wildlife, such as those derived by Sample et al. (1996a), or to doses reported in the toxicological literature. Models for the estimation of exposure from oral ingestion have been reported in the literature (EPA 1993, Sample and Suter 1994, Hope 1995, Pastorok et al. 1996, Freshman and Menzie 1996) and are generally of the form

$$E_j = \sum_{i=1}^m (I_i \times C_{ij}) \quad (4)$$

where

E_j	=	total oral exposure to contaminant (j) (mg/kg/d),
m	=	total number of ingested media (e.g., food, water, or soil),
I_i	=	ingestion rate for medium (i) (kg/kg body weight/d or L/kg body weight/d),
C_{ij}	=	concentration contaminant (j) in medium (i) (mg/kg or mg/L).

Very few wildlife consume diets that consist exclusively of one food type. To meet nutrient needs for growth, maintenance, and reproduction, most wildlife consume varying amounts of multiple food types. Because it is unlikely that all food types consumed will contain the same contaminant concentrations, dietary diversity is of one of the most important exposure modifying factors.

To account for differences in contaminant concentrations of different food types, exposure estimates should be weighted by the relative proportion of daily food consumption attributable to each food type and the contaminant concentration in each food type. In addition, wildlife may drink from different water sources

and consume soils that differ in contaminant concentrations. These differences must also be accounted for. This may be done by modifying Eq. 4 as follows

$$E_j = \sum_{i=1}^m \sum_{k=1}^n p_{ik} (I_i \times C_{ijk}) , \quad (5)$$

where

n	=	number of types of medium (i) consumed (unitless),
p_{ik}	=	proportion of type (k) of medium (i) consumed (unitless),
C_{ijk}	=	concentration of contaminant (j) in type (k) of medium (i) (mg/kg or mg/L).

If the site is spatially heterogeneous with respect to either contamination or wildlife use, the model must be modified to include spatial factors. The most important spatial consideration is the movement of wildlife. Animals travel varying distances, on a daily to seasonal basis, to find food, water, and shelter. The area encompassed by these travels is defined as the home range (we use the term here to include territories). If the site being assessed is larger than the home range of an endpoint species and provides the habitat needs of the species, then the previously listed models are adequate. However, endpoint species often have home ranges that are larger than contaminated sites, or the contaminated site may not supply all of a species' habitat requirements. In those cases, the wildlife exposure model must be modified.

If the contaminated site has similar habitat quality to the surrounding area but is smaller than the home range, use of the contaminated site is simply a function of its area. That is, one can assume that for wildlife that use the entire contaminated area, exposure is proportional to the ratio of the size of the contaminated site to home range size. Eq. 5 can be modified as follows as follows:

$$E_j = \frac{A}{HR} \left[\sum_{i=1}^m \sum_{k=1}^n p_{ik} (I_i \times C_{ijk}) \right] , \quad (6)$$

where

A	=	area (ha) contaminated,
HR	=	home range size (ha) of endpoint species.

Note that A is the area contaminated, not the entire area that has been designated a hazardous waste site (e.g., an operable unit). Because boundaries are often drawn conservatively, they may contain a considerable uncontaminated area.

The previous equation (6) implies that all of the habitat within a contaminated area is suitable and that use of all portions of the contaminated area is equally likely. Because many waste sites are industrial or highly modified in nature, it is unlikely that all areas within their bounds will provide habitat suitable for endpoint species. If it is assumed that use of a waste site will be proportional to the amount of suitable habitat available on the site, Eq. 6 may be modified to read

$$E_j = P_h \left(\frac{A}{HR} \left[\sum_{i=1}^m \sum_{k=1}^n p_{ik} (I_i \times C_{ijk}) \right] \right) , \quad (7)$$

where

P_h = proportion of suitable habitat in the contaminated area.

One complication is the spatial heterogeneity of contaminants on waste sites. These models (Eqs. 4-7) are based on the assumption that either contaminants are evenly distributed on the site, or wildlife forage randomly with respect to contamination on the portion of the site that constitutes habitat so that they are exposed to mean concentrations. However, if contaminant levels are related to habitat quality, that assumption would not hold. For example, contaminant concentrations might be greatest near the center of a site, but the habitat quality might be highest near the edges. In such cases, it might be necessary to model the proportional contribution of each area with a distinct combination of contaminant level and habitat quality

$$E_j = \sum_{l=1}^o \left(\frac{A_l}{HR} \left[\sum_{i=1}^m \sum_{k=1}^n p_{ik} (I_i \times C_{ijkl}) \right] \right), \quad (8)$$

where

o = number of distinct contaminated habitat areas,
 A_l = area (ha) of a distinct contaminated habitat area,
 C_{ijkl} = concentration of contaminant (j) in type (k) of medium (i) from the l^{th} area (mg/kg or mg/L).

As can be seen, if the distribution of contamination and habitat quality is complex, this approach to exposure estimation rapidly becomes ungainly. In such cases, it is advisable to implement the exposure in a Geographic Information System (GIS). Using a GIS, maps displaying the spatial distribution of habitat types may be overlaid with maps of contaminant distribution to accurately determine the degree to which habitat is contaminated. Furthermore, if information on the distribution or movements of wildlife (generated by radiotelemetry or censuses) are available, these data may be combined with the habitat and contaminant data to provide a more accurate visualization of exposure. Examples of the application of GIS to wildlife exposure and risk assessments can be found in Clifford et al. (1995), Banton et al. (1996), Henriques and Dixon (1996) and Sample et al. (1996b).

2.1.2 Exposure-Modifying Factors

Factors other than those described in these models modify contaminant exposure experienced by wildlife endpoint species. These factors include age, sex, season, and behavior patterns.

The models above imply that the endpoint species have uniform body size, metabolism, diet, home ranges, and habitat requirements. However, these properties may differ between juveniles and adults and between males and females. For example, because they are actively growing, metabolism (and therefore food consumption) is generally greater for juveniles of most endpoint species. Diet composition may also differ dramatically between juveniles and adults of the same species. Similarly, the food requirements of females during reproduction are greater than that for males for many endpoint species. These factors may serve to make certain age classes or a particular sex experience greater contaminant exposure than other segments of the population. Because of their greater exposure, contamination may present a greater risk to these segments of the population. If it is known that a particular lifestage or sex is sensitive to contamination, that lifestage should be emphasized in the exposure assessment.

Behavior may modify exposure by increasing or decreasing the likelihood of contact with contaminated media. Wildlife behaviors are frequently seasonal in nature. Some foods may be available and consumed only at certain times of the year. Similarly, some habitats and certain parts of the home range may

be used only in certain seasons. In addition, many species hibernate or migrate; by leaving the area or restricting their activity to certain times of year, their potential exposure may be dramatically reduced. All of these factors should be considered when evaluating contaminant exposure experienced by wildlife, and exposure models should be adjusted accordingly. The simplest approach to modifying the exposure estimates to take into account some of these exposure-modifying factors is to generate multiple exposure estimates. For example, if diet differs by season or by sex, calculate exposure estimates for each sex or season. Comparison of exposure estimates generated for differing exposure scenarios will aid in identifying the segments of population at greatest risk or times of year when risk is greatest.

2.2 ESTIMATION OF EXPOSURE TO RADIONUCLIDES

Estimation of exposure and effects from radionuclides is both qualitatively and quantitatively different from estimation of exposure to chemical contaminants. Exposures to radionuclides may be internal or external, and effects are caused by energetic particles or rays released as part of the decay of atoms. Decay energies of particles or rays emitted by each radionuclide must be accounted for. Unlike chemical exposures where effects of chemicals are generally evaluated individually, the internal and external doses from all radionuclides present must be summed to arrive at the appropriate exposure dose for a given organism. In addition, a number of radionuclides have daughter products that must also be included in the exposure calculations.

Internal exposures result from ingestion of contaminated food, soil, or water or inhalation of contaminated soil or dust (Templeton et al. 1971, IAEA 1976, Blaylock and Trabalka 1978, Woodhead 1984). External exposures result from direct exposure to radiation from the soil and may occur either above or below ground (or a combination of both), depending on the habits of the receptor (e.g., fossorial vs nonfossorial). Evaluation of the resulting radiation doses received by biota requires quantitative information on the radionuclides to which they are exposed. In all cases, the radiation source must be known in terms of the quantity of each specific radionuclide (pCi/g) and the corresponding energy released per disintegration (MeV/dis). Conversions for units of dose and activity generally reported in the literature are presented in Table 1.

Table 1. Comparison of units of activity and absorbed dose of ionizing radiation under the international and conventional systems of measure

Measure	International system	Conventional system	Relationship
Activity	Becquerel (Bq) = one nuclear disintegration/s	Curie (Ci) = 3.7×10^{10} nuclear disintegrations/s	1 Bq = 2.7×10^{-11} Ci 1 Ci = 3.7×10^{10} Bq
Absorbed dose	Gray (Gy) = 1 Joule/kg	rad = 0.01 Joule/kg	1 Gy = 100 rad 1 rad = 0.01 Gy

Models for estimating radiation dose rates (mrad/d) for plants, earthworms, and terrestrial wildlife species are based on methodology from Blaylock et al. (1993) and Baker and Soldat (1992). The general methodology and the equations specific to each exposure route used in estimation of dose rates for biota are described below. In practice, doses from alpha (α), beta (β), and gamma (γ) emissions (only β and γ for external exposures of earthworms and plants and only γ for external exposures of wildlife receptors) should be calculated for each radionuclide of concern, including the dose rates from all short-lived daughter products for the radionuclides. Doses from each radionuclide (plus daughters) should then be summed over all

exposure routes and all radionuclides to arrive at the overall estimate of the dose received for each receptor. Alpha particles have low penetration energy and are not considered for external exposures. Beta particles are unlikely to penetrate the epidermis of larger organisms, so they are only considered in external exposures to plants and earthworms.

2.2.1 External Exposures: Direct Radiation from Soil

The equation for estimating aboveground external dose rates (mrad/d) for terrestrial receptors exposed to contaminated soil uses dose coefficients published by Eckerman and Ryman (1993). These dose coefficients relate the doses to organs and tissues in the body to concentrations of radionuclides in soil and are available for soil contaminated to depths of 1, 5, and 15 cm or soil assumed to be contaminated to an infinite depth. A dose rate reduction factor is used to account for the fraction of time the receptor spends aboveground. This factor is necessary because a different model is used to estimate below-ground exposures to soil radionuclides. The fraction of time spent above or below ground by each receptor species should be estimated based on knowledge of the species' life history and behavior patterns. Dose coefficients assume that the source region is a smooth plane (Eckerman and Ryman 1993), but this is rarely the case in a terrestrial habitat. A representative average dose reduction factor for ground roughness is 0.7, although recommended values range from essentially unity for paved areas to about 0.5 for a deeply plowed field (Eckerman and Ryman 1993). For relatively small mammals (e.g., mice, voles, and shrews) that are effectively much closer than 1 m to the source, an elevation correction factor (ECF) of 2 should be applied to account for the increased dose expected at ground level relative to the effective height of a standard human used to derive the dose coefficients. For large animals the ECF may be set at 1. If desired, more complex modeling may be conducted to arrive at ECFs for organisms of any given effective height above the ground. For plants it may be assumed that the dose represents that to the reproductive part of the plant with an effective height similar to that of the standard human. An ECF of 2 may be appropriate for evaluating low-growing plant species. The equation for aboveground dose from external exposures for a plant or wildlife receptor is

$$D_{abovegrd} = F_{above} F_{ruf} \sum C_{soil,i} DF_{grd,i} CFb ECF, \quad (9)$$

where

$D_{above\ grd}$	=	external dose rate to receptor from aboveground exposures to contaminated soil (mrad/d),
F_{above}	=	dose rate reduction factor accounting for the fraction of time the receptor spends aboveground (unitless),
F_{ruf}	=	dose rate reduction factor accounting for ground roughness (unitless) [Representative average of 0.7 (Eckerman and Ryman 1993) is reasonable default],
$C_{soil,i}$	=	activity of radionuclide i in surface soil (pCi/g),
$DF_{grd,i}$	=	dose coefficient for radionuclide i in soil contaminated to given depth (Eckerman and Ryman 1993) (Sv/s per Bq/m ³),
CFb	=	conversion factor to change Sv/s per Bq/m ³ to mrad g/pCi d (Equals 5.12×10^{14}),
ECF	=	elevation correction factor to adjust dose coefficients to value representative of effective height of animal aboveground.

Dose from alpha radiation is not a concern for external sources, as alpha radiation lacks penetrating power. The effective dose coefficients from Eckerman and Ryman (1993) incorporate both high-energy β and γ emissions. Radionuclide-specific parameters for selected radionuclides are provided in Table 2. These include dose coefficients assuming soil contaminated to a depth of 15 cm. Coefficients for soil contaminated to depths of 1, 5, and 15 cm and to an infinite depth are available in Eckerman and Ryman (1993).

Below-ground exposures are calculated assuming immersion in a continuous soil medium. Dose coefficients are unavailable for the immersion scenario, so exposures can be modeled as dose to soil adjusted for absorption by a small volume of tissue. The exposure fraction reflects the fraction of time the receptor spends below ground. Receptors that do not go below ground (e.g., nonfossorial wildlife: deer, hawks, turkey, etc.) do not receive a dose via this exposure route. Only γ radiations with energies greater than 0.01 MeV were evaluated for wildlife receptors as those with lower energies are unlikely to penetrate skin. Both β and γ radiations were evaluated for earthworms. The equation for below-ground external exposures of earthworms and wildlife receptors is

$$D_{\text{belowgrd}} = 1.05 F_{\text{below}} \sum C_{\text{soil},i} \epsilon_i \text{CFa} , \quad (10)$$

where

$D_{\text{below grd}}$	=	external dose rate to earthworm or wildlife receptor in burrow from contaminated soil (mrad/d),
F_{below}	=	dose rate reduction factor accounting for the fraction of time the receptor spends below ground (unitless),
$C_{\text{soil}, i}$	=	activity of radionuclide i in surface soil (pCi/g),
ϵ_i	=	energy for γ emissions by nuclide i (MeV/nt),
1.05	=	conversion factor to account for immersion in soil vs water (estimated value; Keith Eckerman, Health Sciences Research Division, Oak Ridge National Laboratory, personal communication, June 1996),
CFa	=	conversion factor to go from MeV/nt to g mrad/pCi d. (5.12×10^{-2}).

Note that the conversion factor of 1.05 used to account for the difference between immersion in soil vs water was meant for small volumes of tissue. While it can be roughly applied to large animals, it may be more appropriate to consult a health physicist and conduct more complex calculations of dose from below-ground exposures for large animals expected to spend significant time below ground.

Table 2. Average energy of decay and absorbed fractions for select radionuclides

Radionuclide	Average energy of decay ^a			Absorbed fractions (gamma) ^b					DF _{grd 0-15} (Sv m ³ /s Bq) ^c
	alpha	beta	gamma	A	B	C	D	E	
Actinium-228		0.475	0.971	0.01	0.0127	0.04	0.06	0.14	2.76e-17
Americium-241	5.479	0.052	0.033	0.04	0.05	0.12	0.16	0.3	1.23e-18
Antimony-126		0.283	2.834	0.01	0.01	0.03	0.04	0.11	8.13e-17
Antimony-126m		0.591	1.548	0.085	0.0123	0.03	0.05	0.12	4.44e-17
Astatine-218	6.697	0.04	0.007	0.63	0.79	0.94	0.94	0.94	3.13e-20
Barium-137m		0.065	0.597	0.011	0.015	0.04	0.06	0.15	1.71e-17
Beryllium-7			0.049	0.012	0.017	0.06	0.09	0.2	1.40e-18
Bismuth-210		0.389							1.86e-20
Bismuth-211	6.55	0.01	0.047	0.027	0.04	0.11	0.15	0.29	1.28e-18
Bismuth-212	2.174	0.472	0.186	0.01	0.011	0.04	0.06	0.14	5.36e-18
Bismuth-214		0.659	1.508	0.085	0.0123	0.03	0.05	0.12	4.36e-17
Cadmium-109		0.083	0.026	0.09	0.126	0.16	0.21	0.36	7.88e-20
Calcium-45		0.077							3.35e-22
Carbon-14		0.049							7.20e-23
Cesium-134		0.164	1.555	0.085	0.0123	0.03	0.05	0.12	4.47e-17
Cesium-137		0.187							3.94e-21
Cobalt-57		0.019	0.125	0.01	0.012	0.04	0.06	0.15	2.66e-18
Cobalt-60		0.097	2.504	0.01	0.01	0.03	0.04	0.11	7.25e-17
Curium-242	6.102	0.01	0.002	0.63	0.79	0.94	0.94	0.94	9.07e-22
Curium-243	5.797	0.138	0.134	0.01	0.0105	0.04	0.06	0.15	3.02e-18
Curium-244	5.795	0.009	0.002	0.63	0.79	0.94	0.94	0.94	6.74e-22
Europium-152		0.139	1.155	0.085	0.0123	0.03	0.05	0.12	3.75e-17
Europium-154		0.292	1.242	0.085	0.0123	0.03	0.05	0.12	4.11e-17
Europium-155		0.063	0.061	0.012	0.017	0.06	0.09	0.2	9.75e-19
Iodine-129		0.064	0.025	0.09	0.126	0.16	0.21	0.36	6.93e-20
Lead-212		0.176	0.148	0.01	0.011	0.04	0.06	0.15	3.62e-18
Lead-214		0.293	0.25	0.01	0.01	0.04	0.06	0.14	6.70e-18
Neptunium-237	4.769	0.07	0.035	0.027	0.04	0.11	0.15	0.29	4.16e-19
Plutonium-238	5.487	0.011	0.002	0.63	0.79	0.94	0.94	0.94	8.07e-22

Table 2. (continued)

Radionuclide	Average energy of decay ^a			Absorbed fractions (gamma) ^b					DF _{gd 0-15} (Sv m ³ /s Bq) ^c
	alpha	beta	gamma	A	B	C	D	E	
Plutonium-239	5.148	0.007							1.52e-21
Plutonium-239/240	5.148	0.007	0.002	0.63	0.79	0.94	0.94	0.94	1.52e-21
Plutonium-240	5.156	0.011	0.002	0.63	0.79	0.94	0.94	0.94	7.84e-22
Polonium-210		0.038	0.005	0.63	0.79	0.94	0.94	0.94	2.45e-22
Polonium-211	7.442		0.008	0.63	0.79	0.94	0.94	0.94	2.24e-19
Polonium-212	8.785								3.62e-18
Polonium-214	7.687								2.40e-21
Polonium-216	6.779								4.87e-22
Polonium-218	6.001								2.63e-22
Potassium-40		0.523	0.156	0.01	0.0115	0.04	0.06	0.14	4.57e-18
Protactinium-233		0.196	0.204	0.01	0.01	0.04	0.06	0.14	5.16e-18
Protactinium-234		0.494	1.919	0.085	0.0123	0.03	0.05	0.12	5.38e-17
Protactinium-234m		0.822	0.012	0.55	0.63	0.93	0.93	0.93	4.20e-19
Radium-223	5.667	0.076	0.134	0.01	0.0105	0.04	0.06	0.15	3.10e-18
Radium-224	5.674	0.002	0.01	0.63	0.79	0.29	0.35	0.52	2.62e-19
Radium-226	4.774	0.004	0.007	0.63	0.79	0.94	0.94	0.94	1.65e-19
Radium-228		0.017							0.00e+00
Radon-220	6.288								1.10e-20
Radon-222	5.489								1.14e-20
Sodium-22		0.194	2.193	0.085	0.0123	0.03	0.05	0.12	6.31e-17
Strontium-90		0.196							3.72e-21
Technetium-99		0.101							6.70e-22
Thallium-207		0.493	0.002	0.63	0.79	0.94	0.94	0.94	9.48e-20
Thallium-208		0.598	3.375	0.01	0.01	0.03	0.04	0.11	9.68e-17
Thorium-228	5.4	0.021	0.003	0.63	0.79	0.94	0.94	0.94	4.17e-20
Thorium-230	4.671	0.015	0.002	0.63	0.79	0.94	0.94	0.94	6.39e-21
Thorium-231		0.165	0.026	0.09	0.126	0.16	0.21	0.36	1.94e-19
Thorium-232	3.996	0.012	0.001	0.63	0.79	0.94	0.94	0.94	2.78e-21

Table 2. (continued)

Radionuclide	Average energy of decay ^a			Absorbed fractions (gamma) ^b					DF _{grd} ⁰⁻¹⁵ (Sv m ³ /s Bq) ^c
	alpha	beta	gamma	A	B	C	D	E	
Thorium-234		0.06	0.009	0.63	0.79	0.94	0.94	0.94	1.29e-19
Tin-126		0.172	0.057	0.012	0.017	0.06	0.09	0.2	7.90e-19
Tritium		0.006							0
Uranium-232	5.302	0.017	0.002	0.63	0.79	0.94	0.94	0.94	4.83e-21
Uranium-233	4.817	0.006	0.001	0.63	0.79	0.94	0.94	0.94	7.24e-21
Uranium-233/234	4.817	0.006	0.001	0.63	0.79	0.94	0.94	0.94	7.24e-21
Uranium-234	4.758	0.013	0.002	0.63	0.79	0.94	0.94	0.94	2.14e-21
Uranium-235	4.396	0.049	0.156	0.01	0.0115	0.04	0.06	0.14	3.75e-18
Uranium-235/236	4.396	0.049	0.156	0.01	0.0115	0.04	0.06	0.14	3.75e-18
Uranium-236	4.396	0.049	0.156	0.01	0.0115	0.04	0.06	0.14	3.75e-18
Uranium-238	4.187	0.01	0.001	0.63	0.79	0.94	0.94	0.94	5.52e-22
Yttrium-90		0.935							1.20e-19
Zirconium-89		0.101	1.165	0.085	0.0123	0.03	0.05	0.12	3.85e-17

^a Values were obtained from ICRP (1983).

^b Absorbed fractions for worms, plants, and mouse were derived from data in Blaylock et al. (1993).

Absorbed fraction for other receptors were derived following methodology of Cristy and Eckerman (1987).

Absorbed fractions for beta radiation were 100% for all radionuclides listed.

A = Plants and soil invertebrates. Derived from large insect values presented in Blaylock et al. (1993).

B = Small mammals and birds <<1 kg (e.g., pine vole). Derived from small fish values in Blaylock et al. (1993).

C = Small- to medium-sized mammals and birds (e.g., mink). Derived from values for ~0.76kg human infant after Cristy and Eckerman (1987).

D = Medium-sized mammals and birds (e.g., red fox). Derived from values for ~2.5kg 1-year old human after Cristy and Eckerman (1987).

E = Large mammals (e.g., white-tailed deer). Derived from values for ~28kg human after Cristy and Eckerman (1987).

^c DF_{grd} is the dose coefficient for soil contaminated to a depth of 15 cm (Eckerman and Ryman 1993).

2.2.2 Internal Exposures: Ingestion

Wildlife receptors may receive internal radiation doses after ingesting contaminated prey, soil, or water or after inhaling contaminated dust. Blaylock et al. (1993) provide an equation for estimating the internal dose to fish contaminated with radionuclides. This equation can be modified to address consumers eating a variety of prey types, ingesting soil, and drinking water, as well as plants and invertebrates taking up contaminants directly from the soil

$$D_{ing} = \sum QF C_{tissue} \epsilon_i CFa AF, \quad (11)$$

where

D_{ing}	=	internal dose rate received after ingestion of contaminated prey and soil (mrad/d),
QF	=	quality factor to account for the greater biological effectiveness of α particles (20 for α ; 1 for β and γ emissions; unitless),
C_{tissue}	=	activity (pCi/g) of radionuclide i in tissue of organism,
ϵ_i	=	energy for α , β , or γ emissions by nuclide i (MeV/nt),
CFa	=	conversion factor to go from MeV/nt to g mrad/pCi d (5.12×10^{-2}),
AF	=	absorption factor (unitless).

Radionuclide activity in tissue may be determined a number of ways, depending on data availability. Measured data should be used, if available. In the absence of measured data, soil-to-tissue uptake factors may be used. Uptake factors for selected radionuclides in plants, soil invertebrates, and small mammals are presented in Table 3; additional discussion of uptake factors is presented in Sect. 3.2.

Absorbed energy fractions for α radiations are assumed to equal one for all receptors. While absorption fractions for β radiations are assumed to be one for wildlife receptors, β absorption fractions for plants and earthworms are assumed to equal those for large insects from Blaylock et al. (1993) (assuming small reproductive parts of greatest concern). This is because β radiations are unlikely to have sufficient energy to pass through the wildlife tissues; however, some fraction may have sufficient energy to pass through smaller organisms such as earthworms and plants. Absorption fractions for γ radiations for plants and earthworms were also assumed to be equivalent to those for large insects presented in Blaylock et al. (1993). Absorption fractions for γ radiations derived for infant, 1-yr old, and adult humans using the methodology described in Cristy and Eckerman (1987) were used for wildlife receptors of similar sizes. Table 2 presents absorption factors used for several receptor-radionuclide combinations.

Energies (α , β , and γ) for selected radionuclides were obtained from Eckerman and Ryman (1993) and are provided in Table 2. Because different types of radiation differ in their relative biological effectiveness per unit of absorbed dose, a quality factor derived from data on humans is normally applied (NCRP 1987). The quality factor is determined by the linear energy transfer of radiation, and linear energy transfer for α particles is substantially higher than that for β or γ emissions. A quality factor of 1 should be used for β and γ radiation and 20 for α radiation (Blaylock et al. 1993).

Table 3. Radionuclide-specific soil-tissue uptake factors for plants, soil invertebrates, and small mammals and bioaccumulation factors for birds and mammals

Radionuclide	UF _{plant} ^a				UF _{invert} ^a	BAF _{bird} ^b	BAF _{mamm} ^b	UF _{mamm} ^a
	All plants	Grass	Herb. plants	Tree/shrubs				
228Ac	8.75e-04 c	8.75e-04 d	8.75e-04 d	8.75e-04 d	1.25e-03 e	1.25e-03 f	1.25e-03 c,g	
241Am						4.20e-03 g,j	2.00e-03 j	
212Bi	8.75e-03 c,g	8.75e-03 d	8.75e-03 d	8.75e-03 d	2.00e-02 e	2.00e-02 f	2.00e-02 c	
214Bi	8.75e-03 c,g	8.75e-03 d	8.75e-03 d	8.75e-03 d	2.00e-02 e	2.00e-02 f	2.00e-02 c	
45Ca						2.80e-02 g,j	1.00e-01 j	
244Cm						1.00e-03 f	1.00e-03 k	
57Co						1.40e+00 g,j	5.00e-03 g,j	
60Co						1.40e+00 g,j	5.00e-03 g,j	
134Cs	1.27e-03 l	1.27e-03 l	1.27e-03 l	1.27e-03 l		7.00e+00 g,j	2.56e+00 l	1.62e-02 l
137Cs	1.27e-03 d	1.27e-03 m	1.27e-03 d	1.27e-03 d		7.00e+00 g,j	2.56e+00 m	1.62e-02 m
152Eu	1.05e-02 d	1.05e-02 d	1.05e-02 g,n	1.05e-02 d	1.00e-01 e	1.00e-01 f	1.00e-01 k	
154Eu	1.05e-02 d	1.05e-02 d	1.05e-02 g,n	1.05e-02 d	1.00e-01 e	1.00e-01 f	1.00e-01 k	
155Eu	1.05e-02 d	1.05e-02 d	1.05e-02 g,n	1.05e-02 d	1.00e-01 e	1.00e-01 f	1.00e-01 k	
129I	3.40e-04 d	3.40e-04 g,j	3.40e-04 d	3.40e-04 d	2.00e+00 e	7.00e-03 g,j	2.00e+00 g,j	
40K						1.00e+00 f	1.00e+00 j	
22Na						4.00e+00 f	4.00e+00 j	
237Np	9.00e-03 d	9.00e-03 d	9.00e-03 o	9.00e-03 d	9.00e-03 e	3.84e-03 f	3.84e-03 g,n	
234mPa	6.25e-04 c,g	6.25e-04 d	6.25e-04 d	6.25e-04 d	5.00e-02 e	5.00e-02 f	5.00e-02 c	
210Pb						2.00e-02 f	2.00e-02 j	
212Pb						2.00e-02 f	2.00e-02 j	
214Pb						2.00e-02 f	2.00e-02 j	
238Pu	3.00e-04 l	6.00e-05 l	3.00e-04 l	6.00e-05 l		2.10e-03 g,j	5.00e-04 g,j	
239Pu	3.00e-04 d	6.00e-05 p	3.00e-04 p	6.00e-05 p	9.12e-03 q	2.10e-03 g,j	5.00e-04 g,j	
239/240Pu						2.10e-03 g,j	5.00e-04 g,j	
223Ra	7.50e-02 d	7.50e-02 d	7.50e-02 l,r	7.50e-02 d	7.50e-02 e	4.50e-02 f	4.50e-02 g,j	
224Ra	7.50e-02 d	7.50e-02 d	7.50e-02 l,r	7.50e-02 d	7.50e-02 e	4.50e-02 f	4.50e-02 g,j	
226Ra	7.50e-02 d	7.50e-02 d	7.50e-02 r	7.50e-02 d	7.50e-02 e	4.50e-02 f	4.50e-02 g,j	
228Ra	7.50e-02 d	7.50e-02 d	7.50e-02 l,r	7.50e-02 d	7.50e-02 e	4.50e-02 f	4.50e-02 g,j	
90Sr	4.95e-01 d	1.60e-01 s	4.95e-01 s	4.95e-01 d		5.60e-02 g,j	4.00e-01 g,j	
228Th	9.00e-04 d	4.00e-04 l,p	9.00e-04 g,r	9.00e-04 g,r	5.00e-03 e	5.00e-03 f	5.00e-03 k	3.20e-05 l

Table 3. (continued)

Radionuclide	UF _{plants} ^a				UF _{invert} ^a	BAF _{bird} ^b	BAF _{mamm} ^b	UF _{mamm} ^a
	All plants	Grass	Herb. plants	Tree/shrubs				
230Th	9.00e-04 d	4.00e-04 l,p	9.00e-04 g,r	9.00e-04 g,r	5.00e-03 e	5.00e-03 f	5.00e-03 k	3.20e-05 l
232Th	9.00e-04 d	4.00e-04 p	9.00e-04 g,r	9.00e-04 g,r	5.00e-03 e	5.00e-03 f	5.00e-03 k	3.20e-05 p
234Th	9.00e-04 d	4.00e-04 l,p	9.00e-04 g,r	9.00e-04 g,r	5.00e-03 e	5.00e-03 f	5.00e-03 k	3.20e-05 l
208Tl	1.00e-03 c,g	1.00e-03 d	1.00e-03 d	1.00e-03 d	2.00e+00 e	2.00e+00 f	2.00e+00 c	
232U	1.97e+00 d	9.00e-04 l	3.75e-03 l,r	1.97e+00 l,t		7.00e-01 g,j	1.50e-02 j	3.20e-04 l
233U	1.97e+00 d	9.00e-04 l	3.75e-03 l,r	1.97e+00 l,t		7.00e-01 g,j	1.50e-02 j	3.20e-04 p
234U	1.59e+00 d	9.00e-04 l	3.75e-03 l,r	1.59e+00 t		7.00e-01 g,j	1.50e-02 j	3.20e-04 l
235U	1.97e+00 d	9.00e-04 l	3.75e-03 l,r	1.97e+00 l,t		7.00e-01 g,j	1.50e-02 j	3.20e-04 l
235/236U	1.97e+00 d	9.00e-04 l	3.75e-03 l,r	1.97e+00 l,t		7.00e-01 g,j	1.50e-02 j	3.20e-04 l
238U	1.97e+00 d	9.00e-04 p	3.75e-03 r	1.97e+00 t		7.00e-01 g,i	1.50e-02 i	3.20e-04 p

^a Soil-tissue uptake factors (UF) for plants, soil invertebrates, and small mammals were obtained from available literature. When necessary, values originally reported on a dry-weight basis were converted to a wet-weight basis based on tissue water content.

^b Bird and mammal bioaccumulation factors (BAFs, ratio of tissue activity to activity in food) were obtained from available literature. Values originally reported as biotransfer factors (d/kg) were converted to BAFs by multiplying d/kg by the ingestion rate of the test species. When necessary, values originally reported on a dry-weight basis were converted to a wet-weight basis based on tissue water content.

^c Baes et al. (1984).

^d Assumed the same as other plant types.

^e Uptake factor for earthworms was unavailable. Used the larger of the plant and mammal values.

^f Assumed mammal BAF because of lack of bird-specific values.

^g Elemental form of the analyte was used for isotope.

^j IAEA (1994).

^k NCRP (1989).

^l Assumed uptake same as reported for other isotope of the radionuclide (i.e., ¹³⁷Cs values used for ¹³⁴Cs).

^m Garten (1980a).

ⁿ Trabalka and Garten (1983).

^o Garten et al. (1986).

^p Garten et al. (1987).

^q Garten and Dahlman (1978).

^r Bondietti et al. (1979).

^s Garten and Lomax (1987).

^t Garten (1980b).

2.2.3 Internal Exposures: Inhalation

Wildlife species using burrows may receive an additional internal dose from inhalation of dust originating from contaminated soil. Intake of radionuclide i by inhalation is estimated as (DOE 1995b)

$$D_{inh} = QF F_{below} \sum C_{soil,i} A \frac{1}{AD} \epsilon_i CFa AF, \quad (12)$$

where

D_{inh}	=	internal dose rate from inhalation of contaminated soil (mrad/d),
F_{below}	=	dose reduction factor for fraction of time receptor spends below ground (unitless),
A	=	mass of respirable dust per volume of air breathed (0.1 g/m^3 ; DOE 1995b),
AD	=	air density (1200 g/m^3 ; Eckerman and Ryman 1993),
ϵ_i	=	α , β , or γ radiation energies for radionuclide i (MeV),
CFa	=	conversion factor to go from MeV to mrad g/pCi/d (5.12×10^{-2}),
AF	=	absorption factor (unitless).

Healy (1980) suggests that 0.0001 g/m^3 would be a conservative value when addressing human exposures to dust. Because burrowing animals are likely to spend a greater portion of their time in a confined space (burrow) than humans and are physically closer to the soil surface, an air mass loading of 0.1 g/m^3 is suggested as a conservative estimate of the mass of respirable dust (A) to which these animals may be exposed.

Total internal exposures are obtained by adding ingestion and inhalation dose rates over all radionuclides, including all short-lived daughter products.

2.2.4 Effects Levels for Radionuclides

The discharge of radioactive waste into the environment results in long-term, low-dose exposure to organisms. In most cases, acute mortality can be discounted. Any potential increase in morbidity and mortality that might result from the exposure to chronic irradiation above background is unlikely to be detected because of natural fluctuations in the size of populations.

The International Atomic Energy Agency (IAEA) recommends limiting the dose for terrestrial organisms to 100 mrad/d (IAEA 1992). Studies evaluating reproductive success and survival were used to determine the dose limit. Species-specific effects data were not available, so 100 mrad/d was selected as the threshold dose for all representative wildlife receptors. A dose rate of this magnitude is unlikely to cause observable changes in terrestrial animal populations (IAEA 1992). Higher dose rates may result in impaired reproduction or reduced survivorship. A dose rate of 1 rad/d is generally considered protective of plant and invertebrate populations (IAEA 1992, Barnhouse 1995) based on studies of productivity and community characteristics. This dose rate or less is unlikely to cause observable changes in terrestrial plant populations (IAEA 1992). Higher dose rates may result in reduced productivity or changes in species composition within communities. Therefore, 1 rad/d was selected as the threshold dose for effects on plant and invertebrate populations. Invertebrates tend to be less radiosensitive than plants or vertebrates, and indirect responses to radiation-induced vegetation changes (e.g., habitat alteration) appear more critical than direct effects (e.g., mortality, etc.) from radiation (IAEA 1992).

2.2.5 Uncertainties in Radiological Risk Assessment

A number of areas of uncertainty exist in the estimation of exposure and risks to terrestrial biota from exposure to radionuclides. The methodology outlined above is likely to overestimate dose rates that endpoints may receive. Whereas some of the information needed to implement the methodology is well known, much is unknown or unspecified statistically. A conservative but reasonable approach to model assumptions and radiological exposure scenarios was adopted to avoid underestimating risks to biota. Specific uncertainties identified in the radionuclide models are listed below.

- It is assumed that uptake of radionuclides from soil, food, and water are similar. Radionuclides bound to soil may be less available than those in tissue or water. Many radionuclides are poorly absorbed from soils (e.g., ^{137}Cs bound to clay minerals). Therefore, assuming uptake from soil equal to uptake from food may result in a conservative estimate of actual uptake.
- The dose coefficients obtained from Eckerman and Ryman (1993) used to estimate dose rates from external exposures are developed for application in determining dose rates to humans. These dose coefficients were applied directly for wildlife receptors or adjusted based on the effective height of the receptors, but the actual dose coefficients for wildlife, given differences in size, behavior, and general morphology, may be greater or less than those developed for humans.
- The air mass loading factor of 0.1 g/m^3 used in estimating exposures from inhalation of radionuclide-contaminated dust was selected as a conservative value. Healy (1980) suggested that 0.0001 g/m^3 would be a conservative value for estimating human exposures from inhalation of dust.
- The conversion factor used in the model for below-ground exposures was derived for small volumes of tissue (e.g., a mouse or shrew) immersed in soil assumed to be contaminated to an infinite depth. The actual dose for large animals or in cases where only the first few centimeters of soil are contaminated may be higher or lower. The simplifying assumptions used in the models presented here are generally applicable, but a health physicist could be consulted to develop specific dosimetry models where a more detailed evaluation is desired.
- Absorption factors are not available for many terrestrial organisms. The approach used here was to apply values developed for similar-sized aquatic organisms (Blaylock et al. 1993) or humans (Cristy and Eckerman 1987) to wildlife species. Because size and geometry of wildlife species do not exactly match those of aquatic organisms or humans, actual absorption fractions for wildlife species may be higher or lower than those suggested here.

2.3 PROBABILISTIC EXPOSURE ESTIMATION

Contaminant exposure estimates for wildlife are frequently generated using single, conservative values (e.g., upper 95% confidence limits on the mean, maximum observed value) to represent parameters (e.g., contaminant concentration in soil, food, water, or air; ingestion rates; or diet composition) in the exposure model. These single parameter values, known as point estimates, are selected because they are believed to be protective of most individuals and their use simplifies the calculation of an exposure estimate. While the use of conservative assumptions is suitable in a screening-level assessment, the use of point estimates is not recommended in a baseline or definitive assessment. Employing point estimates for the input parameters in the exposure model does not take into account the variation and uncertainty associated with the

parameters. Contaminant exposure that endpoints may receive in any given area may therefore be either over or underestimated. Consequently, remediation may be recommended for areas where it is unnecessary, or significant risks may be overlooked. Calculation of the exposure model using point estimates also produces only a point estimate of exposure. This exposure estimate provides no information concerning the distribution of exposures or the likelihood that individuals within an area will actually experience potentially hazardous exposures. To incorporate the variation in exposure parameters and to provide a better estimate of the potential exposure experienced by wildlife, it is highly recommended that exposure modeling be performed using probabilistic methods such as Monte Carlo simulation.

A detailed discussion of Monte Carlo simulation is beyond the scope of this report. General discussion of Monte Carlo techniques are provided by Rubenstein (1981) and Law and Kelton (1982). Briefly, Monte Carlo simulation is a resampling technique frequently used in uncertainty analysis in risk assessment (Hammonds et al. 1994). In practice, distributions are assigned to input parameters in a model, and the model output is recalculated many times to produce a distribution of output parameters (e.g., estimates of contaminant exposure). Each time the model is recalculated, a value is selected from within the distribution assigned for each input parameter. As a result, a distribution of exposure estimates is produced that reflects the variability of the input parameters. To determine which input parameters most strongly influence the final exposure estimate, a sensitivity analysis may be performed (Hammonds et al. 1994). Detailed discussions of sensitivity and uncertainty analysis, and the use of Monte Carlo simulations in risk assessment, are provided by Hammonds et al. (1994) and EPA (1996). Burmaster and Anderson (1994) outline 14 principles of good practice for the use of Monte Carlo techniques in risk assessment. Initial guidance for the use and interpretation of Monte Carlo analysis in risk assessment have been developed by the EPA Risk Assessment Forum (EPA 1997) and EPA Region 8 (EPA Region 8 1995). Examples of the application of Monte Carlo techniques in wildlife exposure and risk assessment are presented in MacIntosh et al. (1994), Sample et al. (1996b), and Moore et al. (In Press). Finally, a special issue of the journal *Human and Ecological Risk Assessment* (Vol. 2, No. 4, 1996) has recently been published to commemorate the 50th anniversary of the development of Monte Carlo methods. This issue will contain multiple papers on the application and interpretation of Monte Carlo methods. Software for conducting Monte Carlo simulations include @Risk (Palisade Corporation, Newfield, New York) and Crystal Ball (Decisioneering, Inc., Denver, Colorado).

2.4 EXTRAPOLATION FROM INDIVIDUALS TO POPULATIONS

Exposure models used in a risk assessment must be appropriate for the assessment endpoints considered. The models presented in previous sections are for estimation of exposure of individual organisms, but except for threatened and endangered species, wildlife endpoints are generally considered at the population level (Suter et al. 1995). Because exposure estimates must be integrated with exposure-response information, which is expressed as organism-level responses, the use of these organism-level exposure models is appropriate.

The conversion of individual-level exposure estimates to population-level effects occurs in the risk characterization and can be made in several ways. First, it may be assumed that there is a distinct population on the site so that the exposure of the population is represented by the exposure of all of the individuals. All individuals at the site are assumed to experience equivalent exposure. This assumption is appropriate for small organisms, with limited home ranges, on large sites, particularly if the site constitutes a distinct habitat that is surrounded by inappropriate habitat. For example, a grassy site surrounded by forest or industrial development might support a distinct population of voles. The risks to that population can be estimated directly from the exposures of the individual organisms.

Another approach is to assume that a certain number of individuals are exposed to contaminants out of a larger population. The proportion of the local population exposed at levels that exceed toxic thresholds represents the proportion of the population potentially at risk. This was the logic underlying the preliminary assessment for wide-ranging wildlife on the Oak Ridge Reservation (ORR; Sample et al. 1996b). On the ORR, while most habitat for wide-ranging wildlife species exists outside of source operable units (OUs; contaminated areas), some suitable habitat is present within source OUs. The proportion of the ORR-wide population potentially at risk is represented by the number of individuals that may use habitat on source OUs. The degree to which a source OU is used (and therefore the risk that it may present) is dependent upon the availability of suitable habitat on the OU. An estimate of risks to reservation-wide populations was estimated as follows.

1. Individual-based contaminant exposure estimates are generated for each source OU using the generalized exposure model (Eq. 5). Contaminant data, averaged over the entire OU, were used in the exposure estimate.
2. Contaminant exposure estimates for each OU were compared to Lowest Observed Adverse Effects Levels (LOAELs) from Sample et al. (1996a) to determine the magnitude and nature of effects that may result from exposure at the OU. If the exposure estimate >LOAEL, then individuals at the OU may experience adverse effects.
3. Availability and distribution of habitat on the ORR and within each OU, suitable for each species considered, was determined using a satellite-generated landcover map for the ORR (Washington-Allen et al. 1995).
4. Habitat requirements for the endpoint species of interest are compared to the ORR habitat map to determine the area of suitable habitat on the ORR and within OUs.
5. The area of suitable habitat on the ORR and within OUs was multiplied by species-specific population density values (ORR-specific or obtained from the literature) to generate estimates of the ORR-wide population and the numbers of individuals expected to reside within each OU.
6. The number of individuals for a given endpoint species expected to be receiving exposures >LOAELs for each measured contaminant was totaled. This is performed using the OU-specific population estimate from step 5 and the results from step 2. This number is then compared with the ORR-wide population to determine the proportion of the ORR-wide population that is receiving hazardous exposures.

This approach provides a very simple estimate of population-level effects. It is biased because it does not take wildlife movement into account. Wide-ranging species may travel among and use multiple OUs, therefore receiving exposures greater than that estimated for a single OU. In addition, the proportion of reservation-wide population potentially at risk is limited by the proportion of suitable habitat present in source OUs. For example, if 5% of the suitable habitat for a given species is located within OUs, the proportion of the population potentially at risk cannot exceed 5%.

A third approach is to combine the results of Monte Carlo simulation of exposure with literature-derived population density data to evaluate the likelihood and magnitude of population-level effects

on wildlife. The number of individuals within a given area likely to experience exposures >LOAELs can be estimated using cumulative binomial probability functions (Dowdy and Wearden 1983). Binomial probability functions are estimated using the following equation

$$b(y; n; p) = \binom{n}{y} p^y (1-p)^{n-y}, \quad (13)$$

where

y	=	the number of individuals experiencing exposures >LOAEL,
n	=	total number of individuals within the watershed,
p	=	probability of experiencing an exposure in excess of the LOAEL,
b (y; n; p)	=	probability of y individuals out of a total of n, experiencing an exposure >LOAEL, given the probability that exceeding the LOAEL = p.

By solving Eq. 13 for $y = 0$ to $y = n$, a cumulative binomial probability distribution may be generated that can be used to estimate the number of individuals within an area that are likely to experience adverse effects. This approach was used to estimate the risks that PCBs and mercury in fish presented to the population of piscivores in watersheds on the ORR (Sample et al. 1996b). Monte Carlo simulations were performed to estimate watershed-wide exposures. It was assumed that wildlife were more likely to forage in areas where food is most abundant. Density or biomass of fish at or near locations where fish bioaccumulation data were collected were assumed to represent measures of food abundance. (Biomass data were preferred but were unavailable for all watersheds. Where unavailable, density data were used.) The relative proportion that each location contributed to overall watershed density or biomass data was used to weight the contribution to the watershed-level exposure. The watershed-level exposure was estimated to be the weighted average of the exposure at each location sampled within the watershed. In this way, locations with high fish densities or greater fish biomass contribute more to exposure than do locations with lower density or biomass. Because the watersheds were large enough to support multiple individuals, the weighted average exposure estimate was assumed to represent the exposure of all individuals in each watershed. While simplistic, this approach is believed to provide a better estimate of population-level effects than the previously described method. Use of this method, however, requires exposure data from multiple, spatially disjunct areas and data suitable to weight the potential exposure at each area.

Freshman and Menzie (1996) present an additional approach for extrapolating to population-level effects. Their Population Effects Foraging (PEF) model estimates the number of individuals within a local population that may be adversely affected. The PEF model is an individual-based model that allows animals to move randomly over a contaminated site. Movements are limited by species-specific foraging areas and habitat requirements. The model estimates exposures for a series of individuals, and then sums the number of individuals that receive exposures in excess of toxic thresholds (Freshman and Menzie 1996).

3. PARAMETERS FOR ESTIMATION OF EXPOSURE

Species-specific and contaminant-specific parameter values are required for implementation of any of the models outlined previously. This section summarizes methods for estimation of exposure parameters (e.g., inhalation rates and food, water, and soil ingestion rates) and contaminant uptake into selected wildlife food types. In addition, life history summaries for selected species of interest at DOE sites are presented.

3.1 ESTIMATING EXPOSURE PARAMETERS

Implementation of the exposure model presented in Eq. 4 requires the specification of certain parameters. Although some parameters such as body weight must be obtained from the literature for each endpoint species and others such as soil, water, or air contaminant concentrations and area contaminated are site-specific and must be measured, general methods are available for estimating food and water consumption rates, inhalation rates, and home range/territory size.

3.1.1 Body Weight

Body weight is an extremely important parameter in the estimation of exposure. Not only is it a factor in determining the exposure rate, but because metabolism and body weight are related, body weights may be used to predict food and water consumption rates. On a per individual basis, larger animals consume more food or water than do smaller animals. However, because larger animals have lower metabolic rates than smaller ones, smaller animals have higher food and water consumption rates per unit body weight. This means that smaller animals will experience greater oral exposure per unit body weight than will larger animals.

Body weights for selected terrestrial wildlife are reported in EPA (1993). Additional sources include: Dunning (1984, 1993), Burt and Grossenheider (1976), Silva and Downing (1995), the Mammalian Species series, published by the American Society of Mammalogists, and the Birds of North America series, published by the American Ornithologists Union and the Philadelphia Academy of Natural Sciences.

3.1.2 Estimation of Food and Water Consumption Rates

Field observations of food, water, or soil consumption rates are the best data to use to estimate exposure. With very few exceptions, these data are unavailable for most wildlife species. The second best data to use to estimate exposure are media consumption rates for wildlife species derived from laboratory studies. These data are limited because the influence of ambient conditions, such as activity regimes or environmental variables (temperature, humidity, etc.), on metabolism (and therefore consumption rates) are difficult to approximate in a laboratory setting.

In the absence of experimental data, food consumption values can be estimated from allometric regression models based on metabolic rate. Nagy (1987) derived equations to estimate food consumption (in kg dry weight) for various groups of birds and mammals

$$I_{fd} = (0.0687(BW)^{0.822})/BW \quad \text{Placental Mammals,} \quad (14)$$

$$I_{fd} = (0.0306(BW)^{0.564})/BW \quad \text{Rodents,} \quad (15)$$

$$I_{fd} = (0.0875(BW)^{0.727})/BW \quad \text{Herbivores,} \quad (16)$$

$$I_{fd} = (0.0514(BW)^{0.673})/BW \quad \text{Marsupials,} \quad (17)$$

$$I_{fd} = (0.0582(BW)^{0.651})/BW \quad \text{All Birds,} \quad (18)$$

and

$$I_{fd} = (0.0141(BW)^{0.850})/BW \quad \text{Passerine Birds,} \quad (19)$$

where

$$\begin{aligned} I_{fd} &= \text{food ingestion rate (kg food [dry weight]/ kg body weight/d),} \\ BW &= \text{body weight (kg live weight).} \end{aligned}$$

Food ingestion rates estimated using these allometric equations are expressed as kilograms of dry weight. Because wildlife do not generally consume dry food (unless being maintained in the laboratory), food consumption must be converted to kilograms of fresh weight by adding the water content of the food. Percent water content of wildlife foods are listed in Table 4. Additional data may be obtained from the literature (e.g., Bell 1990, Redford and Dorea 1984, Odum 1993, and Holmes 1976). Calculation of food consumption in kilograms of fresh weight is performed as follows.

$$I_{ff} = \sum_{i=1}^m (P_i \times \frac{I_{fd}}{1 - WC_i}), \quad (20)$$

where

$$\begin{aligned} I_{ff} &= \text{total food ingestion rate (kg food [fresh weight]/kg body weight/d),} \\ m &= \text{total number of food types in the diet,} \\ P_i &= \text{proportion of the } i^{\text{th}} \text{ food type in the diet,} \\ WC_i &= \text{percent water content (by weight) of the } i^{\text{th}} \text{ food type.} \end{aligned}$$

Water consumption rates can be estimated for mammals and birds from allometric regression models based on body weight (Calder and Braun 1983)

$$I_w = (0.099(BW)^{0.90})/BW \quad \text{Mammals,} \quad (21)$$

and

$$I_w = (0.059(BW)^{0.67})/BW \quad \text{Birds,} \quad (22)$$

where

$$\begin{aligned} I_w &= \text{water ingestion rate (L water/kg body weight /d),} \\ BW &= \text{body weight (kg live weight).} \end{aligned}$$

Table 4. Percent water content of wildlife foods^a

Food type	Percent water content		
	Mean	STD	Range ^b
Aquatic invertebrates	Bivalves (w/o shell)	82	4.5
	Crabs (w/shell)	74	6.1
	Shrimp	78	3.3
	Isopods, amphipods		71-80
	Cladocerans		79-87

Table 4. (continued)

	Food type	Percent water content		
		Mean	STD	Range ^b
Aquatic Vertebrates	Bony fishes	75	5.1	
	Pacific herring	68	3.9	
Aquatic plants	Algae	84	4.7	
	Aquatic macrophytes	87	3.1	
	Emergent vegetation			45-80
Terrestrial invertebrates	Earthworms (depurated)	84	1.7	
	Grasshoppers, crickets	69	5.6	
	Beetles (adult)	61	9.8	
Mammals	Mice, voles, rabbits	68	1.6	
Birds	Passerines (w/typical fat reserves)			68
	Mallard duck (flesh only)			67
Reptiles and amphibians	Snakes, lizards			66
	frogs, toads	85	4.7	
Terrestrial plants	Monocots: young grass			70-88
	Monocots: mature dry grass			7-10
	Dicots: leaves	85	3.5	
	Dicots: seeds	9.3	3.1	
	Fruit: pulp, skin	77	3.6	

^a From EPA (1993).

^b Single values indicate only one value available.

3.1.3 Estimation of Inhalation Rates

Similar to food and water ingestion, allometric equations, based on body mass, have also been developed to estimate inhalation rates of resting mammals (Stahl 1967) and nonpasserine birds (Lasiewski and Calder 1971)

$$I_a = (0.54576(BW)^{0.8})/BW \quad \text{Mammals,} \quad (23)$$

and

$$I_a = (0.40896(BW)^{0.77})/BW \quad \text{Non-passerine Birds.} \quad (24)$$

where

I_a = inhalation rate (m³ air/kg body weight /d),
 BW = body weight (kg live weight).

The applicability of Eq. 24 for estimating inhalation rates of passerines is not known. However, the similarity between the models for mammals and birds suggests that Eq. 24 is likely to be suitable for passerines.

3.1.4 Soil Consumption

In addition to consuming food and water, many wildlife consume soil. Soil consumption may occur inadvertently while foraging (i.e., predators of soil invertebrates ingesting soil adhering to worms, grazing herbivores consuming soil deposited on foliage or adhering to roots) or grooming, or purposefully to meet nutrient requirements. Diets of many herbivores are deficient in sodium and other trace nutrients (Robbins 1993). Ungulates, such as white-tailed deer (*Odocoileus virginianus*) have been observed to consume soils with elevated sodium levels, presumably to meet sodium needs (Weeks 1978). Because soils at waste sites may contain very high contaminant concentrations, direct ingestion of soil is potentially a very significant exposure pathway. In contrast to food and water consumption, generalized models do not exist with which to estimate soil ingestion by wildlife. Beyer et al. (1994) report soil consumption estimates for 28 wildlife species. Additional data concerning soil consumption are reported in Arthur and Alldredge (1979), Garten (1980c), Thornton and Abrahams (1983), Arthur and Gates (1988), and Calabrese and Stanek (1995).

3.1.5 Estimation of Home Range and Territory Size

Home ranges and territories represent the spatial areas occupied by wildlife. These areas provide each species with food, water, and shelter and may or may not be defended. Home range or territory size is a critical component in estimating exposure. Species with limited spatial requirements (e.g., small home ranges or territories) may live exclusively within the bounds of a contaminated site and therefore may experience high exposure. Conversely, species with large home ranges may travel among and receive exposure from multiple contaminated sites.

Multiple factors may influence home range or territory size. These factors include habitat quality, prey abundance, and population density. Methods have been developed to estimate home range size. McNab (1963) observed that home range size in mammals was a function of body weight

$$HR = 6.76 (BW)^{0.63}, \quad (25)$$

where

HR = home range (acres),
 BW = body weight (kg live weight).

Differences in home range requirements were observed between “hunters” (includes species that rely on widely distributed foods, e.g., granivores, frugivores, insectivores, and carnivores) and “croppers” (species that rely on foods that are spatially more concentrated, e.g., grazing and browsing herbivores; McNab 1963). Home ranges of “hunters” may be as much as 4 times greater than that of “croppers” of the same body mass. Home ranges for each group may be estimated using the following models

$$HR_h = 12.6 (BW)^{0.71}, \quad (26)$$

and

$$HR_c = 3.02(BW)^{0.69}, \quad (27)$$

where

HR_h = home range for hunters (acres),
 HR_c = home range for croppers (acres).

Note: 1 acre = 0.4047 ha = 4,047 m².

More recent research by Harestad and Bunnell (1979) produced the following relationships between body mass and home range in mammals:

$$HR_{\text{herb}} = 0.002 (bw)^{1.02}, \quad (28)$$

$$HR_{\text{omn}} = 0.59(bw)^{0.92}, \quad (29)$$

and

$$HR_{\text{carn}} = 0.11(bw)^{1.36}, \quad (30)$$

where

HR_{herb} = home range for herbivores (ha),
 HR_{omn} = home range for omnivores (ha),
 HR_{carn} = home range for carnivores (ha),
 bw = body weight (g).

A strong positive relationship also exists between body mass and territory or home range size among birds (Schoener 1968). Predators tend to have larger territories than omnivores or herbivores of the same weight. Territory size also increases more rapidly with body weight among predators than among omnivores or herbivores. Schoener (1968) believes these relationships reflect the higher density of available food for omnivores and herbivores. While Schoener (1968) developed regression models describing the relationship between body size, home range size, and foraging habits, all parameters needed to implement the models are not presented. A summary of home range or territory sizes for 77 species of land birds (and source references) are listed however.

3.2 ESTIMATION OF CONTAMINANT CONCENTRATIONS IN WILDLIFE FOODS

To estimate the magnitude of contaminant exposure that wildlife may experience, contaminant concentrations in food items preferred by endpoint species are needed. These data may be acquired either by direct measurement or estimation.

Direct measurement consists of the collection and analysis of contaminant concentrations in food items. Because direct measurement provides information on the actual contaminant loading in on-site biota, this approach contributes the least uncertainty to exposure estimates and is therefore the preferred approach. For various reasons however (biota phenology incompatible with sampling schedule; insufficient time, personnel, or finances to support field sampling, etc.), direct measurement of contaminant concentrations in biota may not be feasible. When direct measurement of contaminants in biota are not possible, estimation is the only alternative.

Contaminant loads in biota may be estimated using a variety of methods, ranging from mechanistic process models to simple, empirical uptake factors. While mechanistic models for estimation of contaminant concentrations in biota may give more accurate estimates than uptake factors, they generally require considerable information, much of which may not be available in a risk assessment context. Examples of complex contaminant uptake models for plants and fish are presented in Lindstrom et al. (1991) and Thomann and Connolly (1984), respectively. Because of their data requirements, complex models are generally taxa- and location-specific and may not be widely applicable.

The simplest model for estimation of contaminant loads in biota is uptake factors. Uptake factors consist of ratios of the concentration of a given contaminant in biota to that in soil. (The model assumes that exposure to the food item is primarily from contaminants in soil.) In practice, if the contaminant concentration in soil is known (which is likely in almost all ecological risk assessments), the concentration in biota may be estimated by multiplying the soil concentration by the uptake factor. Because contaminant uptake is influenced by characteristics of the organism and by the properties of the contaminant, separate uptake factors are recommended for each contaminant and taxonomic group being considered. Bioavailability of contaminants for uptake can also be influenced by soil conditions. For example, Corp and Morgan (1991) observed that while high amounts of soil organic matter reduced the bioavailability of lead to earthworms, low soil pH increased bioavailability.

The use of uptake factors depends on the assumption that the concentration of chemicals in organisms is a linear, no-threshold function of concentrations in soil. It will not be the case if the chemical in question is well regulated by the organism, either because it is an essential nutrient or because it is a toxicant with effective inducible mechanisms for metabolism or excretion. Such well-regulated chemicals will (at least within the effective concentration range for the mechanism) have nearly constant concentrations, regardless of soil concentrations. Various complex patterns are also possible because of lack of induction at low concentrations, saturation kinetics at high concentrations, toxicity at high concentrations, or other processes. Despite chemical behavior that suggests that alternative models would be more appropriate, uptake factors are commonly used in risk assessments.

In this section, we briefly review methods and models for estimating contaminant concentrations in earthworms and plants. In addition, uptake factors and regression models based on literature-derived data are presented for selected analytes in earthworms and plants. Additional uptake factors and regression models based on literature-derived data for small mammals and sediment-associated invertebrates are presented in Sample et al. (1997a) and Jones et al. (1997), respectively.

3.2.1 Earthworms

Earthworms are considered to be representative of soil invertebrates or terrestrial detritivores in many ecological risk assessments. This is in part because of their importance. Earthworms can constitute a large fraction of the biomass of soil invertebrates, they are important in the formation of soils in temperate environments, and they are a significant fraction of the diet of some vertebrates. In addition, earthworms appear to be more highly exposed to soil contaminants than other soil and litter invertebrates (Davis and French 1969; Ma 1994). Finally, uptake of chemicals from soil by earthworms has been much better studied than uptake by other soil invertebrates but is still much less studied than accumulation by aquatic invertebrates or vertebrates. Although there is some information available on the kinetics of earthworm uptake (Belfroid et al. 1994b), all available operational models are based on equilibrium partitioning with soil or soil pore water. Given the slow kinetics of soil transformation and transport processes relative to air and water, equilibrium is a reasonable assumption.

Soil/Worm Model

If paired soil and earthworm concentrations are available from the site of concern or the literature, a basic soil/worm equilibrium partitioning model may be used.

$$C_v = K_{sv} C_s, \quad (31)$$

where

- C_v = concentration in worms (vermes)(mg/kg),
 K_{sv} = worm/soil partitioning coefficient (kg soil/kg worm),
 C_s = concentration in surface soil (mg/kg).

Values of K_{sv} (equivalent to the uptake factors described previously) are available in the literature for some chemicals (Table 5) but may be highly variable because of soil properties and the form of the contaminant. Steady state may be assumed for field studies but should be demonstrated for laboratory studies. Steady state was reached for a variety of organochlorine chemicals in 10 days (Belfroid et al. 1995). When site-specific values or literature values from a similar soil and contaminant form are available, this is the preferred model.

When site-specific data are collected to derive K_{sv} values, it is important to ensure the quality and relevance of the data. In particular, it is important that the soil and worms be collected from the same location and that the soil be from the surface layer (the A horizon, tilled layer, or equivalent) where the worms would have been exposed. Also, it is important to depurate (i.e. void their gut contents) the worms for three reasons. First, soil ingestion by vermivorous wildlife is accounted for separately in the exposure model, so use of undepurated worms would reduce the accuracy of the model. Second, the mass of ingested material is variable, so it introduces extraneous variance in the K_{sv} estimate. Finally, the bias introduced by the gut contents is not consistent. If the chemical is bioaccumulated by worms to concentrations greater than in soil (i.e., $K_{sv} > 1$), the C_v is underestimated, but if concentrations are greater in soil than worms, C_v is overestimated.

Table 5. Summary of sources of soil-earthworm uptake factors (K_{sv}) and uptake models

Study Location	Analytes with K_{sv} values	Analytes with Models	Reference
Pennsylvania, USA	Cd, Cu, Pb, Ni, and Zn	Cd	Beyer et al. 1982
Maryland, USA		Pb, Cu, Cd, and Se	Beyer et al. 1987
Finland	Al, Cd, Cu, Fe, Hg, Mn, V, and Zn		Braunschweiler 1995
Wales, Great Britain	Pb	Ca, Cd, Cu, Pb, and Zn	Corp and Morgan 1991
Warsaw, Poland	Cd, Cu, Pb, Zn		Czarnowska and Jopkiewicz 1978
Germany	Cd, Pb, and Zn		Emmerling et al. 1997
Denmark		Se	Nielsen and Gissel-Nielsen 1975
Netherlands	Cd, Cu, Mn, Ni, Pb, and Zn		Hendriks et al. 1995
Netherlands	Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn	Pb and Zn	Ma 1982
Netherlands		Cd, Cu, Pb, and Zn	Ma et al. 1983
Seveso, Italy	TCDD		Martinucci et al. 1983

Table 5. (continued)

Study Location	Analytes with K_{sw} values	Analytes with Models	Reference
Models fit to data from multiple locations.		Cd, Cu, Ni, Pb, and Zn	Neuhauser et al. 1995
Montana, USA	As, Cd, Cu, and Zn		Pascoe et al. 1996
Illinois, USA	Cd, Cr, Cu, Ni, and Pb		Pietz et al. 1984
Reading, Great Britain	Cd, Cu, Pb, and Zn	Cd, Cu, Pb, and Zn	Spurgeon and Hopkin 1996
Tennessee, USA	Cd, Pb, Zn		Van Hook 1974

^a TCDD = 2,3,7,8 Tetrachloro Dibenzo-p-dioxin

Soil/Water/Worm Model

It has been proposed that invertebrates are in equilibrium with the aqueous phase of soil. This is consistent with the soil/worm model if the solid, aqueous, and biotic phases of the soil are all in equilibrium. This approach has been used for sediments by the EPA and others (DiToro et al. 1991). It is well supported for sediment invertebrates and is supported by some evidence for earthworms and possibly other soil invertebrates (van Gestel and Ma 1988; Connell 1990; Lokke 1994). However, it has been suggested that the model may underestimate accumulation of a few chemicals for which the dietary route is dominant (Belfroid et al. 1994a). In addition to potentially making extrapolations between soils more accurate than soil/worm partitioning, it has the advantages of making available for use the large literature on water/biota partitioning factors (bioconcentration factors) and the numerous QSARs for water/biota partitioning. However, it adds the burden of estimating soil pore water concentrations. The conventional formula is

$$C_w = C_s / K_d, \quad (32)$$

where

K_d = the soil (or sediment)/water partitioning coefficient (L/kg sediment),

C_w = water concentration (mg/L).

Values of K_d are available from the literature for many metals and some organics but are highly variable (Baes et al. 1984). If literature K_d values are used, this model is not expected to be more accurate than Eq. 31, but K_d values are available for some chemicals for which K_{sw} is not.

For nonionic organic compounds

$$K_d = f_{oc} K_{oc}, \quad (33)$$

or

$$K_d = f_{om} K_{om}, \quad (34)$$

where

f_{oc} = fraction organic carbon in the soil (unitless),
 K_{oc} = water/soil organic carbon partitioning coefficient (kg/kg or L/kg),
 f_{om} = fraction organic matter in the soil (unitless),
 K_{om} = water/soil organic matter partitioning coefficient (kg/kg or L/kg),

This formula adjusts for the organic content (expressed as either organic matter or organic carbon content), which is the major source of variance among soils in the uptake of neutral organic chemicals. This normalization makes this model more accurate than Eq. 31 for neutral organic chemicals. For ionic organic chemicals, Van Gestel et al. (1991) recommend correcting the coefficient (K_{oc} or K_{om}) by dividing by the fraction nondissociated (f_{nd}), which is estimated from

$$f_{nd} = 1/(1 + 10^{pH-pK_a}), \quad (35)$$

where

pK_a = the negative log of the dissociation constant.

When K_{oc} and K_{om} are both unavailable, they may be estimated from QSARs. The model used by the EPA was developed from sediments (DiToro et al. 1991)

$$\log_{10}(K_{oc}) = 0.983 \log_{10}(K_{ow}) + 0.00028, \quad (36)$$

where

K_{ow} = octanol/water partitioning coefficient (unitless).

Van Gestel et al. (1991) provide a formula for K_{om} that is based on soils rather than sediments:

$$\log_{10}(K_{om}) = 0.89 \log_{10}(K_{ow}) - 0.32. \quad (37)$$

Values for K_{ow} are available in the literature for most organic chemicals, or they can be calculated from QSARs. K_{ow} s for selected chemicals are presented in Table 6.

From these formulas, C_v can be calculated as

$$C_v = K_{bw} C_w, \quad (38)$$

where

K_{bw} = biota/water partitioning coefficient (L/kg organism).

K_{bw} values for chemicals in earthworms may be assumed equivalent to bioconcentration factors for aquatic invertebrates from the literature. Alternatively, QSARs can be used to estimate this factor. The model developed by Connell and Markwell (1990) for uptake by earthworms of 32 "lipophilic" organic chemicals ($\log K_{ow}$ 1.0-6.5) is

$$\log K_{bw} = \log K_{ow} - 0.6 \quad (n = 60, r = 0.91). \quad (39)$$

It has been suggested that for lipophilic compounds, earthworm accumulation should also be a function of lipid content of the worms (Connell and Markwell 1990). This is not a component of the standard sediment model and makes no contribution to predictive accuracy in practice because the site-specific lipid content of worms is unknown in nearly all cases and would vary in an unquantified manner seasonally and among species. However, based on a study of marine sediment oligochaetes (Markwell et al. 1989), Menzie et al. (1992) recommend a model for earthworms in soil that contains soil organic content and worm lipid content but not K_{ow} or any other property of the chemical

$$K_{sv} = L (0.66f_{oc})^{-1}, \quad (40)$$

where

L = proportion lipid in worms (unitless).

L was estimated by Menzie et al. (1992) to be 0.02, but Connell and Markwell (1990) used 0.0084 for theoretical calculations.

This model predicts that all chemicals have equal concentrations in earthworms at a site, which was not far from true for the contaminants of concern at the site where it was applied. There, the mean bioconcentration factors for four DDT residues and total chlordane ranged from 0.10 to 0.35, and the estimated mean bioconcentration factor for all chemicals was 0.25. This model is not recommended because the addition of L adds nothing without information that is seldom available (lipid content of test organisms) and because the deletion of K_{ow} is not well justified. It is discussed here because it has been widely adopted in the United States for estimating earthworm concentrations.

Finally, Connell (1990) proposed an extremely reduced formula

$$K_{sv} = 0.44(K_{ow})^{0.05}. \quad (41)$$

This model shows worm concentrations to be a weak function of K_{ow} but not of any soil or worm property. It would be appropriate only if the site soils were similar to the test soils used in the study from which this formula was derived (Lord et al. 1980).

Table 6. Octanol-water partition coefficients for selected chemicals

Chemical and form	Log K_{ow}	Source
Acetone	-0.24	EPA 1995
Aldrin	6.5	EPA 1995
Aroclor 1016	5.6	ATSDR 1989
Aroclor 1242	5.6	ATSDR 1989
Aroclor 1248	6.2	ATSDR 1989
Aroclor 1254	6.5	ATSDR 1989
Benzene	2.13	EPA 1995
beta-BHC	3.81	EPA 1995
BHC-mixed isomers	5.89	EPA 1995
Benzo(a)pyrene	6.11	EPA 1995
Bis(2-ethylhexyl)phthalate	7.3	EPA 1995
Carbon tetrachloride	2.73	EPA 1995
Chlordane	6.32	EPA 1995
Chlordecone (kepone)	5.3	EPA 1995
Chloroform	1.92	EPA 1995
o-Cresol	1.99	EPA 1995
DDT and metabolites	6.53	EPA 1995
1,2-Dichloroethane	1.47	EPA 1995

Table 6. (continued)

Chemical and form	Log K_{ow}	Source
1,1-Dichloroethylene	2.13	EPA 1995
1,2-Dichloroethylene	1.86	EPA 1995
Dieldrin	5.37	EPA 1995
Diethylphthalate	2.5	EPA 1995
Di-n-butyl phthalate	4.61	EPA 1995
1,4-Dioxane	-0.39	EPA 1995
Endosulfan	4.1	EPA 1995
Endrin	5.06	EPA 1995
Ethanol	-0.31	EPA 1992
Ethyl acetate	0.69	EPA 1995
Formaldehyde	-0.05	EPA 1995
Heptachlor	6.26	EPA 1995
Lindane (gamma-BHC)	3.73	EPA 1995
Methanol	-0.71	EPA 1995
Methoxychlor	5.08	EPA 1995
Methylene chloride	1.25	EPA 1995
Methyl ethyl ketone	0.28	EPA 1995
4-Methyl 2-pentanone	1.19	EPA 1992
Pentachloro-nitrobenzene	4.64	EPA 1995
Pentachlorophenol	5.09	EPA 1995
2,3,7,8-Tetrachloro-dibenzodioxin	6.53	EPA 1995
1,1,2,2-Tetrachloro-ethylene	2.67	EPA 1995
Toluene	2.75	EPA 1995
Toxaphene	5.5	EPA 1995
1,1,1-Trichloroethane	2.48	EPA 1995
Trichloroethylene	2.71	EPA 1995
Vinyl chloride	1.5	EPA 1995
Xylene (mixed isomers)	3.2	EPA 1995

All earthworm concentration values in these models are on a fresh weight basis for depurated worms. However, earthworm concentrations in the literature may be reported as fresh or dry weights. Water content of earthworms are reported to range from 82 to 84% (EPA 1993). Concentrations may also be reported for undepurated worms, but there is no basis for correcting those values because of the variability in mass of ingested material.

Soil-Earthworm Uptake Factors

Empirical soil-earthworm uptake factors (K_{sw}) and uptake models have been developed from field data for selected chemicals, primarily metals (Table 5). Most of these studies report uptake from a limited number of locations or represent only a small range of soil concentrations. To best evaluate the relationship between concentrations of contaminants in soil and those in earthworms, a broad range of soil concentrations is needed.

To determine how contaminant uptake varied across locations, contaminant levels, and soil conditions, a literature search was performed for studies that reported chemical concentrations in co-located earthworm and soil samples. Data were obtained for eleven chemicals: arsenic, cadmium, chromium, copper, mercury, lead, manganese, nickel, zinc, PCBs, and TCDD. To ensure relevancy of the data to field situations, only field studies in which resident earthworms were collected were considered. All earthworm tissue burdens were therefore

assumed to be at equilibrium with soil concentrations. Because soil residues in the earthworm gastrointestinal (GI) tract may be highly variable and therefore may significantly bias body burden measurements, only depurated earthworms were included. Samples in which the GI tract had been dissected or manually flushed were also considered suitable. To ensure comparability of data, only 'total' chemical analyses of both soil and earthworms (e.g., resulting from extractions using concentrated acids) were included. Data resulting from DTPA, acetic acid, and other mild extraction methods were excluded. The mean (or composite) soil and earthworm value reported for each sampling location evaluated in each study was considered an observation. If data for multiple earthworm species were reported at a site, each was considered a separate observation. Soil and earthworm data in the database were reported as mg/kg dry weight. If studies reported earthworms in terms of wet weight concentrations, dry weight concentrations were estimated assuming a 84% water content (EPA 1993). Summaries of the analytical methods and data presented for each study included in the database are presented in Appendix A. Summary statistics were calculated for K_{sw} for each chemical (Table 7). To facilitate the use of the UFs in probabilistic risk evaluations, the distribution of the UFs for each analyte was evaluated using a distribution-fitting program (BestFit; Palisade Corp. 1994a). The data were fit to normal and lognormal distributions. Goodness of fit was determined using Kolmogorov-Smirnov tests.

To evaluate if there was a linear relationship between the contaminant concentration in soil and that in earthworms, simple regressions were performed using SAS PROC REG (SAS Inst. Inc. 1988). Contaminant concentrations in both soil and earthworms were natural-log transformed prior to regression analyses. Because data concerning the number of individuals included in composites or means were not available for all observations, no weighting of observations was applied. Simple linear regression models of ln-earthworm concentration on ln-soil concentration were developed for each analyte (Table 8). Plots of the cumulative frequency distributions of the K_{sw} values and scatterplots of soil concentration versus earthworm concentration are presented for each chemical in Figs. 1-11.

With the exception of As and Ni, the distribution of all UFs was best described by the lognormal distribution (Table 7); As and Ni were best fit by a normal distribution. Median UFs for 6 chemicals (As, Cr, Cu, Mn, Ni, and Pb) were <1, indicating no biomagnification (Table 7). Median UFs >1 were observed for the remaining 5 chemicals (Cd, Hg, Zn, PCB, and TCDD; Table 7). [Note: the mean and standard deviation of the natural-log-transformed UFs are presented as parameters for describing the UF distributions for those analytes best fit by a lognormal distribution. While the untransformed UFs are best fit by a lognormal distribution, the natural-log-transformed UFs are normally distributed. These parameters may be used in two ways. They may be applied to normal distribution functions in Monte Carlo simulation software; however the output from the sampling from this distribution must be back-transformed (e.g., e^y , where y =sampling result). Alternatively, they may be incorporated into the LOGNORM2 function in the @RISK Monte Carlo simulation software (Palisade Corp. 1994b). Use of the LOGNORM2 function requires no back-transformation. Comparable results are obtained using either approach]

Regression of ln earthworm on ln soil produced significant model fits for all chemicals except Cr (Table 8). With the exception of Ni, slopes of all regression models were positive (Table 6; Figs. 1a through 11a). Intercepts differed significantly from 0 for all chemicals except Hg, Mn, and Pb (Table 8). r^2 values for the significant models ranged from 0.22 (Cu) to 0.94 (TCDD; Table 8).

Except for chromium, either K_{sw} or regression models could be used to estimate chemical concentrations in earthworm tissues. In the case of chromium, because the regression was not significant, the model should not be used; K_{sw} should be used instead. Because uptake tends to decrease at higher soil concentrations (Fisher and Koszorus 1992), regression models may give more accurate results than K_{sw} values. Comparison of the accuracy and precision of the K_{sw} values and regression models, using independent data, is presented in Sample et al. (1997).

It should be noted that K_v and regression models estimate the tissue concentration in earthworms in mg/kg of dry weight. These values must be converted to mg/kg of wet weight before they are employed in exposure estimation

$$C_{\text{wet}} = C_{\text{dry}} * P_{\text{dry}}, \quad (42)$$

where

- C_{wet} = wet weight concentration,
 C_{dry} = dry weight concentration,
 P_{wet} = proportion dry matter content of worm or other tissue.

3.2.2 Plants

Uptake of contaminants by plants is often dependent on the concentration in soil. In general, uptake increases with soil concentration until the contaminant becomes toxic to the plant (McBride 1995). Instances of apparent saturation have been observed however. For example, the cadmium content in foliage of American sycamore increases with soil concentration until it reaches 50 mg/kg (Carlson and Bazzaz 1977). Contaminants that are also nutrients may be regulated by plants such that uptake varies little relative to soil concentration. Nutrients and chemicals that mimic them are often taken up by active processes, rather than in transpiration water. The various forms of particular metals (e.g., chromium and mercury) complicates the estimation of uptake. Some investigators have observed that the uptake of monovalent cations follows Michaelis-Menten kinetics (Baker 1983), but general or specific models for the uptake of metals by plants are not well developed. Estimation of uptake of metals and other inorganics from soil by plants is generally performed using uptake factors (K_{sp} = plant/soil partitioning coefficient; kg soil/kg plant).

Models for the uptake of organic chemicals by plants are more common, probably because plant physiology plays a greater role in determining uptake of inorganic contaminants. Also, interest in herbicides and in predicting the uptake of pesticides has contributed to research on organic chemical uptake. These models range from the simple ranking of potential for uptake, based on the octanol-water partition coefficient (Scheunert et al. 1994) to the transport of water through xylem and phloem of a single or three-leafed plant, as determined by compartment volumes, cell wall thicknesses, diffusion, and partition coefficients of cell membranes (Boersma et al. 1988, 1991). Fugacity-dependent models include those of Trapp et al. (1990) and Paterson et al. (1994).

Several simple models have been developed to estimate concentrations of organic contaminants in plant tissues. Briggs et al. (1983) studied the uptake of contaminants by plants roots. They observed the following relationship

$$C_r = BCF_r * C_{sw}, \quad (43)$$

and

$$\log BCF_r = 0.77(\log K_{ow}) - 1.52, \quad (44)$$

where

- C_r = concentration of chemical in roots (mg/kg fresh wt.),
 BCF_r = bioconcentration factor for roots (unitless),
 C_{sw} = concentration of chemical in soil water (mg/L).

In similar work with barley, Topp et al. (1986) developed the following model

$$\log BCF_r = 0.63(\log K_{ow}) - 0.959. \quad (45)$$

Table 7. Summary statistics for literature-derived soil-to-biota uptake factors (K_{sv} and K_{sp})

Taxa	Analyte	N	Mean	Standard Deviation	Minimum	Median	90th Percentile	Maximum	Mean of Natural Log-transformed values	Standard Deviation of Natural Log-transformed values	Distribution
Earthworms	As	36	0.2656	0.2116	0.0164	0.2361	0.5214	0.9250			normal
	Cd	114	27.1682	37.5895	0.4286	14.2603	66.0377	190.0000	2.58768	1.28036	lognormal
	Cr	48	0.7080	1.1496	0.0212	0.1607	2.7000	5.3680	-1.48636	1.5555	lognormal
	Cu	103	0.9283	0.9135	0.0130	0.6364	2.2807	4.8890	-0.57464	1.14691	lognormal
	Hg	15	8.5537	11.0986	0.0488	3.9334	30.0000	33.0000	1.16596	1.77202	lognormal
	Mn	16	0.0742	0.0551	0.0249	0.0605	0.1646	0.2280	-2.80288	0.62809	lognormal
	Ni	17	0.9200	0.7418	0.0333	0.7778	1.8881	2.8330			normal
	Pb	119	6.3297	26.7336	0.0007	0.2250	4.3243	228.2610	-1.10093	2.05196	lognormal
	Zn	123	8.2364	11.0731	0.0247	3.7816	25.0000	49.5100	1.03218	1.83458	lognormal
	PCB	16	14.1790	14.4186	4.3333	10.6667	23.4945	65.2270	2.40307	0.64066	lognormal
TCDD	19	11.7409	9.8083	1.1905	11.0108	22.2290	42.0678	2.1132	0.8918	lognormal	
Plants	As	110	0.5529	1.4515	0.000056	0.09791	1.2176	9.074	-2.80737	2.60632	lognormal ^a
	Cd	289	2.0147	3.6572	0.015928	0.9	4.6	35.944	-0.09243	1.29423	lognormal ^a
	Pb	204	0.3413	0.9959	0.000113	0.10235	0.615	10.601	-2.27508	1.5376	lognormal
	Ni	163	0.7235	2.4507	0.000632	0.03827	1.6667	22.214	-2.8878	2.1832	lognormal ^a
	Se	237	20.5818	75.8523	0.033376	1.83973	26.3	627	0.72426	1.91585	lognormal ^a

^a Data not fit well by either normal or lognormal distributions, however, closest fit provided by lognormal.

Table 8. Results of regression analyses on literature-derived soil-biota uptake data

Taxa	Analyte	N	B0±SE	B1±SE	r ²	P model fit
Earthworms	As	36	-1.747±0.3542***	0.9884±0.1804***	0.47	0.0001
	Cd	114	2.8216±0.0766***	0.5512±0.03343***	0.71	0.0001
	Cr	48	2.3957±0.653***	-0.146±0.1863 ^{NS}	0.01	0.44
	Cu	103	1.8059±0.1528***	0.2414±0.04503***	0.22	0.0001
	Hg	15	0.0781±0.2594 ^{NS}	0.3369±0.0915**	0.51	0.0028
	Mn	16	-0.043±1.3719 ^{NS}	0.5759±0.2096*	0.35	0.016
	Ni	17	7.033±0.9409***	-1.548±0.3097***	0.62	0.0002
	Pb	119	0.0752±0.4153 ^{NS}	0.7612±0.07586***	0.46	0.0001
	Zn	123	5.0981±0.1384***	0.2373±0.0239***	0.45	0.0001
	PCB	16	1.7903±0.2358***	1.2909±0.09404***	0.93	0.0001
	TCDD	19	3.533±0.810***	1.182±0.074***	0.94	0.0001
Plants	As	110	-1.915±0.556***	0.673±0.183***	0.11	0.0004
	Cd	289	0.040±0.078 ^{NS}	0.849±0.030***	0.74	0.0001
	Pb	204	-1.625±0.364***	0.864±0.073***	0.41	0.0001
	Ni	163	-1.663±0.463***	0.754±0.087***	0.32	0.0001
	Se	237	0.518±0.163**	1.136±0.070***	0.53	0.0001

model: $\ln(y)=B_0+B_1(\ln[x])$, where y = concentration in biota (mg/kg dry wt.), x = concentration in soil (mg/kg dry wt.).

^{NS} Not Significant: $p>0.05$.

* $p<0.05$.

** $p<0.01$.

*** $p<0.001$.

Travis and Arms (1988) observed that the bioconcentration factor for aboveground foliage for nonpolar organic contaminants was inversely proportional to the $\log K_{ow}$

$$\log BCF_f = 1.588 - 0.578(\log K_{ow}), \quad (46)$$

where

BCF_f = bioconcentration factor for aboveground vegetation (unitless).

Topp et al. (1986) found that bioconcentration factors for organic contaminants in total plants (roots plus foliage) were best described by the molecular weight of the chemical

$$\log BCF_t = 5.943 - 2.385(\log MW), \quad (47)$$

where

BCF_t = bioconcentration factor for total plant (root plus aboveground vegetation; unitless),

MW = molecular weight of chemical (g/mol).

Additional models for the estimation of contaminant uptake by plants by other pathways (e.g., rainsplash, foliar uptake of vapor-phase or particle-bound contaminants) are summarized in Paterson et al. (1990), McKone (1993), and Hope (1995).

With the exception of Eq. 46, all plant BCF models presented here estimate chemical concentrations in terms of wet weight. If Eq. 46 is used, dry weight concentrations may be converted to wet weight using Eq. 42 and water content data obtained from Table 4 or the literature.

In contrast to earthworms, while there have been numerous field and laboratory studies of the uptake of contaminants by plants, few empirical models or K_{sp} values for plants are reported in the literature. A report by Baes et al. (1984) provides point estimates of K_{sp} for all inorganic elements.

To determine how contaminant uptake by plants varied with contaminant levels, an analysis similar to that performed for earthworms and summarized above was performed for plants (Efroymsen et al. 1997). Literature was reviewed for five chemicals: arsenic, cadmium, lead, nickel, and selenium (summary of each paper reviewed is presented in Appendix B). Soil and plant contaminant concentration data were extracted from each paper. Data points represented different locations and plant species. Within studies, replicates were averaged. Experimental treatments in which secondary soil contaminants, aerial contaminants, or other additions were made were not included in the determination of K_{sp} . Studies in which concentrations of contaminants in soil were determined by a partial extraction with diethylene triamine pentaacetic acid (DTPA) or very weak acids or water were excluded from analysis. Although concentrations of DTPA-extracted contaminants from soils sometimes correlate with those taken up by plants (Sadiq 1985), this estimate of bioavailability has been observed not to work for some metals (Sadiq 1985, 1986) or for soils of varying pH (Miles and Parker 1979). Also, studies in which concentrations of analytes in soil or plants were estimated visually from a figure were used only if estimates could be made within about 10%. Studies were included in the analysis even if no correlation between concentrations of contaminants in soils and plants was observed in the study.

K_{sp} values were calculated for each paired soil-plant observation. Summary statistics were calculated for the K_{sp} for each chemical (Table 7). Results of the regression analyses are presented in Table 8. Plots of the cumulative frequency distributions of K_{sp} and scatterplots of soil concentration vs plant concentration are presented for each chemical in Figs. 12 - 16. The distribution of K_{sp} for lead was best described by the lognormal distribution (Table 7). The distributions for the other four analytes, while differing significantly from both the normal and lognormal distribution, was best fit by the lognormal distribution. With the exception of selenium, median K_{sp} for all chemicals was <1 (Table 7). Significant regressions with increasing trends were found for all analytes (Table 8). Additional regression models that incorporate soil pH are presented in Efroymsen et al. (1997).

3.3 LIFE HISTORY PARAMETERS FOR SELECTED SPECIES

To estimate contaminant exposure by terrestrial wildlife using the models described above, species-specific values for the parameters are needed. Because of large within-species variation in values for life-history parameters, data specific to the site in question provides the most accurate exposure estimates and should be used whenever available. Because availability of site-specific life history data is extremely limited, published values from other areas within an endpoint species range must generally be used to estimate exposure.

Life history parameters that determine contaminant exposure have been outlined for eight mammals and five birds. These species were selected because they are likely to occur at DOE facilities (species occurrence will vary according to location of site however) and are considered to be potential endpoints at selected DOE facilities. To avoid repetition, it was decided to focus on species other than those reported in the "Wildlife Exposure Factors Handbook" (EPA 1993), which presents life history data for 15 birds, 11 mammals, and 8 reptiles or amphibians (Table 9). Summaries of life history parameters for selected wildlife species on the ORR are presented in Sample and Suter (1994). Other sources of life history summaries include the Mammalian Species series (published by the American Society of Mammalogists) and the Birds of North America series (published by the American Ornithologists Union and the Philadelphia Academy of Natural Sciences). The Mammalian Species series currently addresses over 300 mammal species, while Birds of North America series addresses 240. Additional information on the Birds of North America may be obtained from the Internet: <http://www.acnatsci.org/bna/>.

Table 9. Summary of species presented in the "Wildlife Exposure Factors Handbook" (EPA 1993)

Birds	Mammals	Reptiles or amphibians
Great Blue Heron	Short-tailed Shrew	Snapping Turtle
Canada Goose	Red Fox	Painted Turtle
Mallard Duck	Raccoon	Eastern Box Turtle
Lesser Scaup	Mink	Racer
Osprey	River Otter	Northern Water Snake
Red-Tailed Hawk	Harbor Seal	Eastern Newt
Bald Eagle	Deer Mouse	Green Frog
American Kestrel	Prairie Vole	Bullfrog
Northern Bobwhite Quail	Meadow Vole	
American Woodcock	Muskrat	
Spotted Sandpiper	Eastern Cottontail Rabbit	
Herring Gull		
Belted Kingfisher		
Marsh Wren		
American Robin		

3.3.1 Little Brown Bat (*Myotis lucifugus*)

Little brown bats are in the order Chiroptera, family Vespertilionidae. The genus *Myotis* includes approximately 80 species; *M. lucifugus* includes six subspecies (Fenton and Barclay 1980). As with most vespertilionids, the little brown bat is strictly insectivorous (Vaughan 1978).

Distribution

The little brown bat is one of the most abundant bats throughout the northern United States and Canada (Harvey 1992). It is widely distributed throughout North America. Its range extends from east to west coasts and from the mountains of northern Mexico to Alaska (Burt and Grossenheider 1976; Fenton and Barclay 1980).

Body Size and Weight

Female little brown bats are somewhat larger than males (Fenton and Barclay 1980). Reported body mass may range from 3.1 to 12 g (Silva and Downing 1995) but averages 7 to 9 g (Burt and Grossenheider 1976). Body weight varies throughout the year, remaining relatively constant from March through August then increasing dramatically in September through October, prior to hibernation (LaVal et al. 1980). Body weights

for little brown bats from several locations are presented in Table 10. Additional data on body weights are reported in Silva and Downing (1995).

Table 10. Body weights (g) for the little brown bat, *Myotis lucifugus*

Location	Sex	N	Mean	Range	Comments	Reference
Massachusetts	not stated	4	7.5±1.1 ^a			Gould 1955
New Mexico	Female (ad) ^b	5	8.47±0.81	7.25-9.43	Collected 19 Aug.; data also presented for 1 and 15 Sept.	Ewing et al. 1970
	Male (ad)	3	6.96±0.27	6.57-7.20		
	Female (yy) ^c	4	6.78±0.21	6.61-7.14		
	Male (yy)	2	5.74±0.06	5.69-5.80		
Alberta, Canada	not stated		10.3	7.4-11.6		Silva and Downing 1995
Indiana	Male		6.15	3.1-10		Silva and Downing 1995
	Female		6.15	3.2-14.4		
Indiana	Male	6	6.03			Stones and Wieber 1965
	Female: nonpregnant, nonlactating	40	6.99			
	Female: pregnant	6	10.27			
	Female: lactating	13	7.77			

^a mean±standard deviation.

^b adult.

^c young of year.

Food Habits and Diet Composition

Little brown bats are strict insectivores, detecting insects using ultrasonic calls (Fenton and Barclay 1980). Although insects are generally captured in flight, some may be taken from the surface of water or vegetation (Fenton and Bell 1979). Foraging is opportunistic; little brown bats have been observed to exploit insect swarms attracted to artificial lights (Fenton and Morris 1976) or large insect hatches (Vaughan 1980). While the diet composition may be highly variable, aquatic insects (e.g., Chironomidae and Trichoptera) are the primary food in most areas studied (Table 11; Fenton and Barclay 1980; Anthony and Kunz 1977; LaVal et al. 1980). However, in Alaska the diet consisted primarily (71.1% by volume) of small moths (Whitaker and Lawhead 1992). Insects consumed generally range from 3 to 10 mm in size (Anthony and Kunz 1977). Additional data concerning diet preferences of little brown bats may be found in Barclay (1991), Belwood and Fenton (1976), Kunz and Whitaker (1983), and Whitaker et al. (1981).

Table 11. Diet composition of little brown bats

Location	Prey Taxon	Percent volume	Percent frequency	Reference
Western Oregon (n=67)	Chironomidae	38.4	62.7	Whitaker et al. 1977
	Unidentified Diptera	10.4	28.4	
	Tipulidae	2.4	7.5	
	Culicidae	0.4	1.5	
	Dipterous larvae	0.1	1.5	
	Insect internal organs	10.6	11.9	
	Isoptera	8.9	13.4	
	Trichoptera	8.4	10.4	
	Unidentified insects	6.3	26.9	
	Unidentified Lepidoptera	3.7	10.4	
	Lepidopterous larvae	1.4	1.5	
	Formicidae	2.3	6.0	
	Unidentified Hymenoptera	0.4	1.5	
	Scarabidae	1.5	1.5	
	Unidentified Coleoptera	0.4	3.0	
	Unidentified Hemiptera	1.5	3.0	
	Cercopidae	1.0	1.5	
	Cicadellidae	0.4	3.0	
	Unidentified Homoptera	0.4	1.5	
	Tettigonidae	0.5	1.5	
Gryllidae	0.1	1.5		
Hemeroibiidae	0.4	1.5		
Nova Scotia adults (n=28)	Coleoptera	7.7		Belwood and Fenton 1976
	Trichoptera	34.6		
	Chironomidae	58.8		
	Other insects	3.8		
Nova Scotia subadults (n=27)	Coleoptera	9.4		Belwood and Fenton 1976
	Trichoptera	26.6		
	Lepidoptera	15.9		
	Neuroptera	11.6		
	Chironomidae	19.5		
	Other Diptera	7.7		
Other insects	9.2			
Watertown, New York; adults (n=12)	Coleoptera	1.2		Belwood and Fenton 1976
	Trichoptera	18.2		
	Lepidoptera	4.2		
	Chironomidae	76.4		
Watertown, New York; subadults (n=12)	Coleoptera	6.6		Belwood and Fenton 1976
	Trichoptera	29.6		
	Lepidoptera	19.9		
	Neuroptera	3.5		
	Chironomidae	35.5		
	Other insects	4.9		
Western Maryland (n=33)	Coleoptera		63.6	Griffith and Gates 1985
	Diptera		54.5	
	Hemiptera		3.0	
	Homoptera		36.4	
	Hymenoptera		39.4	
	Lepidoptera		60.6	
	Neuroptera		24.2	
	Psocoptera		15.2	
Trichoptera		15.2		

Table 11. (continued)

Location	Prey Taxon	Percent volume	Percent frequency	Reference
New Hampshire (n=62) (Paper provides additional breakdown by sex, date, and age)	Chironomidae		85.5	Anthony and Kunz 1977
	Lepidoptera		85.5	
	Culicidae		77.4	
	Tipulidae		67.7	
	Coleoptera		59.7	
	Mycetophilidae		54.8	
	Ephemeroptera		51.6	
	Hymenoptera		33.9	
	Trichoptera		32.3	
	Neuroptera		19.4	
Indiana (n=16)	Unidentified Lepidoptera	21.6	31.3	Whitaker 1972
	Unidentified Trichoptera	13.1	25.0	
	Unidentified Diptera	11.9	31.3	
	Cicadellidae	11.6	43.8	
	Delphacidae	8.8	25.0	
	Coleopterous larvae	6.3	6.3	
	Ichneumonidae	3.8	12.5	
	Carabidae	3.4	18.8	
	Reduviidae	2.8	12.5	
	Scarabidae	2.5	6.3	
	Unidentified Coleoptera	2.2	18.8	
	Tipulidae	1.9	12.5	
	Hemeroptera	1.9	6.3	
	Chironomidae	1.6	12.5	
	Cerambycidae	1.6	6.3	
	Formicidae	1.3	12.5	
	Chrysomelidae	0.9	6.3	
	Chrysomelidae, <i>Diabrotica sp.</i>	0.9	6.3	
	Nitidulidae	0.9	6.3	
	Miridae	0.6	6.3	
Gryllidae	0.3	6.3		
Unidentified insects	0.3	6.3		

Food Consumption Rate

Little brown bats maintained in captivity (at 92°F) and fed mealworms consumed 1 to 4 g food/d, with the greatest consumption observed for pregnant and lactating females (Stones and Wiebers 1965). Food consumption was also greater in summer as opposed to winter. Coutts et al. (1973) observed an average food consumption rate of 0.15 g/g/d for three males and six postlactating females. Feeding rates for bats in the field are likely to be higher. For example, Gould (1955) reports food consumption rates for four "more successful" bats to be 7.7 ± 2.6 g/g/h (mean \pm STD). If 3.5 h/d are spent foraging (Anthony and Kunz 1977), this would translate to a daily consumption rate of 1.12 ± 0.37 g/g/d. This is consistent with Barclay et al. (1991) who suggest that bats may consume their body weight in food per night to meet metabolic needs. Anthony and Kunz (1977) reported daily food consumption rates in New Hampshire to be 2.4 ± 1.1 g/d (mean \pm STD), 3.7 ± 0.5 g/d, and 1.8 ± 0.5 g/d, for pregnant, lactating, and juvenile little brown bats, respectively. Assuming body weights reported in Table 10, these observations translate to 0.23 ± 0.11 g/g/d, 0.48 ± 0.06 g/g/d, and 0.29 ± 0.07 g/g/d.

Water Consumption Rate

A single little brown bat maintained in the laboratory was observed to consume 0.86 mL of water per day (O'Farrell et al. 1971). The average weight of this individual over the course of the study was 7.89 g. Therefore the daily water consumption was 0.11 L/kg/d. In another laboratory study, average water consumption

of male and female little brown bats maintained in the laboratory was observed to be 0.18 L/kg/d (Coutts et al. 1973). Kurta et al. (1989) estimated the drinking water consumption rate of free-ranging pregnant and lactating bats to be 0.177 L/kg/d and 0.205 L/kg/d, respectively. These observations are comparable to water ingestion estimated using Eq. 21. Assuming a body weight of 7.5 g, water ingestion by little brown bats is estimated to average 0.16 L/kg BW/d. (Note: If other body weight values are used, the water ingestion rate should be recalculated.)

Soil Ingestion Rate

No published data were found concerning soil ingestion by little brown bats. As an aerial insectivore, however, soil ingestion is assumed to be negligible.

Respiration Rate

No literature data were found describing inhalation by little brown bats. Using Eq. 23 and assuming a body weight of 7.5 g, the average inhalation rate of little brown bats is estimated to be 1.45 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

Energy utilization by little brown bats is highly efficient. Of 4.15±0.67 kcal/d ingested, only 0.37±0.1 kcal/d was excreted, representing an energy utilization of 91.2±1.5% (O'Farrell et al. 1971). Metabolic rates for little brown bats have been reported to range from 1.47 mL O₂/g BW/h (O'Farrell and Studier 1970) to 2.89±0.89 mL O₂/g BW/h (Altman and Dittmer 1974). Little brown bats enter hibernation September-May in northern portions of their range and November-March in southern areas (Fenton and Barclay 1980).

Habitat Requirements

Little brown bats use three distinct types of roosts: day, night, and hibernation. Day and night roosts are used by active bats in spring, summer, and fall, while hibernation roosts (hibernacula) are used during winter (Fenton and Barclay 1980). Day roosts generally consist of dark or dimly lit locations (buildings, hollow trees, under bark, occasionally in caves) with the appropriate humidity and temperature to mitigate daytime water loss (Fenton and Barclay 1980). Night roosts are occupied after the initial feeding bout of the evening. They may be located in the same building as day roosts but in different locations. Night roosts are generally confined spaces into which the bats pack themselves, possibly for improved thermoregulation (Fenton and Barclay 1980). Hibernacula generally consist of caves or abandoned mines and are used throughout the bat's range. (Harvey et al. 1991) High humidity (>90%) and temperatures above freezing characterize most hibernacula (Fenton and Barclay 1980).

Little brown bats forage primarily in open habitat, frequently over bodies of water (Fenton and Bell 1979; Barclay 1991; Saunders and Barclay 1992). Areas with dense vegetation or other obstructions to flight are avoided (Barclay 1991; Saunders and Barclay 1992). In Missouri, foraging along forest edges has been observed (LaVal et al. 1977).

Home Range

Although no information was found in the literature concerning the home range of little brown bats, the gray bat, a congeneric species, may travel as far as 12 km from roost caves to foraging sites (LaVal et al. 1977).

Population Density

No data were found documenting population density values. Populations may be limited by the availability of roost sites but not by food (Fenton and Barclay 1980). In summer, females form maternity colonies

of hundreds to thousands of individuals (Harvey 1992). Location of males in summer is not well known; it is suspected that they are solitary and scattered in a variety of roost types (Harvey 1992).

Population Dynamics/Survival

Population age structures and survival rates for little brown bats are poorly defined (Fenton and Barclay 1980). While individuals up to 30 years old have been reported (Keen and Hitchcock 1980) and 10-year-old bats are not uncommon, longevity is generally 1.5 years for males and 1.17 to 2.15 years for females (Fenton and Barclay 1980). Annual survival rates in Ontario were estimated to be 0.816 and 0.708 for males and females, respectively (Keen and Hitchcock 1980). Cockrum (1956) presents additional data on longevity.

Reproduction and Breeding

Fertilization occurs in spring, after females leave hibernation. The gestation period is 50-60 days. Only one young is produced per year (Fenton and Barclay 1980). Growth is rapid; young bats can thermoregulate by day 9.5 and are flying in three weeks. Buchler (1980) observed first flights of juveniles at 19-20 days of age. A detailed study of reproduction, growth, and development was performed by O'Farrell and Studier (1973).

Behavior

In New Hampshire, Anthony and Kunz (1977) observed bimodal foraging activity; the first feeding period was before midnight (2200-2400 h) while the second was before dawn (0330-0500 h). In contrast, Saunders and Barclay (1992) found activity was greatest within one hour of sunset.

3.3.2 Great Basin Pocket Mouse (*Perognathus parvus*)

Pocket mice are in the order Rodentia, family Heteromyidae. Pocket mice are the smallest members of this family that includes kangaroo mice and kangaroo rats. A key characteristic of the family is fur-lined cheek pouches (Burt and Grossenheider 1976). Members of this family are all adapted to arid conditions, many, including pocket mice, do not require drinking water (Vaughan 1978; Burt and Grossenheider 1976). *P. parvus* is a semifossorial granivorous species of arid or semiarid habitats (Verts and Kirkland 1988).

Distribution

Pocket mice (*Perognathus spp.*) are found only in western North America, west of the Mississippi river. *P. parvus* occurs throughout the Great Basin region, from southern British Columbia to northern Arizona (Burt and Grossenheider 1976; Verts and Kirkland 1988).

Body Size and Weight

Pocket mice are approximately the size of the house mouse (*Mus musculus*) with longer tails and smaller ears (Scheffer 1938). Males are slightly larger than females; total lengths of males and females from Utah were 174 and 172 mm, respectively (Verts and Kirkland 1988). Tail length is 110 to 120% of body length. Body weights for male and female pocket mice from several locations are presented in Table 12. O'Farrell (1975a) observed that body weights of males increase with increasing elevation.

Table 12. Body weights (g) for the Great Basin pocket mouse, *Perognathus parvus*

Location	Sex	N	Mean	Minimum	Maximum	Reference
Washington	Male	10	17.25			Scheffer 1938
	Female	10	14.3			

Table 12. (continued)

Location	Sex	N	Mean	Minimum	Maximum	Reference
Nevada	Male	10	25.4	21.5	31.0	Verts and Kirkland 1988
	Female	10	20.5	16.5	28.5	
Washington	Male: 500 ft	18	17.4±0.3 ^a			O'Farrell et al. 1975
	Male: 1500 ft	12	18.3±0.3 ^a			
	Male: 2500 ft	11	17.6±0.4 ^a			
	Male: 3500 ft	12	19.1±0.5 ^a			
Washington	Male	12	17.66±1.32 ^b	15.52	19.62	Schreiber 1978
	Female	12	15.82±1.34 ^b	13.16	17.47	

^a mean±standard error.

^b mean±standard deviation.

Food Habits and Diet Composition

Although the diet of *Perognathus parvus* consists primarily of seeds (Scheffer 1938; Martin et al. 1951; Kritzman 1974), insects may be consumed in spring, before seeds become available (Kritzman 1974; O'Farrell et al. 1975). When grass seeds were ripe, they represented 88% of the seeds in cheek pouches of mice in eastern Washington (Kritzman 1974). Food preferences of pocket mice from several locations are listed in Table 13.

Table 13. Diet composition of pocket mice

Location	Foods consumed (%)	Comments	Reference
California	Poison ivy (10-25) Filaree (10-25) Deervetch (10-25) Ryegrass (2-5) Oats (2-5) Nightshade (2-5) Bitterbrush (2-5) Saltbrush, knotweed (1/2-2)	Data are for pocket mice in general. Scientific names not reported. Values in parentheses refer to percentage use as reported by the authors. Data from spring, fall, and winter only.	Martin et al. 1951
Western Prairies and Mt-Deserts	Mesquite (10-25) Locoweed (5-10) Creosote (5-10) Beeplant (5-10) Pigweed (5-10) Cedar (5-10) Fescuegrass (2-5) Saltbush (2-5) Pricklypear (2-5) Bromegrass (2-5) Morning-glory (2-5) Bristlegrass (2-5) Sunflower (2-5) Plantain (2-5) Deervetch (2-5) Barley (2-5) Russianthistle (2-5) Nightshade, knotweed, sagebrush (1/2-2)	Data are for pocket mice in general. Values in parentheses refer to percentage use as reported by the authors. Data from throughout year.	Martin et al. 1951

Table 13. (continued)

Location	Foods consumed (%)	Comments	Reference
Eastern Washington	<i>Amsinckia</i> seeds (2.5) <i>Cryptantha</i> seeds (0.5) <i>Salsola</i> seeds (6.3) <i>Aster</i> seeds (0.4) <i>Franseria</i> seeds (0.1) <i>Descurania</i> pods (3.3) <i>Agropyron</i> seeds (5.5) <i>Bromus</i> seeds (45.6) <i>Festuca</i> seeds (20.0) <i>Gilia</i> seeds (0.8) <i>Microsteris</i> (11.5) Root nodules (0.3) Stem and leaf pieces (2.9) Insect larvae (0.2)	Contents of cheek pouches from 52 <i>P. parvus</i> collected May-October 1969. Data presented as frequency of occurrence over all samples.	Kritzman 1974

Food Consumption Rate

Schreiber (1978) estimates the daily energy requirements for male and female *P. parvus* in Washington in winter to be 2.36 and 2.63 kcal, respectively. In contrast, energy requirements in spring are 6.96 and 6.55 kcal for adult males and females, respectively. Based on estimated daily maintenance energy requirements and caloric content of cheatgrass seeds, Schreiber (1978) estimated the daily food consumption rate. Mean (\pm STD) ingestion for 8 individuals (4 male, 4 female) was 0.076 ± 0.023 g/g/d. Females consumed somewhat more food/g than males (females: 0.079 ± 0.026 g/g/d; males: 0.073 ± 0.020 g/g/d).

Water Consumption Rate

Pocket mice generally do not require water other than that contained in their food (Scheffer 1938, Kritzman 1974, Vert and Kirkland 1988). Schmidt-Nielson et al. (1948) studied water conservation in desert rodents, including *Perognathus baileyi*. Mice survived well and gained weight when maintained for up to six weeks on a dry diet with no drinking water. In contrast, white rats and woodrats (*Neotoma*) maintained under similar conditions lost weight and had all died by 21 and 9 days, respectively (Schmidt-Nielson et al. 1948). Water balance is maintained by excreting concentrated urine, obtaining water from food and water generated through metabolism (Vert and Kirkland 1988); consequently drinking water is not required.

Soil Ingestion Rate

Data concerning soil ingestion by *P. parvus* was not located in the literature. Beyer et al. (1994) report soil ingestion by burrowing rodents (woodchucks and prairie dogs) to range from <2 to 7.7% of their diet. As a burrowing rodent, soil ingestion by *P. parvus* is likely to be comparable to these values.

Respiration Rate

No literature data were found describing inhalation by *P. parvus*. Using Eq. 23 and assuming a body weight of 18 g for males and 16 g for females (Table 12), the average inhalation rate is estimated to be 1.22 m³/kg BW/d for males and 1.25 m³/kg BW/d for females. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

The bioenergetics of *P. parvus* was studied by Schreiber (1978). Annual energy intakes for males and females was estimated to be 2550 kcal/y and 2462 kcal/y, respectively. Summer torpor reduces energy

demand by 3%. In winter, the reduction was 40-43% lower than summer, because of more extensive torpor. Metabolic rates for active, resting, nesting, and torpid *P. parvus* are related to ambient temperature and may be estimated as follows:

$$M_{\text{active}} = 11.5 - 0.24T_a, \quad (48)$$

$$M_{\text{resting}} = 8.6 - 0.24T_a, \quad (49)$$

$$M_{\text{nest}} = 7.0 - 0.165T_a, \quad (50)$$

and

$$M_{\text{torpor}} = 0.38 + 0.014T_a, \quad (51)$$

where

M_{active} = metabolic rate for active individuals (mL O₂/g/h),

M_{resting} = metabolic rate for resting individuals (mL O₂/g/h),

M_{nest} = metabolic rate for individuals in nests (mL O₂/g/h),

M_{torpor} = metabolic rate for torpid individuals (mL O₂/g/h),

T_a = ambient temperature (°C).

Schreiber (1978) also presents models for estimating annual energy expenditure.

Habitat Requirements

P. parvus prefers arid to semiarid environments that are predominantly sandy and dominated by sagebrush (Verts and Kirkland 1988). O'Farrell (1975b) describes the habitat requirements in Washington to be shrub-steppe with light-textured soils. Abundance of *P. parvus* is greater at sites with abundant seed-producing annuals and lower in perennial grasslands or locations where springtime soil temperatures <40°F are extensive (O'Farrell 1975a). While *P. parvus* were captured at all elevations on the Hanford Reservation from 500-3500 ft., 37% of all individuals were collected at lower elevations (e.g., 500 ft.; O'Farrell 1975a).

Home Range

The home range of male *P. parvus* in Washington ranged from 0.156 to 0.4 ha, while those for females ranged from 0.05 to 0.23 ha (O'Farrell et al. 1975). Home range size is inversely related to population density. In southern British Columbia, home ranges range from 0.066 to 0.09 ha (Schreiber 1978). In related species, Blair (1953) reports home ranges of male and female *P. merriami* to be 1.88 and 5.87 acres (0.76 and 2.4 ha), respectively. Average home ranges of male *P. penicillatus* in New Mexico were 2.72±0.48 acres (1.1±0.2 ha), with a maximum of 5.54 acres (2.24 ha). In contrast, average home range of females was 1.09±0.14 acres (0.44±0.06 ha), with a maximum of 1.43 acres (0.58 ha; Blair 1953).

Population Density

Average peak autumn population density in Washington was 118.5 individuals/ha, but ranged from a high of 162 to a low of 76.3 (O'Farrell et al. 1975). Annual average population densities of 28.5/ha (peak of 42/ha) and 82.3/ha have been reported for southeast Washington and the Yakima Valley, respectively (Verts and Kirkland 1988). Schreiber (1978) suggests that at high densities, *P. parvus* may become food stressed. He estimates the maximum sustainable density to be 39-83 individuals/ha.

Population Dynamics/Survival

One, two, and three-year survival rates of *P. parvus* in Washington are reported to be 56-80%, 17-19%, and 2-3%, respectively (O'Farrell et al. 1975). The highest winter survival was observed among juveniles born when precipitation, food supply, and reproduction was lowest. Summer population size was

highly correlated to October-April precipitation (O'Farrell et al. 1975). This rainfall stimulates growth and reproduction in vegetation and consequently affects small mammal numbers.

Reproduction and Breeding

Under favorable conditions, *P. parvus* generally have two litters per female per year; only one during poor years (Kritzman 1974). Duration of the breeding season varies from four months (April-July) to six months (March-August depending on elevation (i.e., shorter at higher elevations; O'Farrell 1975). Scheffer (1938) suggests that the gestation period is 21 to 28 days. Litter sizes average approximately five (Scheffer 1938; Duke 1957) and may range from two to eight (Scheffer 1938, Speth et al. 1968). Males become sexually active in spring (before May) and remain active through August (Speth et al. 1968). O'Farrell et al. (1975) observed the first signs of estrus in females in April, first pregnancies in May, and last pregnancies in August.

Behavior

P. parvus is semifossorial, spending a considerable amount of time underground. Burrows, approximately 25 mm in diameter, ending in a ball-shaped chamber, are constructed 13-30 cm below the soil surface (Scheffer 1938). Burrows may extend as deep as 1 m (Verts and Kirkland 1988). While *P. parvus* is generally nocturnal or crepuscular, individuals may be active during the day (Scheffer 1938). Activity is suppressed by inclement weather.

Social Organization

P. parvus is not considered social, individuals occupy separate nests in the wild (Scheffer 1938, Verts and Kirkland 1988). Conspecifics housed together will fight initially but later tolerate each other (Scheffer 1938). In contrast, *P. parvus* attacks other rodent species it may be housed with (Verts and Kirkland 1988).

3.3.3 Pine Vole (*Microtus pinetorum*)

Pine voles are in the order Rodentia, family Cricetidae. Related species include the meadow vole (*M. pennsylvanicus*) and prairie vole (*M. ochrogaster*). The pine vole is a semifossorial herbivore of wooded habitats (Burt and Grossenheider 1976).

Distribution

The pine vole occurs throughout much of the eastern United States. Its range extends from the Atlantic coast to eastern Texas, north to Wisconsin, southern Ontario, and southern New England (Burt and Grossenheider 1976; Smolen 1981; Johnson and Johnson 1982).

Body Size and Weight

The body form of the meadow vole is cylindrical and slender with reduced eyes, ears, and tail, consistent with a semifossorial lifestyle (Smolen 1981). The body length of adults averages approximately 120 mm (Smolen 1981). Female pine voles are generally slightly larger than males (Table 14; Smolen 1981). Body weights of pine voles from several locations are listed in Table 14.

Table 14. Body weights (g) for the pine vole, *Microtus pinetorum*

Location	Sex	N	Mean	Range	Reference
Virginia	Male	11	25.4±1.5	23.4-28.2	Cengel et al. 1978 ^a
	Female: nonpregnant	11	24.8±1.8	21.6-27.9	
New York and New Jersey	Adults: sex not differentiated	25	25.6	22-37	Benton 1955
Vermont	Adults: sex not differentiated	4	26.1	20.6-30.3	Miller 1964
Connecticut	Adults	18	23.9	20.5-29.0	Miller and Getz 1969
	Sub-adults	10	19.0	16.0-21.0	
	Juveniles	4	13.5	12.0-14.5	
Louisiana	Adults	2	25.6	25.2-26.0	Lowery 1974
Indiana	Female		27.2	22.7-33.8	Silva and Downing 1995
	Male		25.5	23.3-29.5	
Georgia	Male	17	24.2	14.5-28.6	Smolen 1981
	Female	6	27.4	23.1-30.8	

^aValues represent mean and range of means from 11 separate observations

Food Habits and Diet Composition

Pine voles are primarily herbivores; however, snails (Martin et al. 1951) or beetles (Benton 1955) may be consumed. Hamilton (1938) reports that pine voles feed largely on succulent roots and tubers. In New York and New Jersey, the diet of pine voles consists of bulbs, tubers, roots, seeds, fruit, bark, and leaves (Benton 1955). Diet varies by season: grass roots and stems are eaten in summer, fruit and seeds in fall, and bark, roots, and stored foods in winter (Benton 1955). Pine voles may be a serious pest in orchards, eating the bark and roots of fruit trees (Johnson and Johnson 1982, Swihart 1990). Lists of species of plants consumed are presented in Smolen (1981) and Martin et al. (1951). A summary of food habitats of pine voles in North Carolina and Virginia is presented in Table 15.

Table 15. Diet composition of pine voles

Location	Date	Food type	Percent volume	Percent frequency	Comments	Reference
North Carolina (n=11)		<i>Endogone</i> (fungus)	0.4	54.5		Linzey and Linzey 1973
		Unidentified vegetation	78.5	100		
		Fruit	0.2	9.1		
		Unidentified seeds	20.6	36.4		
		Hair	T	36.4		
		Pebbles	0.3	36.4		

Table 15. (continued)

Location	Date	Food type	Percent volume	Percent frequency	Comments	Reference
Virginia (n=5/date and location)	July -M	Grass	20		Values extrapolated from histogram	Cengel et al. 1978
		Forb	78			
		Bulb	2			
	September-M	Grass	60			
		Forb	36			
		Root	2			
		Apple fruit	2			
	September-A	Grass	15			
		Forb	81			
		Root	2			
		Bulb	2			
	November-M	Grass	80			
		Forb	16			
		Root	2			
		Bulb	2			
	November-A	Grass	30			
		Forb	63			
		Root	2			
Bulb		5				
January-M	Grass	82				
	Forb	2				
	Root	9				
	Apple fruit	7				
January-A	Grass	4				
	Forb	88				
	Root	8				
March-M	Grass	85				
	Root	13				
	Bulb	2				
March-A	Grass	20				
	Forb	65				
	Root	15				
May-M	Grass	12				
	Forb	88				
May-A	Grass	4				
	Forb	96				

^aM=maintained orchard.

^bA=abandoned orchard.

Food Consumption Rate

In a study of the efficacy of feeding repellants on consumption of apple twigs by pine voles, mean consumption (in the absence of alternate foods) was 0.051 g/g/d (Swihart 1990). While no other data concerning feeding rates in pine voles were found, data are available for related species. Among meadow voles, food intake when exposed to 14-h days was 0.095±0.002 (mean±SE) g/g/d; intake by individuals exposed to 10-h days was 0.085±0.005 g/g/d (Dark et al. 1983). Mean food consumption by prairie voles

(assumed to weigh 35 g; Burt and Grossenheider 1976) was 0.088 g/g/d and 0.12 g/g/d when ambient temperatures were 21 ° and 28 °C, respectively (Dice 1922).

Water Consumption Rate

Odum (1944) reports the daily water consumption for a single male pine vole to be 0.3 L/kg/d. In prairie voles (*M. ochrogaster*), water consumption was 0.37 and 0.43 L/kg/d for two individuals (Chew 1951). In contrast, Dice (1922) reports mean water consumption for this same species to be 6.2±3.1 mL/individual/d. Assuming a body weight of 35 g (Burt and Grossenheider 1976), mean water consumption was 0.18±0.08 L/kg/d. Using Eq. 21 and assuming a body weight for pine voles of 25 g, water ingestion is estimated to average 0.14 L/kg BW/d. (Note: If other body weight values are used, the water ingestion rate should be recalculated.) Benton (1955) suggests that because of the high water content of their diet, pine voles may not require drinking water.

Soil Ingestion

Data concerning soil ingestion by pine voles was not located in the literature. Beyer et al. (1994), however, reports soil ingestion by meadow voles to be 2.4% of diet. Soil ingestion by pine voles is likely to be comparable or higher because of the greater fossorial nature of pine voles relative to meadow voles.

Respiration Rate

No literature data were found describing inhalation by pine voles. Using Eq. 23 and assuming a body weight of 25 g (Table 14), the average inhalation rate is estimated to be 1.14 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

No literature data were found concerning metabolism in the pine vole. In a related species, the montane vole (*M. montanus*), resting metabolism declined from 3.46±0.15 mL O₂/g/h at 20 °C to 2.05±0.07 mL O₂/g/h at 34 °C and then increased to 2.71±0.09 mL O₂/g/h at 38 °C (Tomasi 1985). In meadow voles, resting metabolism was 2.7 mL O₂/g/h (Altman and Dittmer 1974).

Habitat Requirements

Throughout their range, pine voles occur in a wide variety of habitats, ranging from closed-canopy beech-maple forests with extensive litter (Miller 1964) to grassy fields with brush (Smolen 1981). Pine voles are not restricted to pine forests, as suggested by their common name; in Louisiana, they are more frequently found in hardwood stands (Lowery 1974). Key habitat requirements consist of well-drained soil with thick ground cover of litter or vegetation (Smolen 1981).

Home Range

Pine voles are very sedentary, moving only short distances (Lowery 1974). Home ranges are generally defined by the extent of their burrow system (Smolen 1981). The home range of 17 individuals in an oak-hickory woodland averaged 34.7 m in diameter (range: 13.7-85 m; Benton 1955). In New York, the average home range of 13 individuals was 19.2 m in diameter (Benton 1955). In dry upland hardwood forest, average home ranges were 33.7 m (range: 10-148) and 32.7 m (10-73 m) for females and males, respectively (Miller and Getz 1969).

Population Density

Population density in a 3-ha, dry upland site ranged from 0 to 14.6 voles/ha (Miller and Getz 1969); density in an adjacent mixed conifer-hardwood swamp was <2 voles/ha. Densities are generally greater in

orchards than in natural forests. Density estimates for an orchard in New York ranged from 80 to 120 voles/ha (Hamilton 1938).

Population Dynamics/Survival

Pine vole populations are very local and highly variable (Benton 1955). Miller and Getz (1969) observed mean survival in a high-density upland population to be 2.6 months; maximum observed survival was 12 and 10 months for 2 males and 2 females, respectively. Average survival from one year to the next is reported to be 58% for adults and 57% for juveniles (Smolen 1981).

Reproduction/Breeding

Breeding occurs from January to October in the north portion of the range (Benton 1955) but may be year-round in the south (Lowery 1974). Miller and Getz (1969) estimate the breeding season in Connecticut to extend from mid-February through mid-November. Peak breeding occurs in March and April (Benton 1955). Females are aggressors during mating, which is brief, lasting only a few seconds (Benton 1955). Gestation is estimated to be 20 to 24 days. Hamilton (1938) provides a detailed description of the development of juvenile pine voles. Litter size generally ranges from two to four (Hamilton 1938, Benton 1955). Because female pine voles have only four mammae, large litters are unsuccessful (Smolen 1981). Although litter size is unaffected by day length, juvenile growth is greater under a short photoperiod (8L:16D; Derting and Cranford 1989). Female pine voles are mature in 10 to 12 weeks and are generally breeding by 15 weeks (Smolen 1981).

Behavior

Pine voles are semifossorial, spending considerable time in subsurface burrows and surface runways (Smolen 1981). Burrows are generally 3.8-5 cm in diam. beneath leaves and litter and are rarely 30 cm deep, generally 7.6 to 10 cm at most (Hamilton 1938). In areas with thick litter, surface runways may be constructed (Smolen 1981). Surface activity is not correlated with temperature or humidity (Miller and Getz 1969). Although mostly nocturnal or crepuscular, pine voles may occasionally be active during the day (Lowery 1974). Miller and Getz (1969) report that nocturnal and crepuscular activity was only slightly greater than daytime activity.

Social Organization

Captures of multiple individuals in the same trap suggest a degree of sociability in this species (Miller and Getz 1969). Pine voles are not territorial; multiple individuals may share the same burrow system (Smolen 1981).

3.3.4 Black-Tailed Jackrabbit (*Lepus californicus*)

Black-tailed jackrabbits (also known as California jackrabbits) are in the order Lagomorpha, family Leporidae. Jackrabbits are technically hares, with their young born fully haired, unlike rabbits (Dunn et al. 1982). Three other species of jackrabbit occur in North America: the white-tailed jackrabbit (*L. townsendii*), the antelope jackrabbit (*L. alleni*), and the white-sided jackrabbit (*L. callotis*).

Distribution

The black-tailed jackrabbit is found in the western United States. It ranges from Missouri in the east to the Pacific coast, from the prairies of South Dakota to Texas, and from Washington and Idaho to Mexico in the south (Dunn et al. 1982). It has also been successfully introduced into several eastern states and may be displacing its eastern cousin, the white-tailed jackrabbit (Dunn et al. 1982).

Body Size and Weight

On average, *L. californicus* is smaller than *L. townsendii*. Total body lengths range from 465-630 mm, the tail is 50-112 mm, and the hind foot is from 112-145 mm (Dunn et al. 1982). Representative body weights for black-tailed jackrabbits appear in Table 16. Newborn black-tailed jackrabbits have a total length of 168 mm, and weigh approximately 110 g (Dunn et al. 1982).

Table 16. Body weights (kg) for the black-tailed jackrabbit, *Lepus californicus*

Location	Sex	Mean	Range	Reference
Arkansas	Both	2.3	1.8-3.6	Silva and Downing 1995
Colorado	Both	2.54		Dunn et al. 1982
California	Male	2.47	2.11-2.8	Lechleitner 1959
	Female	2.78	2.3-3.3	
Utah	Male	2.03		Goodwin and Currie 1965
	Female	2.17		

Food Habits and Diet Composition

Jackrabbits are strict herbivores, eating a variety of plants depending on availability and geographic location (Dunn et al. 1982). Black-tailed jackrabbits prefer succulent vegetation when available, with grasses and forbs being important in the summer and shrubs becoming more important in the winter (Dunn et al. 1982). Grasses and sedges may also be important food items. Additional information on foraging habits of black-tailed jackrabbits in different locations are presented in Westoby (1980), Currie and Goodwin (1966), Clark and Innis (1982), Gross et al. (1974), and Dunn et al. (1982).

Food Consumption Rate

Arthur and Gates (1988) estimated a forage intake rate of 145 g (dry weight)/d for black-tailed jackrabbits in Idaho. In Utah, Currie and Goodwin (1966) observed fall, winter, and spring food ingestion rates of 97.3 g (dry weight)/d, 111.4 g/d, and 61.3, g/d, respectively. Assuming a body weight of 2.1 kg (Goodwin and Currie 1965) and a water content for dry grass of 10% (Table 4), daily food ingestion rates are equivalent to 0.076 g/g/d (Idaho), 0.051 g/g/d (fall, Utah), 0.059 g/g/d (winter, Utah), and 0.032 g/g/d (spring Utah).

Water Consumption Rate

Black-tailed jackrabbits are well-adapted to arid environments and are able to regulate water quite efficiently. They have the ability to elevate their body temperature during the day to avoid having to dissipate the heat and hence lose water (Hinds 1977). Black-tailed jackrabbits also can concentrate urine to reduce water loss (Dunn et al. 1982). These factors suggest that black-tailed jackrabbits consume very little water and get most of their moisture from food.

Soil Ingestion

Arthur and Gates (1988) measured a mean (range) ingestion rate of soil for black-tailed jackrabbits in Idaho to be 9.7 (9.0-10.6) g /individual/d, with seasonal peaks occurring in spring and fall. This amount was equivalent to 6.3% of the total dry matter intake for black-tailed jackrabbits. Assuming a body weight of 2.54 kg (Dunn et al. 1982), soil ingestion is estimated to be 0.0038 g/g/d.

Respiration Rate

No literature data were found describing inhalation by black-tailed jackrabbits. Using Eq. 23 and assuming a body weight of 2.54 g, the average inhalation rate is estimated to be $0.45 \text{ m}^3/\text{kg BW}/\text{d}$. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

At rest, the body temperature of adult jackrabbits is approximately 37° to 38°C (Dunn et al. 1982). Hinds (1977) discovered that body temperatures in laboratory jackrabbits do not differ significantly with season or on a diurnal basis. Hinds (1977) observed that the summer thermoneutral zone for black-tailed jackrabbits was 26° to 34°C , with an average basal metabolism of $0.562 \pm 0.15 \text{ mL O}_2/\text{g}/\text{h}$. The winter thermoneutral zone was lower (21° to 28°C), and the average basal metabolism was $0.579 \pm 0.004 \text{ mL O}_2/\text{g}/\text{h}$. Oxygen consumption at ambient temperatures both above and below thermoneutrality increased but at a quicker rate at lower temperatures.

In the summer, evaporative water loss averaged $0.135 \pm 0.009\%$ body mass/h, up to ambient temperatures of 26°C . At this temperature evaporative cooling commences, and water loss increases exponentially. In the winter, the entire range of physiological responses appears to be shifted to lower temperatures, so that water loss is higher in winter. Dry heat transfer and thermal conductance were also estimated by Hinds (1977). Both *L. californicus* and *L. alleni* survive in the desert by exploiting opportunities to minimize the heat load and water expenditure, but *L. alleni* seems to be better adapted to arid conditions. Strategies used by black-tailed jackrabbits to survive in the desert include increasing their body temperature during the day to store heat, concentrating their urine, excreting dry feces, and increasing blood flow to the ears to increase convective and radiative heat loss (Dunn et al. 1982).

Habitat Requirements

Although the black-tailed jackrabbit occupies many diverse habitats, it is primarily found in association with short grass areas in the arid regions of the western United States (Dunn et al. 1982). They inhabit desert shrub areas throughout their range but have also become well adapted to many agricultural situations in western states (Dunn et al. 1982).

Home Range

The home range size of the black-tailed jackrabbit is determined by the pattern of food, cover, and water in the surrounding area (Dunn et al. 1982). In California, Lechleitner (1958) reports that home ranges are usually less than 20.2 ha, with females having larger home ranges than males. In Idaho, home range sizes of less than 16.2 ha are reported (French et al. 1965).

Population Density

Population densities vary greatly by location. Density estimates for areas of the arid southwest range from 0.2/ha in Nevada (Hayden 1966), to 0.9/ha in Utah, and to 1.2/ha in Arizona (Dunn et al. 1982). In more temperate regions, densities ranged from 3.0/ha in California (Leichleitner 1958) to as high as 34.6/ha in agricultural areas in Kansas (Dunn et al. 1982). There also appear to be cycles in population densities, with peak densities occurring every 5 to 10 years, possibly because of density-dependent factors (French et al. 1965, Dunn et al. 1982).

Population Dynamics/Survival

Several extensive studies have been performed on the demographics of black-tailed jackrabbits (Lechleitner 1959; Gross et al. 1974). There is evidence that populations are density dependent (French et al.

1965). Other researchers have also noted the tendency for population levels to cycle. In California, Lechleitner (1959) reported a preimplantation mortality of 6.7% and postimplantation mortality of 6.2%. In Utah, Gross et al. (1974) estimated preimplantation and postimplantation mortality rates of 8.0 and 3.0%, respectively. Juvenile mortality rates in Utah ranged from 24 to 71% (mean=59%; Gross et al. 1974), similar to juvenile mortality rates estimated for other locations (Dunn et al. 1982). Adult mortality rates were measured in Utah over an 8-year period, yielding mean yearly mortality rates of 56-57% with a range from 9 to 87% (Gross et al. 1974).

Reproduction/Breeding

Anatomically, male and female black-tailed jackrabbits are similar to domestic rabbits (Dunn et al. 1982). The length of their breeding season is highly variable, depending on latitude and various environmental factors. Generally, the breeding season is shorter for areas located at higher latitudes with more severe winters (French et al. 1965). This can be as short as 128 days in northern Idaho (French et al. 1965) to over 240 days in California with breeding possible all year round (Lechleitner 1959). Gross et al. (1974) report the mean gestation period to be 40 days, ranging up to 47 days depending on the geographic location and the individual. The number of litters per year can also vary from two in colder climates to as many as seven in warmer climates, with the average annual production throughout the range being about 14 young per female (Dunn et al. 1982). The black-tailed jackrabbit is like other lagomorphs in that it is an induced ovulator with a relatively well-synchronized breeding season (Lechleitner 1959; Gross et al. 1974). The litter size varies from about five in its northern range to two in its southern range (Dunn et al. 1982). Males will reach breeding age in seven to eight months, but females generally will not breed until their second year (Lechleitner 1959; Bronson and Tiemeier 1958).

Behavior

Black-tailed jackrabbits are crepuscular, generally feeding in the early morning and evening hours and overnight (Dunn et al. 1982). They prefer to eat in areas that are inconspicuous but that allow them to detect danger from a moderate distance. They often feed in the open, using hollows or open depressions (Dunn et al. 1982). Coprophagy, which is common in many lagomorphs, has also been observed in the black-tailed jackrabbit (Lechleitner 1957).

3.3.5 Mule Deer (*Odocoileus hemionus*)

Mule deer are in the order Artiodactyla, family Cervidae. Mule deer are also referred to as black-tailed deer, but this designation usually applies to the Pacific Coast subspecies. There are about seven generally recognized subspecies (Mackie et al. 1982). Mule deer are medium-sized cervids and are strictly herbivorous.

Distribution

Mule deer/black-tailed deer are found over most of North America from the 100th meridian to the Pacific coast and from southern Alaska to central Mexico (Mackie et al. 1982; Anderson and Wallmo 1984).

Body Size and Weight

Mule deer are medium-sized members of the cervid family but may vary in both size and weight depending on the geographic location of a particular population. Generally, adult males weigh between 70-150 kg (Anderson and Wallmo 1984). The largest individuals occur in the Rocky Mountains, with males averaging 152.3 cm in length and females 142.4 cm. The average weight of males and females are 74.04 kg

to 58.99 kg, respectively (Mackie et al. 1982). West-coast black-tailed deer are smaller, with adult weights for males and females as low as 50 and 32 kg, respectively (Mackie et al. 1982).

Food Habits and Diet Composition

It is difficult to generalize the typical forage of mule deer; foods eaten vary dramatically in kind, quantity, and nutritional quality as well as in digestibility from one season to another, from one year to the next, and from place to place (Mackie et al. 1982). Mule deer may use many different plants at different times, some may be eaten only in certain seasons, and some parts of plants may be selected over others. In general, diets of mule deer consist mostly of browse, whereas the diets of elk, cattle, and wild horses consist mainly of sedges and grasses (Hansen and Clark 1977). Both rumen and fecal analysis have been used to describe deer diets, and both methods give similar results (Anthony and Smith 1974). Examples of food preferences of mule deer are presented in Table 17.

Food Consumption Rate

Allredge et al. (1974) determined food intake by mule deer in Colorado. Concentrations of ^{137}Cs in deer tissue and diets were used to develop an intake and a retention function. Average intake rates varied by season, age class, and sex (Table 18); mean intake rate was 21.9 g of air-dried forage/kg body weight/d. More specific information on mule deer forage intake rates can be found in Collins and Urness (1983) and Wickstrom et al. (1984).

Wallmo et al. (1977) used several factors including body weight, metabolic weight, activity metabolic rate, forage intake, gross energy, and dry matter digestibility to develop a model to evaluate the ability of ingested forage to supply the energy needs of mule deer. This model can be used to estimate the carrying capacity of seasonal ranges for mule deer populations (Wallmo et al. 1977).

Water Consumption Rate

Mule deer obtain much of their water through succulent forage or as dew on forage plants. This is sufficient to meet their metabolic needs during the spring, summer, and fall; in the winter snow is ingested (Mackie et al. 1982). Observations of mean water intake by penned mule deer range from 24-35 mL/kg/d in winter and 47-70 mL/kg/d in the summer (Anderson and Wallmo 1984). Water consumption by black-tailed deer ranges from 53 mL/kg/d in winter to 104 mL/kg/d in summer (Anderson and Wallmo 1984).

Soil Ingestion

Soil ingestion rates were calculated for mule deer in north central Colorado feeding in a grassland-shrub community (Arthur and Allredge 1979). The intake varied by season, with a year-round average of 16.1 g/individual/d (Table 19). The soil ingested ranged from 0.6 to 2.1% of the deers' diets (dry matter intake). Beyer et al. (1994) report soil ingestion by mule deer to be <2% of their diet.

Respiration Rate

No literature data were found describing inhalation by mule deer. Using Eq. 23 and assuming a body weight of 57.1 kg, the average inhalation rate is estimated to be 0.24 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Table 17. Diet composition of mule deer

Location	Habitat	Season	Percentage of diet						Other Reference
			Trees	Shrubs	Forbs	Grasses	Cactus	Fern	
New Mexico	SW pinyon-juniper		75		16	2.2			6.8 Boeker et al. 1972
Arizona	Sonoran desert	Spring	4.7	37.6	22.8	2.6	29.6		2.7 Short 1977
Arizona	Sonoran desert	Summer	24.1	38	22.4	0.4	14.1		1 Short 1977
Arizona	Sonoran desert	Fall	3.4	48	2.5 Tr.		44.5		1.6 Short 1977
Arizona	Sonoran desert	Winter	4.9	31.7	4.3	1	55.9		2.2 Short 1977
Colorado	Pinyon-juniper range	Winter	81.4		10.7	7.9			Bartmann et al. 1982
Colorado	Pinyon-juniper range	Winter	90.3		8.6	1.1			Bartmann et al. 1982
Colorado	Pinyon-juniper range	Winter		93.8	5.6				1.6 Bartmann et al. 1982
Colorado	Pinyon-juniper range	Winter		89.9	6.2				3.9 Bartmann et al. 1982
Colorado	Sagebrush-steppe range	Winter		62.9	31.2	5.7			0.2 Bartmann et al. 1982
Colorado	Sagebrush-steppe range	Winter		80.7	7.2	12.1			Bartmann et al. 1982
Colorado	Old-growth forest	Fall	52	3	39	3		1	2 Leslie et al. 1984
Washington	Old-growth forest	Winter	49	4	41	2		1	3 Leslie et al. 1984
Washington	Old-growth forest	Spring	61	5	8	4		19	3 Leslie et al. 1984
Washington	Old-growth forest	Summer	60	8	8	4		13	7 Leslie et al. 1984
Washington	Old-growth forest	Fall	3	26	29	7		30	5 Leslie et al. 1984
Washington	Old-growth forest	Winter	2	43	21	6		23	5 Leslie et al. 1984
Washington	Old-growth forest	Spring	25	8	50	6		3	8 Leslie et al. 1984
Utah	Clear-cut forest	Summer	5		92				3 Deschamp et al. 1979
Utah	Dry meadow	Summer	6		83	2			9 Deschamp et al. 1979
Utah	Wet meadow	Summer	4		93				3 Deschamp et al. 1979
Utah	Mature forest	Summer	20		62		18		Deschamp et al. 1979
Utah	Stagnated forest	Summer	20		65		15		Deschamp et al. 1979

Table 18. Forage intake rates (g dry forage/kg/d) for mule deer
(Allredge et al. 1974)

	Mean (\pm SE)
Summer	25.7 \pm 2.4
Winter	20.1 \pm 1.2
Male	22.4 \pm 1.8
Female	21.5 \pm 1.4
Subadults	31.8 \pm 2.3
Adults	18.2 \pm 0.9
Mean for all groups	21.9 \pm 1.1

Table 19. Soil ingestion rates (g/d) by mule deer
(Arthur and Allredge 1979)

	Mean (\pm SE)
Spring	29.6 \pm 20.1
Summer	7.7 \pm 10.2
Fall	8.8 \pm 6.5
Winter	18.3 \pm 10.8

Metabolism

The mean core body temperatures of captive mule deer and black-tailed deer have been calculated. The mean (range) for a yearling male *O.h. hemionus* is 37.1°C (36.3 to 42.1; Thorne 1975). For two male black-tail fawns the temperature was 38.9°C (38.4 to 39.8), and for two adult females the mean temperature was 38.3°C (37.8 to 39.3) (Cowan and Wood 1955b). Mule deer have a preferred ambient temperature range from about -9° to 7°C, but they can tolerate climates with average temperatures between -15° and 30°C, with extremes from -60° to 50°C (Mackie et al. 1982).

Mule deer are homiothermal and lack sweat glands. Thermoregulation from evaporation is difficult; therefore, alternative strategies are used to regulate body temperature (Mackie et al. 1982). Heat production, thermoregulation, and environmental stressors in mule deer are discussed by Nordan et al. (1970), Parker and Robbins (1984), and Parker (1988). Mautz and Fair (1980) observed a linear relationship between heart rate and energy expenditure

$$\text{kcal/kg}^{0.75}/\text{min} = 0.00143(\text{heart rate}) - 0.0186. \quad (52)$$

Although using heart rates as a predictor of energy expenditure for mule deer of similar sizes seems feasible, fluctuations by time of day and ambient temperature may limit the precision of these estimates (Freddy 1984). The average maintenance energy requirement of fawns in winter was 158 kcal ME/kg^{0.75}/d, where

ME = metabolizable energy (Baker et al. 1979). This is the caloric intake needed to maintain body weight equilibrium and includes the unquantified inherent cost of activity and thermoregulation (Baker et al. 1979). Kautz et al. (1982) estimated this value to be between 134 and 204 kcal/kg^{0.75}/d for mule deer fawns. Several studies have been done on the energy costs for different mule deer activities (Kautz et al. 1982; Parker et al. 1984). The costs of bedding, standing, walking, and trotting in kcal/kg^{0.75}/d are 112, 164, 326, and 1,293, respectively (Kautz et al. 1982).

Habitat Requirements

Mule deer are found in all major climatic and vegetational zones of western North America. Generally, mule deer frequent semiarid, open forest, brush, and shrub lands associated with steep, broken, or otherwise rough terrain (Mackie et al. 1982). They are the most populous in mountain foothill habitats but can be found in prairie and semiarid desert habitats as well.

Home Range

Mule deer usually confine themselves to small individual home ranges, with extreme movements occurring only during migration (Mackie et al. 1982). More extreme movements may also occur as a result of severe environmental conditions. The mean annual home range size is 58.8 ha for black-tailed deer and 285.3 ha for mule deer (Anderson and Wallmo 1984). Dasmann and Taber (1956) determined the average home range to be between 640 and 1280 m in diameter for adult does and between 822 and 1280 m for adult bucks. Robinette (1966) observed similar home range sizes in Utah.

Population Density

Population densities vary by habitat type from 0.005 to 0.02 individuals/ha in open prairies and plains, to 0.015-0.045 individuals/ha in broken prairies, and to 0.04-0.07 individuals/ha in mountain regions (Mackie et al. 1982). Winter densities of deer can get much higher with values from 0.3 to 0.5 individuals/ha (Mackie et al. 1982; Anderson and Wallmo 1984; Dasmann and Taber 1956). Populations may also fluctuate from year to year, increasing or decreasing the overall densities.

Population Dynamics/Survival

The abundance of mule deer is determined both by the number of deer that can be supported by a unit of area and the amount of habitat available (Mackie et al. 1982). Local populations may be influenced by many different extrinsic factors, the most important of which are habitat and nutritional limitations. Other limiting factors include weather, diseases, parasites, predation, competition, other wild and domestic ungulates, and hunting (Mackie et al. 1982). Some papers on specific mortality rates of mule deer in Colorado, Utah and Washington are White and Bartmann (1983), Robinette et al. (1957), and Taber and Dasmann (1954).

Mortality of fetuses in mule deer has been estimated at between 3.5 and 10.5%, with postnatal mortality of 22-53% for males and 17-25% for females (Anderson and Wallmo 1984). Average longevity has not been determined, but some wild deer have been observed living to age 20 (Robinette et al. 1957).

Reproduction/Breeding

Mule deer are polygamous, with males wandering and seeking does in estrus. Males are highly aggressive during rut and are antagonistic toward others (Mackie et al. 1982). Females generally do not breed until their second year, with peak breeding occurring between November and December. Gestation usually lasts from 200 to 208 days with the peak births occurring in late June (Anderson and Wallmo 1984). Does usually have one or two fetuses with triplets occurring only about 1.4% of the time. Weaning generally occurs from about week 5 to week 16. The length of the estrous cycle in mule deer was calculated to be between 23

and 29 days (Anderson and Wallmo 1984). Additional information on the fertility of mule deer can be found in Robinette et al. (1955).

Behavior and Social Organization

The degree of sociability in mule deer varies according to season, sex, population, and subspecies, with most being neither highly gregarious, nor strictly solitary (Mackie et al. 1982). Mule deer are most dispersed during the summer and most congregated during the winter, as suitable habitat decreases. There have been scattered reports of group territoriality (Mackie et al. 1982). Additional information on mule deer behavior can be found in Mackie et al. (1982), Kucera (1978), and Dasmann and Taber (1956).

3.3.6 Coyote (*Canis latrans*)

Coyotes are in the order Carnivora, family Canidae. Coyotes are closely related to jackals, having 19 recognized subspecies (Bekoff 1982). Coyotes tend to hunt prey alone or in pairs and are primarily carnivorous. They eat mostly small mammals but also birds, reptiles, insects, fruits, seeds, berries, and nuts (Bekoff 1982).

Distribution

Coyotes are nearctic canids, occupying many diverse habitats, including grasslands, deserts and mountains, between about 10° north latitude and 70° north latitude (Bekoff 1982). They are found throughout the continental United States and much of Canada; some use urban habitats. Coyotes have been extending their range in the past 40 years, possibly because of the extermination of the gray wolf and the destruction of wolf habitat (Thurber and Peterson 1991).

Body Size and Weight

Coyotes range in length from about 1 to 1.5 m, with a tail about 400 mm long (Bekoff 1982). Size and weight vary across different geographic locations and with different subspecies, although adult males tend to be slightly heavier and larger than adult females. The variation in body weights of male and female coyotes from different locations across North America are shown in Table 20. The birth weight of coyotes is about 240-275 g, with the body from head to tail measuring 160 mm (Bekoff 1982).

Table 20. Body weights (kg) for the coyote, *Canis latrans*

Location	Sex	N	Mean±SE	Range	Reference
Iowa	Male		13.4		Bekoff 1982
	Female		11.4		
Minnesota	Male			12-13	Bekoff 1982
	Female			11-12	
	Juvenile male			10-11	
	Juvenile female		10		
California	Male	28	11.2	8.2-12.5	Hawthorne 1971
	Female	26	9.8	7.7-12.0	
Maine	Male	28	15.8±1.24		Richens and Hugie 1974
	Female	20	13.7±1.24		
Kansas	Male		13.1		Bekoff 1982
	Female		11.0		

Table 20. (continued)

Location	Sex	N	Mean±SE	Range	Reference
Ontario	Both: 1959-1960	124	14.6±0.17		Schmitz and Lavigne 1987
	Both: 1983-1984	44	15.5±0.37		
Alaska	Male	26	12.9±0.2		Thurber and Peterson 1991
	Female	28	11.1±0.2		
Arizona	Both	18	10±0.04		Golightly and Ohmart 1983
Oklahoma	Male	7	13.9	12-15.3	Halloran and Glass 1959
Connecticut and Massachusetts	Male			11.7-15.9	Pringle 1960
	Female			11.2-12.3	

Food Habits and Diet Composition

Coyotes are opportunistic foragers (Toweill and Anthony 1988; Todd et al. 1981), consuming a wide variety of foods (Bowen 1981). Coyotes have also been shown to follow a strategy of optimal foraging (MacCracken and Hansen 1987). Coyotes are primarily carnivorous, feeding principally on birds and mammals, but also relying on insects and fruits (Fitcher et al. 1955). Selected information on diet preferences of coyotes is presented in Table 21. The evidence from the studies on stomach and scat contents of coyotes indicates that there is a seasonal shift in food habits (Korschgen 1957; Hawthorne 1972; Bowen 1981; MacCracken and Uresk 1984; Smith 1990). Only a small percentage of a coyote's diet is livestock; actual predation on livestock is rare (Bekoff 1982; Wells and Bekoff 1982).

Table 21. Diet composition of coyotes as determined by stomach content analysis

Location	Percentage volume						Reference
	Mammals	Birds	Insects	Plants	Carrion	Misc.	
12 Western states	64 (29% lagomorphs, 17% rodents, 14% livestock, 2% deer, 2% skunk and badger)	3	1	3	29		Sperry 1933
10 Western states	60 (34% lagomorphs, 15% rodents, 8% livestock, 3% deer)	3		1	36		Sperry 1934
Nebraska	78 (54% lagomorph, 12.5% livestock, 6.9% mice, 4.6% other)	17.7	0.9	1.6		1.8	Fichter et al. 1955

Table 21. (continued)

Location	Percentage volume						Reference
	Mammals	Birds	Insects	Plants	Carrion	Misc.	
Missouri (spring)	77.1 (48.6% lagomorphs, 16.5% livestock, 5.4% mice and rats, 6.6% other)	17.7 (17% poultry)	tr.	0.2	5.0		Korschgen 1957
Missouri (summer)	65 (35.2% lagomorphs, 17.5% livestock, 5.6% mice and rats, 6.7% other)	28 (27.4% poultry)	1.9	0.8	4.3		Korschgen 1957
Missouri (fall)	72.2 (47.7% lagomorphs, 7.2% livestock, 9% mice and rats, 8.3% other)	13.2 (12.8% poultry)	3.5	6.5	4.3	0.3	Korschgen 1957
Missouri (winter)	82.7 (58.1% lagomorphs, 7.6% livestock, 9.5% mice and rats, 7.5% other)	9 (8.5% poultry)	tr.	0.9	6.6	0.8	Korschgen 1957

Food Consumption Rate

Fitch (1948) conducted a captive feeding study with one adult female coyote captured in the San Joaquin Experimental Range, California. Over a one-month period, the coyote consumed a daily average of 0.54 kg of food (body weight not reported). The author observed that the coyote would have eaten even more if given the opportunity and estimated the average food consumption under natural conditions to be about 1.5 lb/d (0.68 kg/d). Huegel and Rongstad (1985) observed food consumption rates of 10-12% of body mass/day among radio-tagged coyotes in northern Wisconsin in winter. Litvaitis and Mautz (1980) estimate the annual ingestion rates of deer, hares, and mice by a 12.9 kg eastern coyote to be 167 kg, 166 kg, and 134 kg, respectively. These values are equivalent to a daily consumption rate of 0.028 to 0.035 g/g/d. Golightly and Ohmart (1983) estimated the minimum energy requirements for desert coyote to be 260 J/g/d. Assuming a diet consisting of small mammals with a caloric density of 21.6 kJ/g (Golley 1961) and a water content of 68% (Table 4), this is equivalent to daily consumption rate of 0.018 g/g/d.

Water Consumption Rate

No literature data were found describing water ingestion by coyotes. Using Eq. 21 and assuming a body weight of 16.3 kg, water ingestion is estimated to average 0.075 L/kg BW/d. (Note: If other body weight values are used, the water ingestion rate should be recalculated.)

Soil Ingestion

No literature data were found concerning soil ingestion by coyotes. Beyer et al. (1994) report soil consumption by red fox to be 2.8% of daily food consumption. Values for coyote may be comparable.

Respiration Rate

No literature data were found describing inhalation by coyote. Using Eq. 23 and assuming a body weight of 16.3 kg, the average inhalation rate is estimated to be 0.31 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

Shield (1972) determined the O₂ consumption rates of several cold-acclimated Alaskan coyotes at a series of ambient temperatures; rates ranged from 7.1 mL O₂/kg/min at 20°C to 20.3 mL O₂/kg/min at -70°C. Golightly and Ohmart (1983) evaluated metabolism and body temperature of coyotes from a desert habitat in Arizona. They observed that minimum O₂ consumption occurred between 22° and 26°C and that the basal metabolic rate (BMR) within this zone was 0.0015 W/g (Golightly and Ohmart 1983). Unlike the kit fox and other desert canids, the coyote did not exhibit any distinct daily rhythms of oxygen consumption. This may be a reflection of the coyote's irregular activity patterns (Golightly and Ohmart 1983). Using BMR values to obtain the minimum energy intake requirements for coyotes, 129.6 J/g/d or 1296 kJ/d are required for a 10 kg coyote in thermal neutrality (Golightly and Ohmart 1983). The minimum energy requirements for a desert coyote were calculated to be 260 J/g/d (Golightly and Ohmart 1983).

Habitat Requirements

Coyotes are very adaptable, occupying diverse habitats ranging from forest to range to desert. Coyotes generally live in dens, built in brush-covered slopes, steep banks, rock ledges, thickets, and hollow logs. Dens of other animals, like badgers, are often used (Bekoff 1982). Coyotes need enough food for a habitat to be suitable, but because they are opportunistic feeders they have adapted well to many diverse habitats. Coyotes in Maine prefer open habitats like bogs and frozen lakes and softwood-dominated mixed habitats to hardwood and hardwood-dominated mixed habitats (Major and Sherburne 1987). In Michigan, coyotes prefer the mixed aspen-conifer and swamp conifer sites, as well as lowland brush habitat (Ozoga and Harger 1966).

Home Range

The home range size of coyotes is highly variable, depending on geography and season (Bekoff 1982). Coyotes in packs that defend ungulate carrion in the winter have compressed home ranges (1430 ha), whereas coyotes living alone or in pairs may have a home range of 3010 ha (Bekoff 1982; Bekoff and Wells 1980). Home range sizes have been reported as high as 6800 ha for male coyotes and as high as 3600 ha for females (Bekoff 1982). Coyotes do not seem to exhibit territoriality unless they are in a pack (Bekoff and Wells 1980).

Population Density

The density of coyote populations varies from year to year and by region. Fichter et al. (1955) report densities of 0.0015 individuals/ha (Fichter et al. 1955). Coyote densities in Alberta during the 1960s and 1970s varied from a low of 0.0014/ha to 0.0044/ha, depending on the abundance of their major food source, hares (Todd et al. 1981). In Michigan, densities of 0.0019/ha to 0.001/ha, have been reported (Ozoga and Harger 1966). Other studies have found population densities of 0.001/ha to 0.023/ha (Bekoff 1982).

Population Dynamics/Survival

The mortality rate of coyotes depends on their age and the level of control to which they are exposed. Pups and individuals less than one year of age have the highest mortality rate (67-68%; Bekoff 1982). Adult mortality varies from 36-45%, with about 3/4 of a coyote population being between 1 and 4 years of age (Bekoff 1982). In order to maintain population stability, net survival of 33-38% is necessary (Knowlton 1972; Nellis and Keith 1976). Maximum ages of wild individuals were recorded at 13.5 years (Nellis and Keith 1976) and 14.5 years (Knowlton 1972).

Reproduction/Breeding

Anatomically and physiologically, coyotes are very similar to domestic dogs and can produce fertile hybrids with them, as well as with red and grey wolves and golden jackals (Bekoff 1982). The number of females that breed in a year is dependent on food availability. Generally, 60-90% of adult females produce litters, along with some female yearlings (Bekoff 1982). Knowlton (1972) estimated that approximately 87% of ovulated implants were represented by viable ova, with a high percentage of these developing into viable young. Gestation lasts about 63 days with an average litter size of 6 (Bekoff 1982). Litter size can vary depending on food availability. The sex ratio in the population is about 1:1 (Bekoff 1982). Young begin to eat solid foods at about 3 weeks of age and are usually weaned by around six weeks of age (Bekoff 1982). During the first eight weeks of life, pup weight increases by about 0.31 kg per week, with the pups reaching adult weight at about 9 months of age (Bekoff 1982). Emergence from the den usually coincides with pups beginning to eat solid foods.

Behavior and Social Organization

Coyotes communicate with a series of postures, gestures, tail movements, facial expressions, and vocalizations. Generally, coyotes are less social than wolves, but they will sometimes form packs. Pack formation occurs when there are large prey items to be eaten or for cooperative group defense purposes (Bekoff 1982). Coyotes may be active at various times during the day but tend to be most active around sunrise and sunset. They also exhibit seasonal differences in activity with more time spent resting during the winter to conserve energy (Bekoff 1982).

3.3.7 Kit Fox (*Vulpes macrotis*)

Kit foxes are in the order Carnivora, family Canidae. They are closely related to the swift fox (*Vulpes velox*), with their common names having been used interchangeably in the past (Samuel and Nelson 1982). They are carnivorous animals, and opportunistic feeders, but seem to rely mostly on rodents and lagomorphs in their diets (McGrew 1979). While they have been exterminated from much of their historical range, populations are returning in some areas (Samuel and Nelson 1982).

Distribution

Kit foxes are distributed throughout the desert and semiarid regions of western North America. They are historically found throughout the Sonoran, Chihuahuan, Mohave, and Painted deserts and much of the Great Basin Desert (McGrew 1979). The similar swift fox (*Vulpes velox*) is found from New Mexico to the Dakotas (Samuel and Nelson 1982).

Body Size and Weight

Kit foxes have a typical fox appearance, with a slim body, large ears relative to their body, and a long bushy tail (McGrew 1979). The kit fox has a body length of about 40 cm, with the tail being 25 to 30 cm (over 40% of the total body length) (McGrew 1979; Samuel and Nelson 1982). Their average adult weight

ranges from 1.5 to 3 kg (McGrew 1979). Weights of kit foxes from several specific locations are listed in Table 22.

Table 22. Body weights (kg) for the kit fox, *Vulpes macrotis*

Location	Sex	N	Mean \pm SE	Range	Reference
Utah	Male	10	2.06	1.7-2.5	Egoscue 1962
	Female	6	1.91	1.6-2.1	
Arizona	Both: summer	11	1.77 \pm 0.06		Golightly and Ohmart 1983
	Both: winter	9	1.87 \pm 0.06		
California	Male	21	2.4 \pm 0.01		White and Ralls 1993
	Female	17	2.1 \pm 0.01		
Arizona	Male	4	1.82 \pm 0.06		Zoellick and Smith 1992
	Female	3	1.67 \pm 0.04		
	Both	7	1.76 \pm 0.05		

Food Habits and Diet Composition

Kit foxes are almost exclusively carnivorous, with primary prey being small mammals and rabbits (McGrew 1979). The endangered San Joaquin kit fox feeds almost exclusively on kangaroo rats, which are also a major food source for other subspecies of kit fox (Morrell 1972). Egoscue (1962) found that black-tailed jackrabbits (*Lepus californicus*) made up over 94% of the kit foxes' diet in Utah. These differences in diet reflect the fact that kit foxes are opportunistic feeders, although not to the extent that coyotes are (McGrew 1979). Kit foxes will supplement their diets with ground-nesting birds, reptiles, and insects but do not appear to switch to diurnal prey or move to areas of greater prey abundance when there is a decline in their primary prey species (Egoscue 1962; Morrell 1972; McGrew 1979).

Food Consumption Rate

Adult kit foxes kept in captivity ate an average of 175 g fresh meat/d (Egoscue 1962), with males consuming 108-348 g/d and females consuming 56-292 g/d. Assuming a mean body weight of 2 kg, mean food consumption equals 0.0875 g/g/d (range = 0.028-0.174 g/g/d). The total family food requirement for the first 64 days following the birth of a litter was estimated to be 44,605 g (Egoscue 1962).

Water Consumption Rate

Kit foxes appear to obtain adequate moisture from their prey species, as they are often many kilometers away from any water source (Egoscue 1962; Morrell 1972). The fact that kit foxes do not utilize evaporative cooling methods for dissipating metabolic heat would support the idea that they are adapted to a low moisture, arid environment (Golightly and Ohmart 1983).

Soil Ingestion

No literature data were found concerning soil ingestion by kit foxes. Beyer et al. (1994) report soil consumption by red foxes to be 2.8% of daily food consumption. Values for kit foxes may be comparable.

Respiration Rate

No literature data were found describing inhalation by kit foxes. Using Eq. 23 and assuming a body weight of 1.5 to 3 kg, the average inhalation rate is estimated to range from 0.44 m³/kg BW/d to 0.5 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

Golightly and Ohmart (1983) studied metabolism and body temperatures of kit foxes and other desert canids from Arizona. The minimum summer oxygen consumption rate was observed between 19° and 31°C; minimum O₂ consumption in winter occurred between 23° and 33°C (Golightly and Ohmart 1983). BMR was 0.0034 W/g in summer and 0.0028 W/g in winter. Kit fox metabolic rates are not consistent with those of other desert-adapted species. Instead, kit foxes exhibit high thermal conductance, which may be an adaptation for dissipating heat loads by nonevaporative means. Foxes may use dens during the day and limit their activities to the night to avoid excessive heat and water loss (Golightly and Ohmart 1983). The kit fox cannot tolerate high ambient temperatures, and the den provides safety and a predictable shelter with a moderated microclimate. Kit foxes also exhibited distinct circadian rhythms in oxygen consumption and body temperature, with peak levels corresponding to early evening and early morning activity periods (Golightly and Ohmart 1983). This is unlike the coyote and allows metabolic rate and water loss to be minimized in the kit fox.

Habitat Requirements

Kit foxes prefer semiarid habitats with less than 20% ground cover, light colored loamy desert soil, and elevations lower than 1675 ft (McGrew 1979). The vegetation of these areas is a shrubby or shrub-grass combination that varies depending on the actual location.

Home Range

Home ranges of kit foxes overlap broadly with different family hunting groups hunting in the same areas but not at the same time. This suggests that no specific hunting territory is maintained or defended (Morrell 1972). Morrell (1972) estimated the home range of kit foxes in the San Joaquin Valley of California to be 260 to 520 ha. Zoellick and Smith (1992) calculated the overall average home range size to be 1120 ± 94 ha for foxes in western Arizona. The male home range averaged 1230 ± 100 ha, and the female home range averaged 980 ± 140 ha. White and Ralls (1993) calculated the home range of kit foxes in California to average 1160 ± 90 ha. White and Ralls (1993) also calculated a mean social group home range of 1370 ± 110 ha.

Population Density

In Utah, Egoscue (1956) estimated the population density of the kit fox to be 0.001 pairs/ha, or at an optimum, 0.008 individuals/ha. Zoellick and Smith (1992) found population densities of 0.0022-0.0028 individuals/ha in western Arizona. White and Ralls (1993) estimated minimum population densities of 0.0015-0.0024 individuals/ha in California. In 1959, the population of the San Joaquin kit fox was estimated to be between 1000 and 3000 total, or about 0.004 individuals/ha (Samuel and Nelson 1982).

Population Dynamics/Survival

The mortality rates of kit foxes are unknown, but their overall abundance has declined dramatically as a result of poisoning and trapping; habitat loss has contributed to the decline (Zoellick et al. 1989). Some fox mortality is the result of being hit by cars and by predation by coyotes and hawks (Egoscue 1962). Most of the kit fox populations that have been studied remain at a relatively stable size, presumably at a level that can be supported by the environment. Egoscue (1956, 1962) and others have often seen a slight bias toward

the number of males in the adult kit fox population. Population numbers have been observed to rise or fall depending on the population of their major food source (Egoscue 1962; Morrell 1972). During a period of low food supply, Egoscue noted that average adult age was only 1.96 years.

Reproduction/Breeding

Males will generally join females at natal dens in October or November, with breeding occurring between December and February (McGrew 1979). Initial observations suggested kit foxes to be monogamous (Egoscue 1962); however, recent research indicates multiple females sharing a den with one male (Morrell 1972). Little is known about courtship behavior, but copulation appears to be similar to other canids. The gestation period in kit foxes is unknown but is assumed to be about the same as the red fox, 49-55 days (Egoscue 1962). Litters are usually born in February or March, with a litter size of 4-5 and a nearly even sex ratio (Egoscue 1962; Morrell 1972; Samuel and Nelson 1982). The male fox stays with the family and hunts for food while the female suckles the pups and rarely leaves the den (McGrew 1979). Pups emerge from the den in about a month and reach adult weight by about five months of age. The family group will split up in October, with the pups usually dispersing beyond their parents home range (Morrell 1972).

Behavior and Social Organization

Few detailed accounts exist of kit fox behavior, although there is some information on reproduction, hunting, and denning (McGrew 1979). Foxes appear to use olfactory clues, similar to other canids, and Egoscue (1962) has described several kit fox vocalizations. Morrell (1972) also described some of these vocalizations. Some of the lack of information on behaviors is because of the nocturnal habits of the kit fox. Dens are a very important part of the kit fox's life, with most having multiple entrances, anywhere from 2 to 24 (Egoscue 1962). A suitable den is a critical habitat component for the kit fox, as dens are used throughout the year (Samuel and Nelson 1982). Family groups tend to have a whole group of dens that they use almost exclusively, but this may change from year to year (Egoscue 1956, 1962). Smaller dens are used during the breeding season and larger dens are used during the winter (Samuel and Nelson 1982). Several researchers have also recently investigated the spacing patterns of kit foxes and their nightly movements (White and Ralls 1993; Zoellick et al. 1989; Zoellick and Smith 1992).

3.3.8 Weasels (*Mustela spp.*)

Weasels are in the order Carnivora, family Mustelidae. Weasels are small to medium sized predators with a characteristic elongated body form. Three species occur in North America, the long-tailed weasel (*Mustela frenata*), the short-tailed weasel (ermine or stoat; *M. erminea*), and the least weasel (*M. nivalis*) (Svendson 1982). Additional *Mustela* species in North America include the mink (*M. vison*) and the black-footed ferret (*M. nigripes*). Because exposure parameters for mink are presented in EPA (1993) and the black-footed ferret is a critically endangered species with an extremely limited distribution, neither species is discussed here.

Distribution

Long-tailed weasels occur from southern Canada, throughout the United States (except for the desert Southwest), through Central America to northern South America (Svendson 1982). Both short-tailed and least weasels have circumpolar ranges, occurring throughout the Holarctic (King 1983, Svendson 1982). In North America, short-tailed weasels occur across the Arctic, south to northern California, Nevada, Utah and Colorado in the west and south to northern Iowa, Wisconsin, Michigan and Pennsylvania in the east (Svendson 1982, Burt and Grossenheider 1976). Least weasels occur from Alaska and the Canadian Arctic, south to Nebraska, Iowa, Illinois, Indiana, Ohio, and Pennsylvania to the southern Appalachians (Svendson

1982, Burt and Grossenheider 1976). Least weasels are not known to occur in the Rocky Mountains or in northern New England. The northern distribution of long-tailed weasels in North America may be limited by snow cover which restricts foraging (Simms 1979a). Southern distribution of least and short-tailed weasels may be limited by competition and interference interactions with long-tailed weasels (Simms 1979a).

Body Size and Weight

Of the three North American weasels, the long-tailed weasel is the largest (total length: 300 - 350 mm), short-tailed weasels are intermediate in size (total length: 225 - 340 mm), and least weasels are smallest (total length: <250 mm in males; <225 mm in females) (Svendson 1982). Tail length is 40-70% of head and body length for long-tailed weasels, 30-45% for short-tailed weasels, and 25% or less for least weasels (Svendson 1982). While both long-tailed and short-tailed weasels have black-tipped tails, the least weasel does not. Summer pelage of these three species is generally brown on top and white to yellowish on the undersides. Winter coats are generally a uniform white.

Sexual dimorphism is pronounced in weasels, with males consistently larger than females. Sexual dimorphism is attributed to the polygynous mating system of weasels; small females have an energetic advantage over large females while rearing young while large males have a competitive advantage during breeding (Erlinge 1979, Moors 1980). Body weights of weasels from several locations are summarized in Table 23. Sanderson (1949) presents data on growth of a litter of long-tailed weasels from 35 to 100 days in age. Growth curves for male and female least weasels maintained in captivity for 15 weeks are presented by Heidt et al. (1968).

Table 23. Body weights (kg) for the weasels

Species	Location	Sex	N	Mean	Range	Reference
Long-tailed weasel	Nevada	Male: adult	4	0.297±0.036 ^a		Brown and Lasiewski 1972
		Female: adult	4	0.153±0.003 ^a		
	Montana	Male: adult	12	0.287		Wright 1947
	Indiana	Male: adult	19	0.200±0.054 ^a	0.102-0.284	Mumford and Whitaker 1982
		Female: adult	6	0.094±0.010 ^a	0.083-0.109	
	North America	Male: adult Female: adult			0.198-0.340 0.085-0.198	Burt and Grossenheider 1976
Short-tailed weasel	New Zealand ^c	Male: adult	11	0.308±0.016 ^b		King et al. 1996
		Female: adult	8	0.209±0.013 ^b		
	Europe	Male: adult			0.208-0.283	King 1983
	Great Britain	Male: adult		0.320		
	Russia	Male: adult			0.134-0.191	
	North America	Male: adult			0.056-0.206	
	Minnesota	Male: adult	12		0.090-0.170	Jones et al. 1983
		Female: adult	4		0.043-0.071	
Colorado	Female: adult	4	0.038	0.030-0.044		

Table 23. (continued)

Species	Location	Sex	N	Mean	Range	Reference
	North America	Male: adult Female: adult			0.071-0.170 0.028-0.085	Burt and Grossenheider 1976
Least weasel	Indiana	Male: adult	26	0.045±0.013 ^a	0.026-0.068	Mumford and Whitaker 1982
		Female: adult	10	0.032±0.090 ^a	0.022-0.052	
	Great Plains, North America	Male: adult	2		0.055-0.063	Jones et al. 1983
		Female: adult	5	0.042	0.032-0.050	
	North America	Male: adult Female: adult			0.039-0.063 0.038-0.039	Burt and Grossenheider 1976

^a Mean ± STD^b Mean ± SE^c Individuals introduced from Great Britain.

Food Habits and Diet Composition

Weasels are specialist predators of small, warm-blooded vertebrates (King 1983). Their diet consists predominantly of small mammals (50-80% of annual consumption) with larger species consuming larger-sized prey (Table 24; Svendsen 1982). Other foods may be consumed, depending on season and availability. Food preferences of weasels from several locations are listed in Table 24.

Table 24. Diet composition of weasels

Species	Location	Prey taxon	Percent	Comments	Reference
Long-tailed weasel	Michigan	Small mammals		Data represent	Quick 1944
		<i>Peromyscus</i>	98.3	frequency of	
		<i>Microtus</i>	28.2	occurrence of prey	
		<i>Tamiasciurus</i>	1.0	types in 294 scats	
		Small birds	6.8	from winter.	
	Colorado	Small mammals		Data represent	Quick 1951
		<i>Microtus</i>	52.0	frequency of	
		<i>Peromyscus</i>	19.5	occurrence of prey	
		<i>Eutamias</i>	18.2	types in 77 scats from	
		<i>Cynomys</i>	2.6	all seasons.	
		<i>Thomomys</i>	3.9		
		<i>Citellus</i>	2.6		
		<i>Ochatona</i>	1.3		
		Insects			
		<i>Vespula</i>	6.5		
		Tettigoniidae	2.6		

Table 24. (continued)

Species	Location	Prey taxon	Percent	Comments	Reference
	Iowa	<i>Microtus</i>	42.85	Data represent percent volume of prey types in 135 scats from winter and spring.	Polderboer et al. 1941
		<i>Reithrodontomys</i>	21.75		
		<i>Peromyscus</i>	10.23		
		<i>Sylvilagus floridanus</i>	8.42		
		<i>Blarina</i>	5.42		
		<i>Mus</i>	1.86		
		Tree Sparrow	1.02		
		Grasshopper	0.60		
		<i>Geomys</i>	0.60		
		<i>Mustela nivalis</i>	5.40		
		Unidentified matter	1.85		
	California	<i>Microtus</i>	97.9	Data represent percent occurrence of prey remains by dens in winter.	Fitzgerald 1977
		<i>Thomomys</i>	1.0		
		<i>Peromyscus</i>	0.5		
		<i>Sorex</i>	0.5		
Short-tailed weasels	California	<i>Microtus</i>	99.1	Data represent percent occurrence of prey remains by dens in winter.	Fitzgerald 1977
		<i>Peromyscus</i>	0.2		
		<i>Sorex</i>	0.35		
		Small birds	0.35		
	Minnesota	Mice	54.5	Data represent percent volume of prey types in 80 stomachs in winter.	Aldous and Manweiler 1942
		Shrews	21.8		
		Hare	6.1		
		Porcupine	5.0		
		Birds	2.7		
		Weasel	2.5		
		Squirrel	2.5		
		Fish	1.2		
		Unknown	3.7		
	Great Britain	Mammals			King and Moors 1979
		Mice and Voles	22.0		
		Rats and Squirrels	4.8		
		Insectivores	0.6		
		Lagomorphs	28.0		
		Birds	33.3		
		Invertebrates	4.2		
Least Weasels	Great Britain	Mammals			King and Moors 1979
		Mice and Voles	55.3		
		Rats and Squirrels	2.6		
		Insectivores	1.3		
		Lagomorphs	19.1		
		Birds	14.5		
		Invertebrates	5.3		

Table 24. (continued)

Species	Location	Prey taxon	Percent	Comments	Reference
	Great Britain	Small rodents	89	Data represent frequency of occurrence of prey types in 215 scats.	King 1980
		Voles	67		
		<i>Clethrionomys</i>	41		
		<i>Microtus</i>	19		
		Unidentified vole	7		
		Mice (<i>Apodemus</i>)	16		
		Unidentified rodents	7		
		Birds	23		
		Passerines	12		
		Non-passerines	2		
		Unidentified birds	3		
		Eggs	7		
		Lagomorph	0.5		
		Mole	0.5		
	Sweden	<i>Microtus</i>	46	Data represent frequency of occurrence of prey types in 148 scats.	Erlinge 1975
		<i>Clethrionomys</i>	9		
		<i>Apodemus</i>	10		
		<i>Arvicola</i>	16		
		Lagomorph	15		
		Soricidae	1		
		Birds	2		
		Reptile	1		

Food Consumption Rate

Observations of three long-tailed weasels (sex not reported) indicate that four mice/day would "sustain them in apparent health" (Quick 1951). Brown and Lasiewski (1972) report the mean (\pm STD) metabolism of male and female long-tailed weasels to be 1.36 ± 0.2 and 0.84 ± 0.12 kcal/hr, respectively. Assuming that male and female weasels weigh 0.297 kg and 0.153 kg (Brown and Lasiewski 1972), respectively, the diet consists exclusively of small mammals with an energy content of 5163 kcal/kg dry weight (Golley 1961), and the water content of small mammals is 68% (EPA 1993), male and female weasels consume 0.067 and 0.080 kg food/kg BW/d. For comparison, food ingestion by male and female long-tailed weasels, estimated using Eq. 14 is 0.266 and 0.299 kg food/kg BW/d, respectively [assuming BW from Brown and Lasiewski (1972), diet consisting only of small mammals, and water content of small mammals is 68% (EPA 1993)].

No data were found concerning food ingestion by short-tailed weasels. Using Eq. 14 and assuming body weights for males and females reported by Burt and Grossenheider (1976; Table 23), a diet consisting only of small mammals with water content 68% (EPA 1993), food ingestion rates of 0.29 to 0.34 kg food/kg BW/d are estimated for males and 0.33 to 0.41 kg food/kg BW/d for females.

Food ingestion by least weasels has received more attention than that for other weasels. Golley (1960) observed food consumption of 0.41 and 0.42 kg/kg/d for a single least weasel (assumed to weigh 0.36 kg) on a diet of *Microtus* or white mice (*Mus*), respectively. Moors (1977) observed mean (\pm STD) food ingestion by male and female least weasels to be 0.33 ± 0.06 and 0.36 ± 0.08 kg/kg/d, respectively. The

greatest food ingestion rates are reported by Gillingham (1984); mean (\pm STD) ingestion by six individuals (sex not reported) was 0.56 ± 0.03 kg/kg/d.

Water Consumption Rate

Weasels require a constant supply of drinking water, drinking small amounts frequently (Svendson 1982). Long-tailed weasels are reported to consume 25 mL water/d (Svendson 1982). No other literature data were found describing water ingestion by weasels. Using Eq. 21, water ingestion rates may range from 0.11 L/kg BW/d for long-tailed weasels weighing 0.297 kg to 0.15 L/kg BW/d for least weasels weighing 0.022 kg. If other body weight values are used, the water ingestion rate should be recalculated.

Soil Ingestion

No literature data were found describing soil ingestion by any weasel species. Beyer et al. (1994) report soil consumption by red fox to be 2.8% of daily food consumption. Values for weasels may be comparable.

Respiration Rate

No literature data were found describing inhalation by weasels. Using Eq. 23, inhalation rates may range from 0.70 m³/kg BW/d for long-tailed weasels weighing 0.297 kg to 1.17 m³/kg BW/d for least weasels weighing 0.022 kg. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

Brown and Lasiewski (1972) found that cold-stressed long-tailed weasels lost body heat more rapidly and had metabolic rates 50-100% greater than would be expected for a 'normal' shaped animal of similar weight. Higher metabolic rates and greater thermal conductance for weasels relative to other mammals are also reported by Casey and Casey (1979) and Chappell (1980). Similarly, Iversen (1972) observed that the basal metabolic rate of small mustelids (<1 kg BW, includes both short-tailed and least weasels) was greater than that for larger mustelids (>1 kg BW). Metabolism for small mustelids was described by the following equation:

$$M = 0.958BW^{0.55} \quad (53)$$

where

M = basal metabolic rate (kcal/d)
 BW = body weight (kg)

The higher metabolic rates and thermal conductance of weasels are attributed to greater surface area, shorter fur, and the inability of weasels to attain a spherical posture that would reduce heat loss (Brown and Lasiewski 1972).

Habitat Requirements

Habitat preferences of weasels are highly variable. All species tend to be most abundant in habitats with large small mammal populations and near bodies of water. Quick (1944) observed that long-tailed weasels in Michigan spent 53% of their time in crop and fallow land, 29 % in plowed fields, and 18% in forested areas. Stubble and plowed fields appeared to be preferred hunting areas. Similar observations were made by Polderboer et al. (1941). In contrast, Gamble (1981) found that long-tailed weasels preferred late seral stage habitats where prey species diversity was greatest. In southern Ontario, long-tailed weasels used habitats ranging from grassland to forest, with no apparent preference (Simms 1979b).

Short-tailed weasels occur from agricultural lowlands, woodlands, and meadows to montane habitats 3,000 - 4,000 m in elevation; dense forests and deserts are avoided (Svendson 1982). In southern Ontario, short-tailed weasels were observed to prefer early successional habitats and avoid forests (Simms 1979b).

Habitats used by least weasels include marshes, meadows, cultivated fields, brushy areas, and open woods (Svendson 1982). In Wisconsin, high marsh habitats with the water table at or near the surface for a good part of the year are preferred (Beer 1950). Erlinge (1974) observed spruce plantations and regenerating clearings to be most preferred by least weasels.

Home Range

Home ranges of weasels vary by sex, habitat, food availability and season, with smaller species having smaller home ranges (Svendson 1982). King (1975) reports home ranges for least weasels in a deciduous forest in Great Britain to be 7-15 ha for males and 1-4 ha for females. In the Bialowieza Forest of eastern Poland, home ranges for male least weasels increased from 11-37 ha during a rodent outbreak to 117-216 ha during a rodent population crash (Jedrzejewski et al. 1995). Erlinge (1977) reports home ranges for male and female short-tailed weasels in Sweden to be 2-3 ha and 8-13 ha, respectively. In contrast, home ranges for short-tailed weasels in Ontario ranged from 20-25 ha and 10-15 ha for males and females, respectively (Simms 1979b). Home ranges for long-tailed weasels have been reported to range from 5-16 ha in Iowa (Polderboer et al. 1941) to 81-121 ha in Michigan and Colorado (Quick 1944, 1951).

Population Density

Weasel population densities vary considerably by season, food availability, and species (Svendson 1982). For example, densities of least weasels in the Bialowieza Forest of eastern Poland range from 0.52 to 2.73 individuals / km² in winter, declining to 0 to 1.9 individuals / km² in early spring (Jedrzejewski et al. 1995). Midsummer densities varied from 4.2 to 4.8 individuals / km² in years of moderate prey abundance, to 10.2 individuals / km² during a rodent population peak, to 1.9 individuals / km² during the prey population crash. In a study of a 95 ha area in southern Ontario comprised predominantly of early successional habitat, Simms (1979b) observed an overall density of short-tailed weasels of 5.97 individuals / km². However, if only preferred habitat types are considered, density is 10.53 individuals / km². Svendson (1982) reports that densities of long-tailed weasels may range from 6 to 7 individuals / km², while in the Rocky Mountains of Colorado, 0.77 individuals / km² are reported (Quick 1951).

Population Dynamics/Survival

Population fluctuations of weasels are associated with the abundance of prey species. Keith and Cary (1991) observed that 81% of the variation in abundance of weasels (*M. frenata* and *M. erminea*) was attributed to fluctuations in the abundance of hares, voles and mice in Alberta, Canada. In the Bialowieza Forest of eastern Poland, abundance of least weasels was observed to be positively correlated with the abundance of voles and mice (Jedrzejewski et al. 1995).

Longevity of weasels is not well documented. Mean age at death for least weasels in Great Britain was 11 months (King 1975). The lifespan for short-tailed weasels in the wild is reported to be 4 to 6 years (Svendson 1982). In a study of short-tailed weasels in New Zealand, the mean age of individuals captured was 15 months; maximum longevity was 5 years (King et al. 1996). Age-specific mortality of first year individuals was 76%. In Colorado, marked adult long-tailed weasels were observed in the same area for 3 years (Svendson 1982).

Reproduction/Breeding

Both long-tailed and short-tailed weasels display delayed implantation (Svendson 1982). Fertilized ova develop to the blastocyst stage in approximately 14 days, then remain free in the uterus for the next 9 to

10 months (King 1983). Active gestation, from implantation of the embryo to parturition, takes approximately 4 weeks (King 1983). The least weasel, in contrast, does not have delayed implantation; kits are born approximately 41 days following fertilization (Svendson 1982). Additional reproductive parameters for North American weasels are summarized in Table 25.

Table 25. Summary of reproductive characteristics for North American weasels (data from Svendson 1982)

Species	Age at sexual maturity	Breeding season	Gestation	Litter size	Number litters/year
Long-tailed weasel	♂: 1 yr ♀: 3-4 months	July-August	~ 278 days; 27 days implantation	6-9	1
Short-tailed weasel	♂: 1 yr ♀: 3-4 months	July-August	~ 270 days; 21-28 days implantation	6-9	1
Least weasel	♂: 3-4 months ♀: 3-4 months	All year	~ 41 days; no delayed implantation	3-6	2-3

Behavior

Weasels are active year-round and do not hibernate (Svendson 1982). While commonly considered to be nocturnal, weasels tend to be most active during the daytime (Svendson 1982). Erlinge (1980) observed seasonal changes in daily activity; short-tailed weasels tended to be nocturnal in winter and diurnal in summer.

3.3.9 Green Heron (*Butorides virescens*)

The green heron (also known as the green-backed heron) is in the order Ciconiformes, family Ardeidae. This small, compact wading bird is part of a world-wide complex of related species, considered by some to be a single species (Davis and Kushlan 1994). This species is notable in that it has been observed to use a variety of baits and lures to catch prey.

Distribution

In eastern North America, the green heron occurs from the Atlantic Coast to the Great Plains, from southeastern Canada to the Gulf Coast and Florida (Davis and Kushlan 1994). In the west, it is found along the Pacific Coast to Vancouver Island. Range of the green heron is limited by aridity, altitude, and high latitude (Davis and Kushlan 1994).

Body Size and Weight

The green heron is small and stocky (41-46 cm long) with neck and legs shorter than those in other herons (Davis and Kushlan 1994). Dunning (1993) reports the mean body weight of green herons from Florida to be 212±5.92 g (mean±STD; n=34; sex not stated). In Louisiana, the mean body weight of 16 adults and 14 juveniles was 241 g and 219 g, respectively (Davis and Kushlan 1994). Meyerriecks (1962) reports body weights for two males and a female to be 158 g, 191.6 g, and 181.5 g, respectively.

Food Habits and Diet Composition

The diet of green herons consists primarily of fish (40 to >90%; Table 26). Other prey items include crayfish and other crustaceans, insects, spiders, and amphibians. Fish consumed are generally small in size.

In Michigan, Alexander (1977) observed the following size distribution of fish consumed: 0 to 25.4 mm, 60%; 25 to 51 mm, 37%; 51 to 76 mm, 1.1%; and 76 to 100 mm, 2.2%. Prey consumed by herons in Louisiana ranged from 10 to 100 mm (Davis and Kushlan 1994).

Table 26. Diet composition of green herons

Location	Prey taxon	Percent volume	Percent frequency	Reference
Louisiana (n=27) data from late summer	Fish	93	93	Davis and Kushlan 1994
	Mosquitofish (<i>Gambusia affinis</i>)	1	11	
	Shiners (<i>Notropis</i> spp.)	2	7	
	Sunfish (<i>Lepomis</i> spp.)	35	26	
	Pirate perch (<i>Aphredoderus sayanus</i>)	2	4	
	Threadfin shad (<i>Dorosoma petenense</i>)	53	48	
	Crustacea	1	22	
	Crayfish (Cambarinae)	1	11	
	Prawns (<i>Palaemonetes kadiakensis</i>)	<1	11	
	Insecta	6	63	
	Coleoptera	<1	4	
	Hemiptera	1	19	
	Odonata	2	48	
	Orthoptera	3	26	
	Arachnida	1	22	
Water spiders (<i>Dolomedes</i> spp.)	1	22		
Throughout United States (N=255)	Noncommercial fishes	38.52		Meyerriecks 1962
	Food fishes	5.91		
	Undetermined fish fragments	0.96		
	Crustaceans	20.64		
	Insects	23.65		
	Spiders and other invertebrates	10.32		
Michigan (n=12)	Fish	67		Alexander 1977
	Red belly dace	7.7 ^a		
	Creek chub	3.3 ^a		
	Darter	3.3 ^a		
	Brook stickleback	62.2 ^a		
	Fathead minnow	13.3 ^a		
	Mudminnow	7.7 ^a		
	Largemouth bass	2.2 ^a		
	Crustaceans	1		
	Insects	9		
	Amphibians	10		
	Vegetation	3		
Unidentified	10			

^a Values represent percent of total fish species consumed.

Food Consumption Rate

Kushlan (1978) developed a model for estimation of daily food ingestion rates by herons

$$\log I_f = 0.966 (\log BW) - 0.64, \quad (54)$$

where

$$\begin{aligned} I_f &= \text{food ingestion rate (g fresh wt. /individual/d),} \\ BW &= \text{body weight (g).} \end{aligned}$$

Assuming a body weight of 212 g (Dunning 1993), green herons are estimated to consume 0.19 g/g/d. This estimate is comparable to that observed for two nestling green herons, just prior to fledging (16% of body

mass/d; Junor 1972). In contrast, Alexander (1977) estimates that green herons in Michigan consume 50% of their body mass in food per day. No data are presented to support this estimate, however.

Water Consumption Rate

No literature data were found describing water consumption by green herons. Using Eq. 22 and assuming a body weight of 212 g (Dunning 1993), the average water ingestion rate is estimated to be 0.098 L/kg BW/d. If other body weight values are used, the water consumption rate should be recalculated.

Soil Ingestion

Data concerning soil ingestion by green herons were not located in the literature. As a piscivorous, nonfossorial species, soil ingestion is likely to be negligible.

Respiration Rate

No literature data were found describing inhalation by green herons. Using Eq. 24 and assuming a body weight of 212 g (Dunning 1993), the average inhalation rate is estimated to be 0.58 m³/kg BW/d. If other body weight values are used, the inhalation rate should be recalculated.

Metabolism

No literature data on metabolism were located.

Habitat Requirements

Green herons are highly flexible, using almost any available fresh or salt water habitat within their range (Meyerriicks 1962). Their primary requirement is dense vegetation. Green herons forage in swamps, marshes, riparian zones along creeks or human-made ditches, pond or lake edges, etc. (Davis and Kushlan 1994). These herons generally avoid open flats frequented by other, longer-legged herons.

Home Range

Davis and Kushlan (1994) report that green herons defend feeding territories from conspecifics; however, specific data on home range and territory size in this species are lacking.

Population Density

Because green herons are generally solitary and widely dispersed, population density estimates are problematic (Davis and Kushlan 1994).

Population Dynamics/Survival

There are few data on survivorship or longevity in green herons. Banding records indicate longevity of at least 7 years (Davis and Kushlan 1994). Limited data on populations indicate somewhat increasing abundance in the eastern United States, with range expansions at its northern and western limits (Davis and Kushlan 1994).

Reproduction/Breeding

Data on reproduction in green herons was derived from Bent (1926), Meyerriicks (1962), DeGraaf et al. (1981), and Davis and Kushlan (1994). Green herons may nest singly or in colonies. Nests are frequently in trees or shrubs near water, typically 3 to 4.5 m in height. In New York, eggs may be present from April 29 to August 4. Clutch sizes range from three to six eggs but are typically four to five eggs. Incubation lasts 19 to 21 days. Hatching success averages 78.9%. The nestling period lasts 16 to 17 days. Green herons

produce one clutch/year in northern latitudes, two per year in the south. Green herons are sexually mature at one year of age but generally do not breed until their second year.

Behavior

Green herons use the fewest number of feeding behaviors reported for North American day herons (Davis and Kushlan 1994). Of 36 potential behavior types, green herons used only 15. Green herons are also less active than other herons. Green herons are known to bait for fish using bread crusts, feathers, insects, worms, sticks, and plastic (Davis and Kushlan 1994).

Green herons are migratory in the northern parts of their range (Meyerriecks 1962). Migration generally occurs at night, either singly or as flocks of 50 or more individuals.

Social Organization

Green herons are not social outside the breeding season (Meyerriecks 1962). They are typically solitary foragers. During the breeding season, they may nest singly or form small colonies of up to 30 pairs (DeGraaf et al 1981). Green herons may also be found as part of mixed breeding colonies with other heron species (Davis and Kushlan 1994).

3.3.10 Burrowing Owl (*Speotyto cunicularia*)

The burrowing owl is in the order Strigiformes, family Strigidae. This owl is unique among North American owls in that it is diurnal, forms loose colonies, and is very tolerant of human activity (Haug et al. 1993).

Distribution

The burrowing owl has a very broad distribution in the Americas. This species occurs in suitable habitat throughout western North America, from southern Canada to southern Mexico (Johnsgard 1988, Haug et al. 1993). Populations also occur in southern Florida, the western Caribbean islands, and in Central and South America to Tierra del Fuego.

Body Size and Weight

The burrowing owl is a small owl with total body lengths of males and females ranging from 19 to 25 cm (Haug et al. 1993). Earhart and Johnson (1970) report that, in contrast to other North American owls, male borrowing owls are longer winged and heavier than females. More recent data do not support this observation (Haug et al. 1993). Body weights of borrowing owls from several locations are presented in Table 27.

Table 27. Body weights (g) for burrowing owls, *Speotyto cunicularia*

Location	Sex	N	Mean	Reference
Colorado	Male	38	146.3 ± 1.9 ^a	Haug et al. 1993
	Female	31	156.1 ± 3.6	
Florida	Male	111	148.8 ± 1.5	
	Female	162	149.7 ± 1.7	
Throughout North America	Male	31	158.6 (120-228) ^b	Earhart and Johnson 1970
	Female	15	150.6 (129-185)	

^a mean ± SE.

^b mean (range).

Food Habits and Diet Composition

Burrowing owls are opportunistic feeders, foraging on arthropods, small mammals, and small birds (Earhart and Johnson 1970; Johnsgard 1988; Haug et al. 1993; Table 28). Diets vary by season, according to availability of prey (Thomsen 1971; Marti 1974; Haug et al. 1993). Food habits of burrowing owls from several locations are summarized in Table 28. Size of prey taken by burrowing owls is small; mean weight is 3 g with 91.2 % being ≤ 1 g (Marti 1974). Vegetation observed in diet of owls from California is attributed to stomach contents of prey (Thomsen 1971; Table 28).

Table 28. Diet composition of burrowing owls

Location	Prey taxon	Percent	Comments	Reference
California	Meadow vole	27.63	Values represent mean total biomass observed in pellets over four seasons	Thomsen 1971
	Jackrabbit	2.28		
	Pocket gopher	1.25		
	Norway rat	0.38		
	House mouse	0.25		
	Hoary bat	0.025		
	Western meadowlark	0.075		
	Blackbird	0.1		
	Shorebirds	0.05		
	Unidentified birds	3.05		
	Toad	0.28		
	Jerusalem cricket	11.25		
	Unidentified orthoptera	0.075		
	Coleoptera	16.05		
	Isopoda	0.05		
	Sand and dirt	4.13		
Stones	0.9			
Vegetation	32.35			
Idaho	Mammals	68	Values represent percent biomass in pellets	Gleason and Craig 1979
	Birds	1		
	Amphibians	3		
	Arachnids	4		
	Insects	25		

Table 28. (continued)

Location	Prey taxon	Percent	Comments	Reference
Colorado	Mammals		Values represent	Marti 1974
	<i>Sylvilagus</i> spp.	0.23	mean percent of	
	<i>Perognathus</i> spp.	0.17	numbers observed	
	<i>Reithrodontomys</i> spp.	1.17	in pellets collected	
	<i>Peromyscus maniculatus</i>	5.38	over six months	
	<i>Microtus ochrogaster</i>	2.03		
	Other mammals	0.22		
	Birds	0.12		
	Reptiles	0.03		
	Crayfish	0.38		
	Insects			
	Gryllidae	9.78		
	Acrididae	9.37		
	Cicindelidae	0.30		
	Carabidae	50.27		
	Scarabidae	10.13		
	Silphidae	2.83		
Tenebrionidae	3.15			
Curculionidae	1.40			
Other insects	2.58			
Spiders	0.23			

^a Mean and range of observations from three locations.

Food Consumption Rate

Coulombe (1970) reports the mean (\pm STD) daily energy expenditure by burrowing owls in summer (21-26°C) and winter (10°C) to be 0.18 ± 0.05 kcal/g/d and 0.14 ± 0.036 kcal/g/d, respectively. Using Eq. 20 [assuming a diet of 90.7% invertebrates and 9.3% small mammals (Table 28; Marti 1974), caloric densities and water content of invertebrates and small mammals of 5.278 kcal/g and 76.3% (Bell 1990) and 5.163 kcal/g (Golley 1961) and 68% (Table 4), respectively], mean daily food consumption by burrowing owls is estimated to be 0.046 g/g/d in summer and 0.036 g/g/d in winter. These estimates are substantially lower than that estimated using the same assumptions and Eq. 18 (summer = 0.165 g/g/d; winter = 0.153 g/g/d).

Water Consumption Rate

No literature data were located concerning water ingestion rates for burrowing owls. Using Eq. 22, owls weighing 0.15-0.16 kg are estimated to consume approximately 0.11 L/kg/d.

Soil Ingestion

Sand, dirt, and rocks accounted for 0.12 to 15% of the volume of pellets of burrowing owls from California (mean \pm STD: 5.0 ± 5.9 ; Thomsen 1971).

Respiration Rate

Burrowing owls are adapted to high CO₂ and low O₂ concentrations they experience in burrows. While respiration rates for bobwhite increased sharply in response to decreasing O₂ concentration, that for burrowing owls remained constant (Boggs and Kilgore 1983). Average (\pm SE) respiration rates for resting

burrowing owls under normal conditions is 129 ± 4.5 mL/min. or 1.12 m³/kg/d (Boggs and Kilgore 1983). This measured value is almost twice that estimated using Eq. 24: 0.6 m³/kg/d for owls weighing 0.15 - 0.16 kg.

Metabolism

The metabolism and physiology of burrowing owls was extensively studied by Coulombe (1970). Oxygen consumption varied in relation to ambient temperature and was described by the following

$$VO_2 = 1.44 - 0.0324 (T_A - 13.66) \text{ for } T_A < 25^\circ\text{C}, \quad (55)$$

$$VO_2 = 1.05 \pm 0.56 (\bar{x} \pm 95\% \text{ CI}) \text{ for } T_A 25\text{-}37^\circ\text{C}, \quad (56)$$

and

$$VO_2 = 1.32e^{0.0911(T_A - 41.27)} \text{ for } T_A > 37^\circ\text{C}, \quad (57)$$

where

$$\begin{aligned} VO_2 &= \text{oxygen consumption in cm}^3/\text{g/h}, \\ T_A &= \text{ambient temperature.} \end{aligned}$$

Habitat Requirements

The typical habitat of burrowing owls consists of dry, open, treeless plains, heavily grazed or low-quality grassland, or desert vegetation (Johnsgard 1988; Haug et al. 1993). Other areas include golf courses, cemeteries, road-sides, airports, vacant lots, etc. (Haug et al. 1993). Burrowing owls are frequently associated with burrowing mammals (MacCracken et al. 1985; Rich 1986; Green and Anthony 1989; Desmond and Savidge 1996). Although the presence of burrows appears to be a critical requirement for western owls, owls in Florida usually excavate their own burrows (Haug et al. 1993). In Saskatchewan, burrowing owls foraged in grass-forb areas but avoided croplands and grazed pasture (Haug and Oliphant 1990).

Home Range

Although the mean home range size of owls in Saskatchewan was 241 ha (range = 14 - 481 ha; Haug and Oliphant 1990), 95% of all movement occurred within 600 m of nest burrows. Territories are generally limited to the immediate area around burrows; adjacent pairs may share foraging ranges (Johnsgard 1988). In California, Thomsen (1971) observed a mean territory size of 0.8 ha (range: 0.04 - 1.6 ha).

Population Density

Nest density is probably influenced by the availability of nest burrows (Johnsgard 1988). In the Imperial Valley of California, mean (\pm STD) density was 0.035 ± 0.018 individuals/ha (range: 0.003 - 0.06 ; Coulombe 1971). Desmond and Savidge (1996) report that burrowing owl densities varied according to the size of the prairie dog towns they were associated with; small towns (<35 ha) had 0.1 - 30 owls/ha while large towns (≥ 35 ha) had 0.03 - 0.4 owls/ha. Densities of owls, within owl clusters in large prairie dog towns ranged from 0.9 - 2.5 owls/ha. As the size of the prairie dog town increased, the abundance of owls increased, but their density decreased (Desmond and Savidge 1996).

Population Dynamics/Survival

Evidence suggests that burrowing owl populations are declining across much of their range (Haug et al. 1993). The annual survival of burrowing owls in California was 30% for juveniles and 80% for adults (Thomsen 1971). Longevity in excess of 8 years has been reported (Haug et al. 1993).

Reproduction/Breeding

Data on reproduction in burrowing owls was derived from Martin (1973), Johnsgard (1988), Green and Anthony (1989), and Haug et al. (1993). Burrowing owls nest in underground burrows that they may or may not excavate themselves. Eggs may be present from mid-March to May. Clutch sizes range from 3 to 12 eggs but are typically 6 to 8 eggs. Incubation lasts 27 to 30 days. Hatching success ranges from 55 to 90.3%. The nestling period lasts 40 to 45 days. Generally, only one clutch/year is produced. Burrowing owls are sexually mature at 1 year of age.

Behavior

Burrowing owls are migratory only in the northern part of their range; birds in Florida and southern California are sedentary (Johnsgard 1988). While burrowing owls are generally crepuscular in their foraging (Coulombe 1971), hunting has been observed during both day and night. Insects are generally hunted by day and small mammals at night (Haug et al. 1993). Thomsen (1971) observed dust bathing in this species.

Social Organization

Burrowing owls are semicolonial, forming loose colonies (Haug et al. 1993). Migrant birds, however, are solitary.

3.3.10 Cooper's Hawk (*Accipiter cooperii*)

The Cooper's hawk is in the order Falconiformes, family Acciptridae. Cooper's hawks are generally woodland species. They are intermediate in size between the other two congeneric accipiters in North America: the sharp-shinned hawk (*A. striatus*) and the northern goshawk (*A. gentilis*; Rosenfield and Bielefeldt 1993).

Distribution

The Cooper's hawk is found in forested areas throughout the conterminous United States, southern Canada, and south to central Mexico (Rosenfield and Bielefeldt 1993).

Body Size and Weight

The Cooper's hawk is medium sized (approximately that of a crow), with short, rounded wings and a long, rounded tail (Rosenfield and Bielefeldt 1993). Males are significantly smaller than females (Storer 1966). Birds in the eastern United States are larger than birds in the western United States. Body weights of Cooper's hawks are presented in Table 29.

Table 29. Body weights (g) for the Cooper's hawk, *Accipiter cooperii*^a

Location	Status	Sex	N	Mean ± STD
Eastern United States	Migrant	Male	51	349 ± 20
		Female	57	529 ± 36
	Breeding	Male	15	338 ± 20
		Female	31	566 ± 40
	Juvenile, migrant	Male	53	335 ± 26
		Female	58	499 ± 40
Western United States	Migrant	Male	177	281 ± 19
		Female	416	439 ± 35
	Breeding	Male	48	280 ± 19
		Female	20	473 ± 41
	Juvenile, migrant	Male	183	269 ± 22
		Female	310	399 ± 36
Juvenile, breeding ^b	Male	9	276 ± 26	
	Female	5	486 ± 29	

^a All data from Rosenfield and Bielefeldt (1993).

^b nonbreeding, summer birds.

Food Habits and Diet Composition

The diet of Cooper's hawks has been well studied. Sherrod (1978) and Rosenfield and Bielefeldt (1993) provide reviews of literature concerning diet composition. In general, Cooper's hawks are reported to forage primary on medium-sized birds (approximately 60-80%), with small mammals making up the remainder. However, Bielefeldt et al. (1992) suggest that the methods used in most dietary studies overestimate the proportion of birds in the diet and that small mammals may constitute the primary food. Species consumed include the American robin, jays, northern flicker, European starling, grouse, quail, pheasant, crows, doves, sparrows, chipmunks, hares, squirrels, deer mice, and bats. The diet composition of Cooper's hawks from several locations is presented in Table 30.

Table 30. Diet composition of Cooper's hawks

Location	Prey taxon	Percent	Comments	Reference
Northwestern Oregon	Birds ($\bar{x}_{size} = 79.2g$)	74	Diet composition determined from prey remains at nests. Species composition listed in appendix	Reynolds and Meslow 1984
	Mammals ($\bar{x}_{size} = 296.4g$)	25		
Eastern Oregon	Birds ($\bar{x}_{size} = 123.7g$)	47		
	Mammals ($\bar{x}_{size} = 147.5g$)	43		

Table 30. (continued)

Location	Prey taxon	Percent	Comments	Reference
Northwest Washington	Birds	85	Diet composition determined by direct observation of prey deliveries to nests. Primary prey types were American robin and California quail	Kennedy and Johnson 1986
	Mammals	15		
Michigan	Birds	84.4	Diet composition determined by analysis of gullet contents of nestlings and residues in nests	Hamerstrom and Hamerstrom 1951
	Mammals	15.6		
New York and Pennsylvania	Birds	81.8	Diet composition determined from pellets prey remains at nests. Primary prey types were starlings, flickers, eastern meadowlarks, and chipmunks.	Meng 1959
	Mammals	18.2		
Wisconsin	Birds	52 (42-60) ^a	Diet composition determined by crop content analysis	Bielefeldt et al. 1992
	Mammals	48 (40-58) ^a		
Michigan	Birds	29		
	Mammals	71		

^a Mean and range of observations from three locations.

Cooper's hawks take prey ranging in size from 37 to 85% of their body weight (Rosenfield and Bielefeldt 1993). Mean prey size taken by Cooper's hawks in eastern and western Oregon was 134.7 g and 136.3 g, respectively (Reynolds and Meslow 1984). Males generally take smaller prey than females (Rosenfield 1988). In Washington, the percentage of prey taken that was < 91 g was 81% for males and 65% for females (Kennedy and Johnson 1986).

Food Consumption Rate

Craighead and Craighead (1969) observed a food consumption of 0.197 g/g/d for a single male maintained in captivity during fall and winter. Average consumption by two females and a male, during spring and summer, was 0.165 g/g/d (range = 0.16 to 0.173; Craighead and Craighead 1969). Using Eq.s 18 and 20, food ingestion rates of Cooper's hawks are estimated to range from 0.1 g/g/d to 0.13 g/g/d [assuming body weights of 566 g and 280 g (Table 26) and water content of birds and mammals of 68% (Table 4)].

Water Consumption Rate

No literature data were located concerning water ingestion rates for Cooper's hawks. Using Eq. 22, water ingestion rates of Cooper's hawks are estimated to range from 0.07 L/kg/d to 0.09 L/kg/d [assuming body weights of 566g and 280g (Table 26)].

Soil Ingestion

No literature data were located concerning soil ingestion by Cooper's hawks. Soil ingestion is likely to be negligible and consist only of that associated with prey that are consumed.

Respiration Rate

No literature data were located concerning inhalation rates for Cooper's hawks. Using Eq. 24, inhalation rates of Cooper's hawks are estimated to range from 0.47 m³/kg/d to 0.55 m³/kg/d [assuming body weights of 566g and 280g (Table 26)].

Metabolism

While generally viewed as "sit and wait" predators, accipiters are more active than previously thought. Consequently, their metabolic rates are generally higher than those observed in other Falconiformes (Kennedy and Gessaman 1991). Mean metabolic heat production of male and female Cooper's hawks at rest are 2516.25 and 2655.50 mW, respectively (Kennedy and Gessaman 1991).

Habitat Requirements

Cooper's hawks are a forest species, occurring in deciduous, mixed, and evergreen forests; floodplain forests; and wooded swamps (DeGraaf et al. 1981; Rosenfield and Bielefeldt 1993). Forest edges are often used and may serve as primary hunting sites. They have also been observed to use urban habitats (Clark 1977). Nesting habitat in Oregon was intermediate in both age and density of trees, relative to those used by sharp-shinned (younger and denser) and goshawks (older and more open; Reynolds et al. 1982). In the central Appalachians, the nest habitat of Cooper's hawks was characterized as mature forest with well developed understory and herb layer (Titus and Mosher 1981).

Home Range

Cooper's hawks require considerable space. Home ranges during the breeding season may range from 400 to 1800 ha (Rosenfield and Bielefeldt 1993). The mean size of winter ranges of four Cooper's hawks in Michigan was 192 ha (range=67 to 435 ha; Craighead and Craighead 1969). Summer home range size for this population was highly variable, ranging from 18 to 531 ha; but mean size (203 ha) was comparable to that in winter.

Population Density

Density data for Cooper's hawks are based on the abundance of nests. As a consequence, the data are biased because nonbreeding individuals are not represented. Regardless, available data indicate this species to be diffuse throughout its range. Craighead and Craighead (1969) report densities of 0.017 pairs/ha in Michigan and 0.046 pairs/ha in Wyoming. In Oregon, mean density was 0.00045 pairs/ha (Reynolds and Wight 1978).

Population Dynamics/Survival

Although eastern populations declined in the mid-1900s and the species is listed as threatened or endangered in several eastern states, evidence suggests the presence of recovering breeding populations in many areas (Rosenfield and Bielefeldt 1993). Mean age at death reported from banding data was 16.3 months, with maximum longevity being 12 years. Mortality in the first year is 72 to 78%, then 34 to 37% in subsequent years (Rosenfield and Bielefeldt 1993).

Reproduction/Breeding

Data on reproduction in Cooper's hawks was derived from DeGraaf et al. (1981), Palmer (1988), and Rosenfield and Bielefeldt (1993). Cooper's hawks nest in extensive forests, woodlots of 4 to 8 ha, and occasionally in isolated trees. Nests are constructed of sticks, placed in a main crotch or on a horizontal limb against the trunk of live trees, typically 10.7 to 13.7 m in height. Eggs may be present from May to June. Clutch sizes range from three to six eggs, but are typically four to five eggs. Incubation lasts 34 to 36 days.

Hatching success ranges from 74 to 96%. The nestling period lasts 30 to 34 days for eastern birds and 27 to 30 days for western birds. Only one clutch/year is produced. Cooper's hawks generally do not breed until they are at least 2 years old.

Behavior

Cooper's hawks are diurnal, spending approximately 20% of the day hunting (Rosenfield and Bielefeldt 1993). Birds from the northern portion of their range are migratory, although some stay resident year-round, even in Canada (Palmer 1988). Southern birds may be locally migratory or more or less resident, leaving high elevations for more protected low elevations during winter.

Social Organization

Outside of the breeding season, Cooper's hawks are solitary. Small groups may form during migration, but these are incidental and are not the result of social interactions (Rosenfield and Bielefeldt 1993).

3.3.11 Western Meadowlark (*Sturnella neglecta*)

The western meadowlark is in the order Passeriformes, family Emberizidae. This bird is one of the most abundant and widely distributed birds in North America. It is similar in appearance to the eastern meadow lark (*Sturnella magna*), differing only in song (Lanyon 1994).

Distribution

Western meadowlarks range throughout western North America, west of the Mississippi River to the Pacific Coast (Lanyon 1994). They occur from the southern half of British Columbia, Alberta, Saskatchewan, and Manitoba in the north, to central Mexico in the south.

Body Size and Weight

The western meadowlark is a medium-sized terrestrial songbird, approximately 24 cm in length (National Geographic Society 1987) with a long, slender bill, short tail, and long legs (Lanyon 1994). Males meadowlarks weigh more than females. Body weights for western meadowlarks from different locations throughout their range are presented in Table 31.

Table 31. Body weights (g) for the western meadowlark, *Sturnella neglecta*

Location	Sex	N	Mean	Reference
South Dakota	Male	3 ^a	111.9±2.2 ^b	Wiens and Rotenberry 1980
	Female	3 ^a	86.3±3.0 ^b	
Texas	Male	3 ^a	110.9±3.0 ^b	
	Female	3 ^a	90.1±1.1 ^b	
Washington	Male	4 ^a	113.2±1.5 ^b	
	Female	4 ^a	94.2±3.5 ^b	
Nevada	Male	3	111.5±0.8	

Table 31. (continued)

Location	Sex	N	Mean	Reference
Saskatchewan	NS ^c	NS	103	Wiens and Innis 1974
Colorado	NS	NS	110	

^a Number of sampling dates.

^b mean \pm standard deviation of means for n sampling dates.

^c Not stated.

Food Habits and Diet Composition

Western meadowlarks are ground foragers that consume both plant material (primarily seeds) and invertebrates (Bent 1958; Lanyon 1994; Rotenberry 1980). Bent (1958) reports the diet to consist of approximately 30% plant and 70% insect foods. Food preferences of western meadowlarks are summarized in Table 32. The mean size of insects consumed by western meadowlarks in Washington ranges from 7.7 to 14.6 mm (Rotenberry 1980).

Table 32. Diet composition of western meadowlarks

Location	Prey taxon	Percent volume	Reference
Throughout North America (n=1920)	Plant material	36.7	Lanyon 1994
	Grain	30.8	
	Weed seeds	5.3	
	Miscellaneous	0.6	
	Arthropods	63.3	
	Coleoptera	21.3	
	Orthoptera	20.3	
	Lepidoptera	12.2	
	Hemiptera	1.7	
	Hymenoptera	5.6	
	Diptera	0.1	
	Arachnida	0.2	
Miscellaneous insects	1.9		

Table 32. (continued)

Location	Prey taxon	Percent volume	Reference
Washington (n=23) ^a	Angiospermae		Rotenberry 1980
	Graminae	1.6	
	Miscellaneous forbs	0.3	
	Arachnida		
	Araneida	0.7	
	Solpugida	0.6	
	Insecta		
	Coleoptera		
	Curculionidae	14.8	
	Tenebrionidae	14.4	
	Scarabidae	5.2	
	Carabidae	7.6	
	Larvae	0.6	
	Miscellaneous	0.8	
	Hymenoptera		
	Formicidae	2.1	
	"Wasps"	1.5	
	Lepidoptera		
	Larvae	10.3	
	Diptera		
	Asilidae	0.4	
	Miscellaneous	0.3	
	Neuroptera	0.8	
Hemiptera	1.1		
Orthoptera	29.6		
Homoptera			
Cicadidae	7.4		
Miscellaneous	0.3		

^a Values represent means from 4 sampling dates.

Food Consumption Rate

Bryant (1914, cited in Lanyon 1984) estimates that daily food consumption by western meadowlarks is approximately three times its stomach capacity. Mean dry mass per stomach in Washington ranges from 0.35 to 1.3 g (mean±STD: 0.79±0.40; Rotenberry 1980). Assuming a body weight of 108.8 g and a diet consisting almost exclusively of insects (Rotenberry 1980) with a water content of 76.3% (Bell 1990), the mean daily food ingestion by western meadowlarks is estimated to be 0.028±0.014 g/g/d. This estimate is comparable to that obtained using Eqs. 19 and 20: 0.026 g/g/d (assuming body weight=108.8 g, diet=100% insects, water content= 76.3%).

Water Consumption Rate

Pierce (1974) reports *ad libitum* water consumption by western meadowlarks to be 18.6% of their body weight per day (0.186 L/kg/d). Minimum water consumption for weight maintenance was 66% of the *ad libitum* rate. This is equivalent to that estimated using Eq. 22 and assuming a body weight of 108.8 g (0.12 L/kg BW/d).

Soil Ingestion

Western meadowlarks are reported to ingest grit, probably to aid in digestion or as a source of inorganic nutrients (Gionfriddo and Best 1996). Grit was observed in 44% of the stomachs considered. The mean particle size in stomachs of adults was 1.4 mm with 2 ± 3 particles/stomach (Gionfriddo and Best 1996). Data relating grit ingestion to food ingestion rate were not found in the literature, however. Consequently, estimation of a soil ingestion rate from these data is problematic.

Respiration Rate

No literature data were located concerning inhalation rates for western meadowlarks. Eq. 24, although developed for nonpasserine birds, may be used; however, significant uncertainty in the resulting estimate must be acknowledged.

Metabolism

Nocturnal and diurnal resting metabolic rates for western meadowlarks are 1.73 and 1.97 mL O₂/g/h, respectively (Pierce 1974). These values are low relative to other birds and represent adaptations to hot, open environments.

Habitat Requirements

Western meadowlarks are common in open habitats including native grasslands, pastures, hay and alfalfa fields, weedy borders, cropland, roadsides, orchards, and, occasionally, desert grasslands (Lanyon 1994). In areas where their ranges overlap, western meadowlarks generally prefer more arid habitats than eastern meadowlarks (Lanyon 1956; National Geographic Society 1987).

In an extensive study of habitat associations and avian communities in a shrub-steppe environment in Washington, Wiens and Rotenberry (1981) found western meadowlarks to be broadly distributed over most of the available habitat. While the density of meadowlarks did not correlate well with overall habitat variation, density was positively correlated with sagebrush, grass, and litter cover and negatively with bare ground.

Home Range

Male western meadowlarks defend multipurpose territories in which they forage, breed, and raise young (Lanyon 1994). Territories in Wisconsin varied from 1.2 to 6.1 ha but were generally 2.8 to 3.2 ha. Kendeigh (1941) reports territories to range from 4 to 13 ha in Iowa. Schaefer and Picman (1988) report a mean territory size of 7 ha in Manitoba.

Population Density

Wiens and Rotenberry (1981) report densities of western meadowlarks in shrub-steppe habitat in Washington ranging from 0.02 to 0.88 individuals/ha. In an Iowa prairie, Kendeigh (1941) observed approximately 0.05 birds/ha. In a state-wide census of breeding birds in North Dakota, Stewart and Kantrud (1972) estimated the mean density of western meadowlarks to be 0.11 pairs/ha.

Population Dynamics/Survival

In good habitat, western meadowlarks can be very abundant. Stewart and Kantrud (1972) estimate western meadowlarks to be the fourth most abundant breeding bird in the North Dakota (behind horned larks, chestnut-collared longspur, and red-winged blackbirds). The state-wide population was estimated to be over 2×10^6 pairs. Although the longevity of captive birds ranges from 3 to 5 years, some individuals have lived as long as 10 years (Lanyon 1994). Survivorship in wild populations is unknown.

Reproduction/Breeding

Data on reproduction in western meadowlarks was derived from Bent (1958) and Lanyon (1994). Western meadowlarks make well-concealed nests on the ground, often in a shallow depression and frequently in thick vegetation. Eggs may be present from April to July, throughout the range. Clutch sizes range from 3 to 6 eggs but average 4.8 eggs. Incubation lasts 13 to 14 days, rarely 15 to 16 days. A hatching success of 53% has been reported in British Columbia. The nestling period lasts 10 to 12 days. Western meadowlarks may raise up to two clutches/year. Sexual maturity is reached in one year.

Behavior

Although western meadowlarks will tolerate other ground-nesting species in their territories, they aggressively defend against both conspecifics and eastern meadowlarks (in areas where both species are sympatric; Lanyon 1994).

Social Organization

During fall and winter, western meadowlarks form loose flocks of up to 200 individuals. The flocks may include eastern meadowlarks (Lanyon 1994).

3.3.12 Swallows

Swallows are in the order Passeriformes, family Hirundinidae. Eight species of swallows occur in North America: tree swallow (*Tachycineta bicolor*), violet-green swallow (*Tachycineta thalassina*), purple martin (*Progne subis*), bank swallow (*Riparia riparia*), northern rough-winged swallow (*Stelgidopteryx serripennis*), cliff swallow (*Hirundo pyrrhonota*), cave swallow (*Hirundo fulva*), and barn swallow (*Hirundo rustica*) (National Geographic Society 1987). All are aerial foraging species that forage over open fields or bodies of water (Imhof 1976).

Distribution

Swallow species are found throughout North America. Tree, bank, northern rough-winged, cliff, and barn swallows breed across the northern 3/4 of the United States into Canada and Alaska (except the rough-winged, which extends only to southern Canada; National Geographic Society 1987). Violet-green swallows occur in the west, from Alaska to Mexico. Purple martins breed east of the Rocky Mountains and along the Pacific Coast. Cave swallows occur only in Texas and southern New Mexico (West 1995).

Body Size and Weight

Swallows are small, long-winged birds. Body lengths range from approximately 13 cm for bank swallows to 20 cm for purple martins. Body masses for North American swallow species range from <15 to approximately 50 g (Table 33).

Food Habits and Diet Composition

The diet of swallows consists primarily of insects; however, some plant matter may be consumed (Beal 1918). The diet composition of swallow species in North America is summarized in Table 34. Flies (Diptera) are generally very important food items for swallows, comprising as much as 40% of the diet of some species (Quinney and Ankney 1985; Blancher and McNicol 1991; Table 34). Chironomid midges are an important food item of tree swallows, accounting for 33% of the diet of nestlings (Blancher and McNicol 1991). Because many swallows forage extensively over water (Brown and Brown 1995; DeJong 1996; Robertson et al. 1992; DeGraaf et al. 1981), aquatic prey constitute a significant portion of their diet.

Blancher and McNicol (1991) found prey of aquatic origins to account for 64.9, 71, and 54.9% of the diet of nestling, egg-laying female, and other adult tree swallows, respectively. Swallows generally consume small insects. Quinney and Ankney (1985) report that 99% of the insects consumed by tree swallows are ≤ 10 mm in length. Blancher and McNicol (1991) observed that $\sim 90\%$ of prey were ≤ 25 mm in length.

Food Consumption Rate

Brown and Brown (1995) report that cliff swallows forage at a rate of 3.4, 3.8, and 3.5 kcal/h during nest building, incubation, and nestling periods, respectively. Female tree swallows in New Brunswick, Canada, were observed to require 5.73 ± 1.40 kJ/g/d (mean \pm STD; $n=10$; Williams 1988). Assuming that the diet consists exclusively of insects (Quinney and Ankney 1985) and that the energy and water content of insects is 22.09 kJ/g dry weight and 76.3%, respectively (Bell 1990), daily food consumption by tree swallows is 0.198 ± 0.048 g/g/d.

Water Consumption Rate

No literature data were located concerning water ingestion rates for swallows. Estimated water ingestion rates among swallows may range from 0.24 L/kg BW/d to 0.16 L/kg BW/d (based on Eq. 22 and body weights of 15 and 50 g). In practice, water ingestion rates should be recalculated using body weights for species of interest.

Soil Ingestion

Swallows are reported to ingest grit, probably to aid in digestion or as a source of inorganic nutrients (Barrentine 1980; Mayoh and Zach 1986). Although Barrentine (1980) found grit in 80% of the stomachs of nestling barn swallows, the occurrence of grit in the stomachs of adults was only 22% (Gionfriddo and Best 1996). Among nestlings, particles ranged from 0.84 to 4 mm in diameter, with 4.8 ± 4.5 (mean \pm STD) particles/stomach (Barrentine 1980). In contrast, the mean particle size in stomachs of adults was 1.2 mm, with 1 ± 4 particles/stomach (Gionfriddo and Best 1996). Grit was found in 35 and 20% of the stomachs of nestling and adult tree swallows, respectively (Mayoh and Zach 1986). The number of particles and the mass of grit was greater in nestlings than adults: the number of particles was 10.2 ± 2.2 (mean \pm SE) in nestlings vs 0.8 ± 0.8 in adults and mass (mg) was 17.2 ± 2.6 in nestlings vs 6.1 ± 6.1 in adults. Data relating grit ingestion to food ingestion rate was not found in the literature, however. Consequently estimation of a soil ingestion rate from these data is problematic.

Respiration Rate

No literature data were located concerning inhalation rates for swallows. Eq. 24, although developed for nonpasserine birds, may be used; however, significant uncertainty in the resulting estimate must be acknowledged.

Metabolism

Williams (1988) studied the field metabolism of tree swallows during the breeding season to evaluate whether aerial foraging species have higher energy requirements than other species. Resting and night-time basal metabolic rates were determined to be 79.3 ± 12.6 and 59.5 mL O₂/h, respectively, for birds weighing 21.6 ± 1.9 g. The results indicated that swallows have higher metabolic rates than birds with less energy-intensive lifestyles (e.g., ground foraging species). Additional information on the metabolism of swallows is included in a bioenergetics-based model of PCB accumulation by nestling tree swallows (Nichols et al. 1995).

Habitat Requirements

As aerial foraging species, all swallows require open areas that do not inhibit flight activities. Areas that may be used include open fields, farmland, suburban yards, marshes, bodies of water, riparian edge, broken forest, etc. (DeGraaf et al. 1981; Brown and Brown 1995; Robertson et al. 1992; Bent 1942; West 1995; DeJong 1996). Preferred habitats are generally near water. Some habitats are avoided, for example dense forest, desert, and alpine areas (Brown and Brown 1995). Prior to human development, nests were placed on cliffs or within tree cavities. Now, many human-made structures such as bridges or buildings may be used for nesting. Proximity to a mud source for nest building may also be a requirement for some species (Brown and Brown 1995). Purple martins originally nested in tree cavities but now rely extensively on human-made multiroom nest boxes (DeGraaf et al. 1981). As a cavity nester, tree swallows need dead trees (Robertson et al. 1992). Bank and northern rough-winged swallows frequently use burrows in earthen banks near water bodies (DeJong 1996; Stoner 1936; DeGraaf et al. 1981).

Home Range

Prior to incubation, tree swallows may travel up to 60 km from nest to forage. However, during incubation and nesting, males may travel 4-5 km and females 2-3 km in search of food (Robertson et al. 1992). Bank and barn swallows generally forage within 0.8 km or less from nest sites (Stoner and Stoner 1941; DeGraaf et al. 1981). Among cliff swallows, foraging is generally restricted to a 1.5-km radius around the colony; however, birds may travel up to 6 km to forage (Brown and Brown 1995).

Population Density

Because of their colonial nature and patchy distribution, densities of swallows can be highly variable, difficult to estimate, and dependant on habitat and availability of suitable nest sites. Additionally, density estimates based on breeding pairs are biased because nonbreeding floaters are not accounted for (Robertson et al. 1992). Some representative density estimates follow. Densities of foraging barn swallows of 0.64 individuals/ha have been reported in Illinois (DeGraaf et al. 1981). Breeding densities for barn swallows range from 0.077 pairs/ha in 'favorable' habitat in South Dakota to 0.27 pairs/ha in mixed agricultural/residential habitat in Maryland (DeGraaf et al. 1981). Among tree swallows, breeding densities have been reported to range from 3.5 to 500 pairs/ha, the later estimate resulting from nest boxes placed at an artificially high density (DeGraaf et al. 1981). The breeding density of northern rough-winged swallows in Michigan was approximately 0.18 pairs/ha (Lunk 1962).

Population Dynamics/Survival

First-year mortality among swallows is high: 68, 79, and 83% for cave, tree, and cliff swallows, respectively (West 1995; Robertson et al. 1992; Brown and Brown 1995). After the first year, survivorship improves, ranging from 40 to 60% (Robertson et al. 1992; Brown and Brown 1995). For rough-winged swallows, a 33% adult survival is required for population maintenance (DeJong 1996). Maximum longevity in swallows ranges from 5 years (rough-winged swallows; DeJong 1966) to 11 years (cliff and tree swallows; Robertson et al. 1992; Brown and Brown 1995).

Reproduction/Breeding

Reproductive parameters for North American swallows are summarized in Table 35. Reproductive success for rough-winged swallows in Michigan are reported to be 73, 61, and 65% for hatching, fledging, and overall nesting, respectively (Lunk 1962). Success rates for tree swallows are somewhat higher: hatching success = 88.4%, fledging success = 80.2, and overall nesting success = 78.8% (Robertson et al. 1995).

Behavior

Most North American swallows are migratory, traveling to winter ranges in the southern United States, Mexico, and South America (DeJong 1996; West 1995; Robertson et al. 1992; Brown and Brown 1995). Many swallows drink water while in flight, tipping their bills into water during low flight (DeJong 1996; Robertson et al. 1992; Brown and Brown 1995).

Social Organization

Swallows are generally considered highly social, gregarious birds. Many swallows are colonial, congregating in large breeding colonies. Bank swallow colonies may include 10 to more than 300 nests (DeGraaf et al. 1981). Cliff swallows are the most colonial; colonies of 1000 nests are common, with 3700 nests in the largest colony (Brown and Brown 1995). Rough-winged swallows are the least social (DeJong 1996), commonly forming groups of 3 to 12 individuals. These swallows nest singly or in small groups of 2 to 25 pairs, often at edges of bank swallow colonies.

Table 33. Body weights (g) for swallows

Species	Location	Sex and age	N	Mean	Range	Reference
Cave swallow	Yucatan, Mexico	Male: adult	3	19.0		West 1995
		Female: adult	3	17.7		
	Texas	Both: adult	25	20.4	18.4-22.3	Dunning 1993
Northern rough-winged swallow	Pennsylvania	Both: adult	47	15.9±0.58	10.3-18.3	Dunning 1993
	Not stated	Male: adult	9	14.59±0.54		DeJong 1996
		Female: adult	6	13.3±0.63		
Tree swallow	Southern Ontario	Male: adult > 2 years	86	20.4±1.5	17-24	Robertson et al. 1992
		Female: adult > 2 years	134	21.5±1.7	18-25.5	
	Pennsylvania	Both: adult	82	20.1±1.58	15.6-25.4	Dunning 1993
Cliff swallow	Nebraska	Male: adult during nesting	6797	23.9		Brown and Brown 1995
		Female: adult during nesting	3566	24.15		
	California	Both: adult	88	21.6±2.04	17.5-26.7	Dunning 1993
Purple martin	Maine	Both: adult	22	49.4±1.49		Dunning 1993
Violet-green swallow	California	Male: adult	16	14.4	13.0-16.3	Dunning 1993
		Female: adult	15	13.9	12.5-15.2	
Barn swallow	Morocco	Male: adult	1337	16.2	12.1-28.2	Dunning 1993
		Female: adult	994	15.8	11.0-24.8	
Bank swallow	New York	Both: adult	249	14.6	12.0-18.6	Stoner 1936

Table 34. Diet composition of swallows in North America

Species	Location	Taxa	Percent volume	Percent frequency	Comments	Reference
Purple martin	Throughout the United States and Canada (n=205)	Hymenoptera	23		Other consists of Ephemeroptera, spiders, and sowbugs	Beal 1918
		Diptera	16.09			
		Hemiptera/Homptera	14.58			
		Coleoptera	12.53			
		Lepidoptera	9.39			
		Orthoptera	1.09			
		Odonata	15.1			
		Other	8.09			
Cliff swallow	Throughout United States (N=375)	Ants	8.24		Other consists of Odonata, Ephemeroptera, spiders, and snails	Beal 1918
		Other Hymenoptera	20.51			
		Diptera	13.95			
		Hemiptera/Homptera	26.32			
		Coleoptera	26.8			
		Orthoptera	0.71			
		Other	2.97			
Barn swallow	27 states and Canada (n=467)	Ants	9.89			Beal 1918
		Other Hymenoptera	12.82			
		Diptera	39.49			
		Hemiptera/Homptera	15.1			
		Coleoptera	15.63			
		Lepidoptera	2.39			
		Orthoptera	0.51			
Odonata	4					

Table 34. (continued)

Species	Location	Taxa	Percent volume	Percent frequency	Comments	Reference
Tree swallow	22 states and Canada (n=343)	Ants	6.37		90% of plant material consumed consisted of fruit of waxberry (<i>Myrica carolinensis</i>). Other consisted primarily of spiders	Beal 1918
		Other Hymenoptera	7.58			
		Diptera	40.58			
		Coleoptera	14.39			
		Lepidoptera	5.02			
		Orthoptera	0.37			
		Odonata	4			
		Other	4.64			
		Plant Material	16.9			
Violet-green swallow	Arizona, California, Oregon, Colorado, Wyoming, and Alaska. (N=110)	Ants	9.42		Other consisted primarily of Ephemeroptera	Beal 1918
		Other Hymenoptera	17.48			
		Diptera	19.36			
		Hemiptera/Homptera	35.96			
		Coleoptera	10.57			
		Lepidoptera	3.12			
		Other	4.09			

Table 34. (continued)

Species	Location	Taxa	Percent volume	Percent frequency	Comments	Reference
Bank swallow	21 states and Canada (n=394)	Ants	13.39		Other consists of Ephemeroptera (which accounted for 43% of diet in April), spiders, and snails	Beal 1918
		Other Hymenoptera	20			
		Diptera	26.63			
		Hemiptera/Homptera	7.96			
		Coleoptera	17.9			
		Lepidoptera	2.21			
		Odonata	2.11			
		Other	10.53			
	New York (n=64)	Coleoptera	36.13		Stoner 1936	
		Diptera	31.59			
		Homoptera	17.81			
		Hemiptera	6.13			
		Hymenoptera	5.66			
		Other	1.02			
Northern rough- winged swallow	15 states and Canada (n=136)	Ants	11.99		Other consists of Odonata, Ephemeroptera, spiders, and snails	Beal 1918
		Other Hymenoptera	18.91			
		Diptera	32.89			
		Hemiptera/Homptera	14.9			
		Coleoptera	14.83			
		Lepidoptera	1.11			
		Orthoptera	0.12			
		Other	5.04			
		Plant Material	0.21			

Table 35. Summary of reproductive characteristics for North American swallows

Species	Nest habitat	Egg dates	Clutch size	Number of clutches per year	Incubation period	Nestling period	Age of first breeding	References
Purple martin	Tree cavities, multiroom bird houses	May 21-July 13 (New York)	3 to 8, typically 4 to 5	1	16 to 18 days	26 to 31 days	1 year	DeGraaf et al. 1981
Cliff swallow	Mud cups on cliffs, cave entrances, buildings, bridges, culverts	May 20-5, June peak in Nebraska	1 to 6, typically 3 to 4	1	10 to 19 days, typically 13 to 15 days	20 to 26 days	1 year	Brown and Brown 1995
Barn swallow	Mud cups on human-made structures, especially buildings (barns)	May 11-August 3 (New York)	4 to 6, typically 4 to 5	1 to 2 in warmer areas	Approx. 15 days	16 to 23 days	1 years	DeGraaf et al. 1981
Tree swallow	Tree cavities or nest boxes	Laying starts in early May	2 to 8, typically 4 to 7	1, rarely 2	11 to 19 days, typically 14 to 15 days	15 to 25 days, typically 18 to 22 days	1 year, if possible	Robertson et al. 1992
Violet-green swallow	Tree cavities or nest boxes	May 1-July 1 (California)	4 to 7, typically 4 to 5	1	13 to 14 days	Approx. 23 days	No data	Bent 1942
Bank swallow	Burrows in earthen banks	May 15-July 13 (New York)	4 to 6, typically 5	Up to 2	14 to 16 days	18 to 22 days	1 year	Stoner 1936; DeGraaf et al. 1981
Northern rough-winged swallow	Burrows in earthen banks	Mid-May to mid-June	4 to 8, typically 4 to 6	1	15.5 to 16.5 days	17 to 21.5 days	1 year	DeJong 1996
Cave swallow	Mud cups on cliffs, cave entrances, buildings, bridges, culverts	April-July (New Mexico)	3 to 5, occasionally 1 to 2	2	No data	20 to 23 days	1 yr	West 1995

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