

Prepared in cooperation with U.S. Bureau of Land Management

Captive Breeding, Husbandry, Release, and Translocation of Sciurids

Scientific Investigations Report 2023–5055

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By Sharon A. Poessel

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
Length		
centimeter (cm)	0.3937	inch (in.)
meter (m)	3.281	foot (ft)
meter (m)	1.094	yard (yd)
Mass		
gram (g)	0.03527	ounce, avoirdupois (oz)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$^{\circ}\text{F} = (1.8 \times ^{\circ}\text{C}) + 32.$$

Captive Breeding, Husbandry, Release, and Translocation of Sciurids

By Sharon A. Poessel

Abstract

Captive breeding and release programs have been instrumental in preventing the extinction of some wildlife species, but these programs have been less successful for other species. Evaluating initial guidelines for procedures to start a captive breeding and release program for a particular species is an important first step in the process of initiating such a program. The Mohave ground squirrel (*Xerospermophilus mohavensis*) is a diurnal sciurid endemic to the Mojave Desert in southern California. Ongoing drought conditions in California, impacts of climate change, and reliance of Mohave ground squirrels on sufficient precipitation for successful reproduction appear to have resulted in recent extirpations of the species from part of its restricted range. Thus, designing a captive breeding and release program has been identified as a top priority for this species. The purpose of this report is to review and document the scientific literature on captive breeding and release, and wild-to-wild translocation, programs for other related sciurid species, as well as some non-sciurid rodent species. This review is important because captive breeding has never been attempted for Mohave ground squirrels, so models of similar species can provide good metrics and guidance in program development. We then use this review to identify key questions that underpin effective design of a captive breeding and release, or translocation, program for Mohave ground squirrels.

Introduction

As populations of many species decline and ecosystems worldwide become increasingly altered, maintenance of animals in captivity is becoming a more common approach to species conservation. Captive breeding and release programs, in particular, have prevented the extinction of some species (for example, black-footed ferrets [*Mustela nigripes*; Jachowski and Lockhart, 2009] and California condors [*Gymnogyps californianus*; Walters and others, 2010]), but have been less successful in others (for example, Key Largo woodrats [*Neotoma floridana smalli*]; McCleery and others, 2014). Thus, evaluating the appropriateness of a captive breeding and release program for a wildlife species, including an assessment of the benefits and risks, is an important step in

the process of initiating such a program (International Union for Conservation of Nature/Species Survival Commission [IUCN/SSC], 2013, 2014).

The Mohave ground squirrel (*Xerospermophilus mohavensis*) is a small, diurnal, semi-fossorial sciurid endemic to the Mojave Desert in southern California. The species, which is active aboveground only in spring and early summer, has a restricted distribution but appears to have been recently extirpated in the southern portion of its range (Leitner, 2021). Reproduction in spring is highly dependent on rainfall in the previous winter because food resources are sparse when rainfall is low (Leitner and Leitner, 2017). Thus, ongoing drought conditions in California and impacts of climate change can result in multiple consecutive years of reproductive failure in Mohave ground squirrels and, consequently, a decline in population size.

A recently completed conservation strategy for the Mohave ground squirrel outlined a number of planning goals for the species, including reducing climate change impacts, identifying and implementing conservation actions to protect habitat, and developing a research program to inform conservation and management (California Department of Fish and Wildlife, 2019). Furthermore, at a recent research planning workshop, designing a captive breeding and release program was identified as a top priority for the species, so that such a program could be quickly implemented if required (Katzner and others, 2022). However, a number of questions were raised concerning how such a program would be best designed.

The purpose of this report is to review and document the scientific literature on captive breeding and release programs for other sciurid species. Because few sciurid species are maintained in such conservation programs, we also include literature on husbandry methods for those species held in captivity for non-conservation purposes (usually research or zoo collections). Furthermore, in some cases, we include information on captive breeding and release protocols for non-sciurid rodent species to supplement existing data for sciurids. In a separate section later in the report, we also review wild-to-wild translocation programs (hereinafter, “translocations”) for sciurid species. Finally, we use this review to identify key questions that underpin effective design of a captive breeding and release, or translocation, program for Mohave ground squirrels.

Capture of Founder Animals

Once a decision has been made to initiate a captive breeding and release program, the first subsequent step is to choose the source population, decide how many animals from each age and sex class will be captured, and then capture the animals that will comprise the founding population in captivity. For most captive breeding programs, the primary objectives for founder animals are to maintain genetic diversity, maximize reproductive potential, and minimize impacts to the source population (Shier, 2014; Smyser and Swihart, 2014). A further consideration is whether a wild population should be prioritized for capture because of concern that it may be lost due to future development or private landowner actions (Kenagy and others, 1989).

The U.S. Fish and Wildlife Service (USFWS) established a captive breeding program at the Phoenix Zoo in Arizona for the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), a sciurid species extant in only one population. Captive breeding and husbandry protocols for this species are not publicly available. However, a public environmental assessment that includes some information on a captive breeding strategy was prepared (USFWS, 2010). The preferred alternative from the assessment stated that the goal was to capture up to 16 juvenile squirrels, 8 males and 8 females (although up to 8 adults could be captured if 16 juveniles were not trapped). Juveniles would be captured at the time of dispersal from their natal area, because removing this cohort from the wild population would have less impact than would removing adults. A further stipulation was that no more than 10 percent of the population would be trapped in any single year (USFWS, 2010).

Captive breeding programs also have been established for non-sciurid rodent species of conservation concern. The goal of the Pacific pocket mouse (*Perognathus longimembris pacificus*) program was to have 30 founders, with 10 individuals (2 adult males, 2 adult females, 3 juvenile males, and 3 juvenile females) captured from each of the 3 remaining extant populations (Shier, 2014). To minimize impacts to the source populations, these captured individuals would consist of no more than 10 percent of the adults or 20 percent of the juveniles in each population (Shier, 2014). To maximize genetic diversity in the captive Allegheny woodrat (*Neotoma magister*) population, in 1 year biologists captured eight individuals across seven extant populations in one state, and four additional animals from another state (age class was not specified; Smyser and Swihart, 2014). The sex ratio was deliberately female-biased to maximize reproductive potential. The following year, five of these founders were returned to the wild and replaced with six other wild animals (Smyser and Swihart, 2014). Finally, for Amargosa voles (*Microtus californicus scirpensis*), a rodent species endemic to the Mojave Desert, founders of the captive colony were 10 male and 10 female juveniles captured in 1 year, with an additional 6 males and 6 females captured 2 years later (Allan and others, 2018).

Housing

Sciurids have been housed in a variety of conditions. Although sciurids in zoos are sometimes kept in large spaces resembling colonies in natural settings, the studies evaluated were designed for conservation or research purposes and rarely included a colony of animals kept in a single enclosure. The largest enclosures from the studies reviewed were wire cages (122×244×61 centimeters [cm]) for California ground squirrels (*Otospermophilus beecheyi*) that were placed on the ground outside and subjected to natural light and weather (Marsh and Howard, 1968). All other housing conditions documented were smaller laboratory cages (ranging from 15×15×31 cm to 48×27×20 cm) placed inside a building. Such a design has been used for Cascade golden-mantled ground squirrels (*Callospermophilus saturatus*; Kenagy and others, 1989), Richardson's ground squirrels (*Urocyon richardsonii*; Dobson and Michener, 1995), Columbian ground squirrels (*U. columbianus*; Murie and others, 1998), white-tailed and black-tailed prairie dogs (*Cynomys leucurus* and *C. ludovicianus*; Harlow and Frank, 2001), and 13-lined ground squirrels (*Ictidomys tridecemlineatus*; Landau and Holmes, 1988; Vaughan and others, 2006; Merriman and others, 2012). The latter species was studied in two different institutions, one in Michigan (referred to as the “Michigan” study; Landau and Holmes, 1988) and one as part of a long-term breeding colony maintained for research at the University of Wisconsin, Oshkosh (the “Wisconsin” study; Vaughan and others, 2006; Merriman and others, 2012).

In all studies in which indoor housing was described in detail, temperatures were maintained at 20–22 degrees Centigrade (°C). Animals were subject to either natural light and photoperiod (Landau and Holmes, 1988; Dobson and Michener, 1995; Harlow and Frank, 2001), a 12 hour light:12 hour dark cycle (Kenagy and others, 1989), or lighting that was adjusted every 2 weeks to simulate actual local sunrise and sunset (Vaughan and others, 2006; Merriman and others, 2012). Generally, these conditions were maintained year-round except during the hibernation season (described below).

Materials inside animal cages also varied among studies. The outdoor enclosures for California ground squirrels included a wooden nest box (30×53×30 cm; Marsh and Howard, 1968). Bedding materials used in indoor enclosures were either wood shavings (Kenagy and others, 1989; Murie and others, 1998; Vaughan and others, 2006) or aspen chips (Dobson and Michener, 1995; Merriman and others, 2012). The animals in the Wisconsin 13-lined ground squirrel colony were further provided with open-ended, plastic tubes that were placed on the floor of the cages to simulate horizontal burrows (Vaughan and others, 2006; Merriman and others, 2012).

For some species, housing conditions were changed during the breeding season. Males and females were placed together in larger cages for mating (ranging from 24×45×20 cm to 90×65×35 cm; Kenagy and others, 1989; Vaughan and others, 2006; Merriman and others, 2012). In the Wisconsin 13-lined ground squirrel colony, plywood nest boxes were

initially placed in the breeding enclosures, but these were discontinued because they were not used for nesting and were difficult to clean (Vaughan and others, 2006). Nesting materials described were either cotton balls (Kenagy and others, 1989) or paper towels (Dobson and Michener, 1995; Murie and others, 1998; Vaughan and others, 2006).

Housing conditions were changed again for hibernation. Prairie dogs were moved to a 6 °C chamber with low lighting and were placed in nesting cages (15.2×15.2×30.5 cm) containing cotton insulation (Harlow and Frank, 2001). For 13-lined ground squirrels just before hibernation, either paper towels (Vaughan and others, 2006) or pulp-based materials (Tek-Fresh 7099, Harlan Laboratories, Indianapolis, IN; Merriman and others, 2012) were added as bedding, and the animals usually shredded these items to make hibernation nests. Once squirrels became torpid, they were then moved to a “cold room” that was maintained in complete darkness at 3–5 °C (Landau and Holmes, 1988; Vaughan and others, 2006; Merriman and others, 2012). Each squirrel was placed in a separate hibernation cage, a clear plastic kitchen container (24×21×17 cm) with holes and locking lids (Vaughan and others, 2006; Merriman and others, 2012).

In addition to California ground squirrels, two non-sciurid rodent species have been housed outdoors. Key Largo woodrats were placed in an outdoor compound exposed to natural sounds and scents (Alligood and others, 2011). This compound was protected from predators by a double-layer fencing system and from weather by a roof mounted on wood rafters. Woodrats were housed in separate enclosures (93×62×60 cm) that were stackable in threes. Some cages were connected with a system of wire mesh tubes mounted from the ceiling of the compound that included runways and feeding or nesting stations to simulate natural foraging and social behaviors (Alligood and others, 2011). Amargosa voles sometimes were housed in stock tank mesocosms (147×99×64 cm) that were covered with a tight-fitting screen with a latched wooden door to prevent animal escape (Allan and others, 2018). These mesocosms were placed within outdoor chain link runs (214×214×305 cm) with attached roofs and floors that provided protection from predators, while simultaneously helping to transition the animals to natural conditions (Allan and others, 2018).

None of the captive breeding programs reviewed used a vertical burrowing structure in animal enclosures. However, the captive breeding program for black-footed ferrets, a burrowing carnivore species, housed each animal in an indoor enclosure with a simulated burrow (Poessel and others, 2011). Each enclosure consisted of a wooden cage (1.2×1.2×0.6 meters [m]) elevated from the ground, with a nest box attached directly to the cage and a second nest box placed on the floor beneath the cage. This second nest box was connected to the bottom of the cage with a piece of ribbed, black tubing that simulated a vertical tunnel. Another black plastic tube was suspended from the ceiling of the cage as an additional shelter (Poessel and others, 2011).

Diet

Sciurids in captivity usually have been maintained on a mixed diet of protein and vegetables. Diet components typically are either natural, processed, or both. Regardless of the components, an important goal of the diet of captive sciurids is to provide opportunity to maintain wear of their elodont incisors (Merriman and others, 2012).

Protein sources varied among studies. California ground squirrels were fed laboratory pellets (Marsh and Howard, 1968). Purina rodent chow was provided to Michigan 13-lined, Cascade golden-mantled, Richardson's, and Columbian ground squirrels (Landau and Holmes, 1988; Kenagy and others, 1989; Dobson and Michener, 1995; Murie and others, 1998), as well as white-tailed and black-tailed prairie dogs (Harlow and Frank, 2001). In the Wisconsin colony of 13-lined ground squirrels, the base diet was changed over the years from rodent chow to commercial dog chow (IAMS) or cat chow (Purina), due to the higher protein content of the dog and cat food (Vaughan and others, 2006; Merriman and others, 2012).

Another common protein source provided to sciurids was seeds. Sunflower seeds were used as a supplement to the base diet for both Richardson's and Wisconsin 13-lined ground squirrels (Dobson and Michener, 1995; Vaughan and others, 2006; Merriman and others, 2012). Breeding 13-lined ground squirrels also were fed large, live mealworms (Merriman and others, 2012). Pups (and, eventually, all animals in this colony) were provided kitten formula through a medicine dropper or plastic pipette (Merriman and others, 2012).

The vegetable component of the diet also varied among studies. A variety of greens were fed to California ground squirrels (Marsh and Howard, 1968). Lettuce leaves, which can be a valuable water source, were provided to Richardson's and Columbian ground squirrels (Dobson and Michener, 1995; Murie and others, 1998). Carrots and celery were fed to 13-lined ground squirrels in the Wisconsin colony (Vaughan and others, 2006; Merriman and others, 2012).

Water was usually provided *ad libitum*. For both Columbian and 13-lined ground squirrels, water was available from a glass or plastic bottle with a metal sipper tube (Murie and others, 1998; Vaughan and others, 2006). Although none of the sciurid studies stated that they provided water in bowls or dishes, some of them did not describe the details of water provisioning (Marsh and Howard, 1968; Landau and Holmes, 1988; Kenagy and others, 1989; Harlow and Frank, 2001; Merriman and others, 2012). However, water was provided in bowls for Key Largo woodrats (Alligood and others, 2011), Allegheny woodrats (Smyser and Swihart, 2014), and Amargosa voles (Allan and others, 2018).

Thirteen-lined ground squirrels naturally fattened towards the end of the active season (that is, the season when animals were awake and active; Merriman and others, 2012). Just before hibernation, they reduced consumption of food and production of waste (Vaughan and others, 2006). When an individual squirrel was placed in the cold room, a small

number of sunflower seeds was placed in the hibernation cage, but no other food or water was provided until arousal the following spring (Merriman and others, 2012).

Environmental Enrichment

Environmental enrichment in enclosures can provide multiple benefits to animals in captivity, including reduction in stress (Poessel and others, 2011), enhancement of memory and learning (Schrijver and others, 2002), and reduction of stereotypic behaviors (Jones and others, 2011). The 13-lined ground squirrels in the Wisconsin colony were provided a variety of enrichment items, described as cage enrichment, novel foods, and manipulanda (Merriman and others, 2012). Cage enrichment included different types of nesting material and plastic tubes (see “Housing” section above). Novel foods included seeds, mealworms, vegetables, alfalfa (when seasonally available), kitten formula (see “Diet” section above), and live crickets (but only if cages were designed to prevent cricket escape). Fresh vegetables were sometimes provided in food balls, and dried corn on the cob also was sometimes supplied. Scattering food items throughout the cage substrate also simulated foraging behavior. Finally, manipulanda included chew sticks and chewable rodent huts, but the squirrels ignored these items. Running wheels also were provided, and the squirrels readily used these. However, the researchers noted that caution should be exercised with the provision of running wheels because squirrels can develop repetitive running behavior after the wheel is removed (Merriman and others, 2012).

Captive breeding programs for non-scuriid rodents also have used environmental enrichment. Key Largo woodrats received willow, pinecones, grapevine, cardboard tubes, and running wheels, and these items were rotated twice per week (Alligood and others, 2011). Allegheny woodrats received eastern red cedar limbs for vertical structure, cardboard tubes for hiding or shredding, elevated platforms for resting, running wheels (on a rotational basis) for exercise, rodent block that was either buried in a bowl of sand, hidden in a cardboard box packed with hay, or scattered in the enclosure, and various nesting materials, such as cedar slab wood, crinkle paper, or facial tissue in a spinning hay holder attached to the side of the enclosure (Smyser and Swihart, 2014). Finally, Amargosa voles received 454-gram (g) compostable cups filled with potting soil to encourage natural digging behaviors (Allan and others, 2018).

Sociality

Few studies of either scuriid or non-scuriid rodent species have addressed sociality or intra-specific interactions among captive animals. Individuals are usually housed singly, except during the breeding season (see “Reproduction”

section below). Thirteen-lined ground squirrels are considered to be an asocial species, and they have not been observed grooming each other, outside of courtship behavior during the breeding season (Merriman and others, 2012). However, adults may require social interactions with conspecifics via vocal communication and alarm calling (Merriman and others, 2012). Additionally, a controlled study showed the importance of social interactions to juvenile 13-lined ground squirrels (Lahvis and others, 2015). The authors of that study concluded that juvenile individuals of this species, despite their asocial status, should be housed in social groups (that is, in the same enclosure) rather than in isolation (Merriman and others, 2012; Lahvis and others, 2015).

Two additional observations are useful to understand when making decisions regarding social housing of captive animals. First, some 13-lined ground squirrels were housed in pairs or groups in the same enclosure just before hibernation (Merriman and others, 2012). When one animal in the group entered torpor, the cagemates would begin to eat the hibernating animal. Wild 13-lined ground squirrels always hibernate singly in separate hibernation chambers. Thus, current practice in the Wisconsin colony is to move all animals to single housing well in advance of hibernation (Merriman and others, 2012). Second, Amargosa voles raised together indoors were moved to outdoor enclosures (see “Housing” section above; Allan and others, 2018). After being moved, male voles displayed aggression to each other outdoors, but female voles could be safely housed in groups outdoors (Allan and others, 2018). This illustrates that social housing conditions and tolerances can vary by sex and species.

Health

Monitoring the health of scuruids is an essential component of a captive breeding program. Cross-contamination of parasites from wild to captive animals was identified as the primary health issue in the 13-lined ground squirrel colony in Wisconsin (Merriman and others, 2012). To protect against such cross-contamination, individuals captured in the wild were injected with ivermectin and wiped with flea and tick spray to treat parasites. They were then quarantined for 1–2 weeks (inside the same room used for hibernation in winter) before being moved into the captive colony (Vaughan and others, 2006; Merriman and others, 2012). For animals housed in groups, parasite transmission was reduced with regular changes of bedding (Vaughan and others, 2006). This population also was monitored regularly for a variety of typical rodent diseases, none of which were ever detected (Merriman and others, 2012).

The environmental assessment for the Mount Graham red squirrel discussed a 30-day quarantine period, both for captured animals brought into captivity and for captive animals prior to release back into the wild (USFWS, 2010). This was to prevent the introduction of disease or parasites

into the breeding facility or wild populations. During this period, animals receive a complete physical examination, infectious disease testing, and vaccinations (USFWS, 2010).

Health conditions for non-sciurids in captivity also have been monitored. After capture, Pacific pocket mice were inspected for pelage condition and ectoparasites, weighed, and quarantined for 14–30 days (Shier, 2014). Fleas, ticks, and lice were collected, and fecal samples from the mice were taken to test for endoparasites. Ectoparasites were rare, and fecal assays for endoparasites were negative. All mice gained weight while in captivity, indicating that they were in good condition and adjusted well to the captive environment (Shier, 2014). Captured *Amargosa* voles were also quarantined for a 2-week period (Allan and others, 2018). Voles were examined once per month for a health checkup, including evaluation of mass, body condition, alertness, hydration, breathing, facial appearance, and presence of ectoparasites. Voles developed tumors, abscesses, and other diseases while in captivity. Voles also were found to be highly sensitive to anesthesia, so doses of anesthetic drugs for this species had to be less per unit of body weight than those used for most small mammals (Allan and others, 2018).

Survival

Survival of animals in a captive breeding and release program can be measured in two ways: (1) survival of animals while in captivity, and (2) survival of animals after release into the wild. In the first years of the captive breeding program for 13-lined ground squirrels in Wisconsin (2002–05), 11 percent of animals captured during this period died in captivity (6 of 53; Vaughan and others, 2006). Causes of death included ingestion of rodenticide before capture, a self-inflicted leg injury, failure to thrive, and a non-contagious vestibular disorder (running in circles with the head held to the side). Individuals died during hibernation in only two cases, two wild-captured juveniles, each housed alone, and three captive-bred juveniles housed together. Subsequently, the diet of these animals was changed to a higher-protein food (see “Diet” section above), and the protocol was changed to house hibernating animals singly (see “Sociality” section above). Since that time, no animals have died during hibernation from causes other than old age (Vaughan and others, 2006; Merriman and others, 2012).

Survival of adult female Columbian ground squirrels that gave birth in captivity and were subsequently released with their litters was similar to that of wild animals, indicating that time in captivity had no negative effect on survival (Murie and others, 1998). Sixty percent of captive-born litters survived to emergence intact, 26 percent experienced partial loss, and 14 percent were a total loss. The percentage of litters that were a total loss was somewhat lower for captive-born litters than for wild-born litters. Finally, post-release survival of captive-born juveniles was similar to survival of wild-born juveniles

(Murie and others, 1998). However, because this study was an experiment and animals were only in captivity for a short period of time (2–6 days), these results likely are not relevant to a long-term captive breeding and release program.

The Key Largo woodrat program was evaluated by comparing survival of captive, captive-born and released, and wild-born woodrats (McCleery and others, 2013). The 3-month survival rate was highest for captive woodrats (0.988), followed by wild-born woodrats (0.942), followed by captive-born and released woodrats (0.561). The cause of death for all but one of the fatalities in the wild was predation. The authors concluded that, because of their low rate of survival, releasing woodrats bred in captivity under current protocols was not an effective management tool for increasing the wild population (McCleery and others, 2013).

Finally, as of 2014, 13 mortalities were reported in the Pacific pocket mouse captive breeding program (Shier, 2014). One adult male had a broken leg, and one adult female contracted bacterial endocarditis. Eleven pups also died. Of these, five from one litter and three from another litter were all birthed by inexperienced females that did not lactate. Three others were runts from different litters, and one of these runts was cannibalized by the female (see “Reproduction” section below). Overall, pup survival rate was 73 percent (Shier, 2014).

Reproduction

Reproduction protocols for captive breeding programs for sciurids, as well as non-sciurids, have been well described in the literature. These protocols include information on pairing of animals, breeding readiness and success, gestation, litter size, litter success, double litters, maternal infanticide, body condition and growth, and weaning. We briefly discuss each of these topics below.

Pairing of Animals

An important first step before breeding animals in captivity is determining which adults will be placed together and how they will be paired. In the Wisconsin colony of 13-lined ground squirrels, animals were captured from the wild and used as breeders at least every third generation (Merriman and others, 2012). Individual squirrels have been bred until at least 5 years of age. If a particular male and female bred successfully, and the young had a behavioral phenotype “favorable” to being maintained in this research colony, then that pair was re-bred for multiple years (Merriman and others, 2012). However, what is favorable for a research colony may not be relevant for conservation purposes. For example, the behavioral phenotype of young animals in a conservation program may not be important because many of these individuals likely will be released to the wild rather than remain in the captive population.

In this colony, all males were removed from the cold room (defined in the “Housing” section above) at the same time and placed in the “warm room” where animals were kept during the active season (Vaughan and others, 2006; Merriman and others, 2012). Two weeks later, all females were removed from the cold room, placed in single housing for 48 hours, and then males and females were placed together. As many as three females were placed with one male; usually this meant that an experienced male was placed with 1–3 young females from the same litter. In the early years of the program, the male was left with the female(s) until a female produced a litter or until the male's testes regressed (Vaughan and others, 2006). More recently, 28 days after they were first placed together, the male and each female were moved to separate cages (Merriman and others, 2012).

Pairing decisions for some of the non-sciurid species in captive breeding programs for conservation purposes typically have been based on genetics. For example, pairing of Key Largo woodrats in captivity was based on consultations with a geneticist and the USFWS using information from the Association of Zoos and Aquariums (AZA) studbook for that species (Alligood and others, 2011). For Allegheny woodrats, only wild-caught animals were allowed to breed (Smyser and Swihart, 2014). For Pacific pocket mice, pairing decisions also were made by a genetics team (Shier, 2014). Finally, for Amargosa voles, pairs were chosen based on pedigree data and a goal to preserve genetic diversity (Allan and others, 2018).

Different strategies have been used to encourage mating of pairs. The enclosures of male and female Key Largo woodrats were connected with a wire mesh tube with an exclusion door on the male's cage (Alligood and others, 2011). This door was opened only after a 7-day introductory period that allowed the pair to have visual and olfactory, but no physical, contact (Alligood and others, 2011). One Allegheny woodrat male was paired with two females (Smyser and Swihart, 2014). All three animals were housed in separate enclosures that were connected by a system of access tubes and doors that also could be used to restrict interactions between animals (Smyser and Swihart, 2014). A female Pacific pocket mouse was allowed to select one of two males placed in adjacent enclosures, and she was deemed to have chosen a male based on the amount of time spent next to that male's enclosure (Shier, 2014). The pair was then placed in the same enclosure (Shier, 2014). Finally, an Amargosa vole pair was placed together in a mating cage, but the animals were separated if aggressive behavior was observed (Allan and others, 2018).

Breeding Readiness and Success

Captive breeding programs are more successful if adult animals can be placed together when both males and females have achieved breeding readiness. In the 13-lined

ground squirrel colony in Wisconsin, the purpose of the 2-week delay in pairing males and females was to allow male testes to enlarge, so males could achieve breeding readiness before being placed with females (Vaughan and others, 2006; Merriman and others, 2012). Time since emergence from hibernation appears to be a critical factor in determining whether females will mate with males (Landau and Holmes, 1988). Behavioral receptivity of females differed from estrus, which was determined by daily vaginal lavages. Females were in estrus within 2 days after removal from the cold room, and estrus lasted for 2–5 weeks. However, if females were not paired with a male within 2 weeks of removal from the cold room, behavioral receptivity terminated, and regardless of estrus status, these females did not get pregnant when subsequently paired with a male (Landau and Holmes, 1988).

Hibernation appeared to be an important breeding cue for females, but not for males. Breeding success was lower for female 13-lined ground squirrels that did not hibernate than for those that did (Merriman and others, 2012). Without knowing the timing of arousal from hibernation, determining when a non-hibernating female entered estrus, and thus when she should be paired with a male, was difficult. By contrast, males that did not hibernate still developed enlarged testes and were fertile at the same time as males that had hibernated (Merriman and others, 2012).

Captivity may influence breeding readiness of some sciurids. Two male round-tailed ground squirrels (*X. tereticaudus*) held in captivity for greater than or equal to (\geq) 6 months had large testes and motile spermatozoa in late summer, well past the typical spring breeding season for the species (Neal, 1965). The authors suggested that captivity may have delayed regression of the testes. By contrast, one captive male Harris's antelope squirrel (*Ammospermophilus harrisi*) had small testes in late summer, similar to those of wild males (Neal, 1965). For 13-lined ground squirrels, the only males reported to have large testes after mating season were those housed with females who did not become pregnant (Vaughan and others, 2006).

For non-sciurid rodent species, determining breeding readiness and when females come into estrus can be more challenging because some of these species breed year-round. Sexual maturity of males generally can be determined by descended testes, but females may not show obvious physical changes due to estrus. Thus, for both Key Largo and Allegheny woodrats, observations of behaviors and interactions between a male and female whose enclosures were adjacent to each other were used to determine when they were ready for mating (Alligood and others, 2011; Smyser and Swihart, 2014). By contrast, the genitals of female Pacific pocket mice showed visible changes and produced a discharge during estrus (Shier, 2014). Hence, males were paired with females during peak estrus (determined by observation of a taut vulva with noticeable mucous or blood; Shier, 2014).

Gestation and Litter Size

Gestation periods reported in the literature for sciurid species range from 23 to 35 days, and for non-sciurid rodent species, they range from 21 to 40 days. Litter sizes of sciurid species range from 1 to 12, and for non-sciurid rodent species, they range from 1 to 6. Gestation periods and litter sizes are reported in [table 1](#).

Litter Success

Litter success rates vary among sciurid species kept in captivity. During the first and second seasons that California ground squirrels were in captivity, only 2 of 20 and 5 of 31 females, respectively, produced a litter (10 percent and 16 percent litter success rates; Marsh and Howard, 1968). All five litters in the second season were from enclosures that contained one male and two females (Marsh and Howard, 1968). For 13-lined ground squirrels in Michigan, females that

mated within 1 week of removal from the cold room had a 100 percent litter success rate in the first year (8 of 8 females) and a 40 percent success rate in the second year (2 of 5 females; Landau and Holmes, 1988). Reported litter success rates of 13-lined ground squirrels in Wisconsin varied from 11 to 75 percent (Vaughan and others, 2006). Finally, of 101 female Richardson's ground squirrels that were brought into captivity while pregnant, 97 gave birth (96 percent litter success rate; Dobson and Michener, 1995).

For non-sciurids, litter success rates are also variable. For example, less than (<) 15 percent of copulations in Key Largo woodrats have resulted in pregnancy, and five stillbirths have occurred (Alligood and others, 2011). The litter success rate for Allegheny woodrats over a 2-year period was 58 percent (19 of 33 pairings; Smyser and Swihart, 2014). For Pacific pocket mice, in the first 2 years of the program, 5 of 14 and 7 of 13 copulations resulted in pregnancy (36 and 54 percent success rate, respectively; Shier, 2014). Finally, nearly 80 percent of Amargosa vole pairings (57 of 72) resulted in successful litters (Allan and others, 2018).

Table 1. Gestation periods and litter sizes for sciurid and non-sciurid rodent species.

[Gestation periods (in days) and litter sizes reported in the literature]

Species	Gestation period	Litter size	Reference
Sciurids			
Round-tailed ground squirrels (<i>Xerospermophilus tereticaudus</i>)	28–35	4–9	Neal, 1965
Harris's antelope squirrels (<i>Ammospermophilus harrisi</i>)	30	6–7	Neal, 1965
California ground squirrels (<i>Otospermophilus beecheyi</i>)	Not reported	3–8	Marsh and Howard, 1968
Cascade golden-mantled ground squirrels (<i>Callospermophilus saturatus</i>)	Not reported	3–5	Kenagy and others, 1989
Richardson's ground squirrels (<i>Urocitellus richardsonii</i>)	23	Not reported	Dobson and Michener, 1995
Columbian ground squirrels (<i>Urocitellus columbianus</i>)	24	1–5	Murie and others, 1998
13-lined ground squirrels (<i>Ictidomys tridecemlineatus</i>)	28–30	6–12	Vaughan and others, 2006; Merriman and others, 2012
Non-sciurids			
Key Largo woodrats (<i>Neotoma floridana smalli</i>)	37–40	Not reported	Alligood and others, 2011
Allegheny woodrats (<i>Neotoma magister</i>)	37–39	1–3	Smyser and Swihart, 2014
Pacific pocket mice (<i>Perognathus longimembris pacificus</i>)	Not reported	2–6	Shier, 2014
Amargosa voles (<i>Microtus californicus scirpensis</i>)	21	1–6	Allan and others, 2018

Double Litters

Production of two litters in the same breeding season is rare among the sciurid species, both in the wild and in captivity, but it has occasionally occurred. That said, we found no definitive records in the literature of any captive sciurid females successfully raising two litters in the same season. Two round-tailed ground squirrel females were captured from the wild when pregnant late in the breeding season, and the authors surmised that these females may have been older and bred twice, although they acknowledged that second litters in the same season are not common (Neal, 1965). The managers of the 13-lined ground squirrel colony in Wisconsin attempted several times to breed females twice in the same year, but the 1 time a female successfully bred twice, no pups survived to weaning (Merriman and others, 2012). That female killed her first litter 1 day after birth, re-bred with a male, produced a second litter, and then killed that litter as well (see “Maternal Infanticide” subsection below; Merriman and others, 2012). Because non-sciurid species have life cycles that differ from sciurid species, and some non-sciurid rodents can successfully breed year-round (for example, Amargosa voles; Allan and others, 2018), those species are not reviewed here.

Maternal Infanticide

As noted in the previous subsection, female sciurids held in captivity sometimes kill their young after birth. One female Columbian ground squirrel cannibalized her pups shortly after birth in each of 2 consecutive years (Murie and others, 1998). In the first years of the captive breeding program for 13-lined ground squirrels in Wisconsin, maternal cannibalism occurred occasionally, usually within the first 4 days of birth, but this appeared to end after a higher-protein diet was introduced (see “Diet” section above; Vaughan and others, 2006). However, in later years of the program, even though animals were fed the high-protein diet, maternal infanticide occurred, with up to 35 percent loss of litters in a season, usually in the first 2 days after birth (Merriman and others, 2012).

The managers of this program drew two qualitative conclusions from their experiences. First, they recommended that pups not be handled by caretakers during their first week of life to reduce the risk of infanticide (Vaughan and others, 2006). Second, because infanticide rates were much lower for wild-captured females than for captive-bred females, they suggested that maternal stress resulting from captivity may have been a potential cause of infanticide (Merriman and others, 2012).

Maternal infanticide has been observed in non-sciurid species as well. As reported in the “Survival” section above, at least one Pacific pocket mouse pup was cannibalized by its mother shortly after birth (Shier, 2014). Additionally, although numbers were not reported, Amargosa vole pups that died were often cannibalized by the female (Allan and others, 2018).

Body Condition and Growth

At least two sciurid studies have analyzed body condition and weight gain of females and pups during the lactation and post-natal growth period. For Cascade golden-mantled ground squirrels, lactating females increased food consumption an average of 2.1 times the pre-lactation level, but body mass increased only slightly during the first 30 days of lactation (Kenagy and others, 1989). The average mass at birth of individual pups was not related to litter size, but at the time of weaning, pups in larger litters weighed less than pups in smaller litters. Growth rate of pups was generally linear from birth to weaning, and this rate was still linear, but faster, after weaning, when they began to eat solid foods. After 60 days, pups reached adult body mass (Kenagy and others, 1989).

Female Richardson's ground squirrels brought into captivity when pregnant appeared to adjust to captive conditions and diet, and they made modest gains in mass by the time of parturition (Dobson and Michener, 1995). Litter mass and litter size were smaller for yearling females than they were for older females. Further, just after emergence from hibernation, body masses of yearlings were lower than for older adults. However, by late pregnancy, their masses were similar, indicating that yearling females were still growing during the gestation period. Finally, for all age classes, females with greater post-parturition mass had heavier offspring, and females that gave birth later in the season had smaller litters but heavier pups (Dobson and Michener, 1995).

Weaning

Ages of young at weaning are similar among sciurid species. These ages usually range from 30 to 35 days. Cascade golden-mantled ground squirrel pups were fully independent at 30–35 days old, and the mean age of earliest handling of food (that is, rodent chow) by pups was 34 days old (Kenagy and others, 1989). Thirteen-lined ground squirrel pups were also weaned at 30–35 days old, at which time the litter was separated from the female and placed together in a larger cage (Vaughan and others, 2006; Merriman and others, 2012).

Ages at weaning are more variable among non-sciurid species. These ages range from 20 to 65 days. Key Largo woodrat pups reduced their nursing and began eating solid food at approximately 25 days old but were not separated from the female until day 65 (Alligood and others, 2011). Allegheny woodrat pups began consuming solid food at an age of 21 days but were not transferred to separate housing until they were 45 days old (Smyser and Swihart, 2014). Finally, Amargosa vole pups were weaned and separated from the female at 20–21 days old (Allan and others, 2018).

Hibernation

Most sciurid species that we reviewed follow an annual cycle that involves activity aboveground in the spring and summer and hibernation belowground in autumn and winter. For the most part, animals retained this cycle while in captivity. White-tailed and black-tailed prairie dogs were placed in a hibernation room as part of an experiment comparing hibernation and physiological conditions between the two species (Harlow and Frank, 2001). The 13-lined ground squirrels in Michigan were placed in the cold room for hibernation in the autumn and were removed the following spring (Landau and Holmes, 1988).

More detailed information on hibernation has been provided for the 13-lined ground squirrel colony in Wisconsin, and the remainder of this section is drawn from the protocols for this colony. By late summer/early autumn body temperatures of squirrels were lower, and squirrels began to cycle in and out of torpor, indicating they were nearing hibernation readiness (Vaughan and others, 2006). Methods used by staff members to determine whether an animal was ready for hibernation were evaluation of the type of nest made (a covered dome rather than a shallow cup), of the amount of time spent in the nest, and of food intake (which decreased as hibernation approached; Merriman and others, 2012). In later years of the program, squirrels were implanted with transmitters that recorded body temperatures, which were used to confirm immergence into torpor (Merriman and others, 2012). Once squirrels were moved to the cold room, which was kept dark throughout the hibernation season, caregivers checked on them daily (Vaughan and others, 2006). If any individual aroused and remained awake for more than 48 hours, that squirrel was returned to the warm room for another 1–2 weeks, then brought back to the cold room for another hibernation attempt (Vaughan and others, 2006).

Each year, some individuals in the colony did not enter torpor, and in late autumn these animals were placed in the cold room without food and water (Merriman and others, 2012). If an individual was still aroused after 48 hours, then that squirrel was moved between the warm room and the cold room on a weekly basis until mid-December. At that time, non-hibernating animals were kept in the warm room throughout the winter. No animal failed to hibernate 2 years in a row (Merriman and others, 2012).

As described in the “Reproduction” section above, by late March to early April, all males were removed from the cold room, whether they were aroused or not, to synchronize breeding, and females were removed 2 weeks later (Vaughan and others, 2006; Merriman and others, 2012). Two or three males were removed from the cold room in late February, to accommodate early-arousing females (Merriman and others, 2012). This annual cycle of hibernation and arousal results in reproduction occurring only once per year, in the spring. Reproduction once per year is the norm, not only for 13-lined

ground squirrels, but for other sciurid species as well. Because many non-sciurid rodent species do not hibernate, those are not reviewed here.

Pre-Release Conditioning

The goal of a captive breeding and release program is eventually to release captive-bred animals back into the wild. Although some of these programs have been successful, others have failed (Fischer and Lindenmayer, 2000). An important reason for such failures is that captive-bred animals often lack sufficient survival skills for life in the wild (Greggor and others, 2019). Some animals have reduced survival post-release due to deficient locomotion, lack of spatial orientation, or inability to recognize natural foods or predators (McPhee, 2003). Further, animals in captivity for multiple generations can show increased among-individual variation in predator-avoidance behaviors, suggesting relaxed selection while in captivity, which, in turn, decreases survival after release (McPhee, 2003).

For prey species, such as sciurids, mortality caused by predation is one of the primary reasons a release program might fail (Griffin and others, 2000; Greggor and others, 2019; Tetzlaff and others, 2019; Rowell and others, 2020). Thus, implementing a pre-release training program that teaches anti-predator skills to naïve animals is increasingly recognized as important to captive breeding and release programs (Griffin and others, 2000; Tetzlaff and others, 2019; Rowell and others, 2020). Such training has the potential to increase the expression of anti-predator behaviors by animals post-release (Griffin and others, 2000) and equip animals with survival skills (Greggor and others, 2019).

One effective training method is to pair a predator, either a live or model predator, with a desired anti-predator behavior (Griffin and others, 2000). For example, a predator model could be presented simultaneously with a mildly aversive stimulus, such as thrown rubber bands, squirted water, mild electric stimulation, or flashes of light (Griffin and others, 2000; Greggor and others, 2019). Alternatively, the model could be paired with a frightening stimulus, such as a recording of a conspecific alarm call, loud noises, or being chased by the model (Griffin and others, 2000; Greggor and others, 2019). Frightening stimuli are likely to be more effective than startling stimuli (Griffin and others, 2000). The most useful stimuli are those that are ecologically relevant for the species, that is, a predator in the wild is likely to occur with the stimulus, such as a conspecific alarm call (Rowell and others, 2020). Some studies have noted that too much training can result in habituation, which could reduce post-release survival (Griffin and others, 2000).

Evidence suggests that, because anti-predatory skills are learned during early developmental years, juveniles likely are able to learn about predators more easily than are adults (Griffin and others, 2000). Anti-predator experiments

have been conducted for juvenile black-tailed prairie dogs in outdoor enclosures (Shier and Owings, 2006, 2007). In the first set of experiments, one group of juveniles was exposed to three different predators (a live black-footed ferret, a taxidermically-mounted red-tailed hawk [*Buteo jamaicensis*], and a live prairie rattlesnake [*Crotalus viridis*]), each paired with a prairie dog alarm call (Shier and Owings, 2006). A second group was the control with no exposure. After the experiment, the juveniles were released. Relative to control animals, the trained animals were less active and spent more time vigilant, in or near shelter, and alarm calling. Trained animals also had higher survival than control animals 1 year post-release (Shier and Owings, 2006). In the second set of experiments, captive-reared juveniles were exposed to the three different predators either with or without the presence of an experienced adult prairie dog (Shier and Owings, 2007). Animals trained with an adult were more wary of the predators than were animals trained without an adult. Further, juveniles trained with an adult were more likely to survive 1 year post-release than were juveniles trained without an adult, and survival of animals trained with an adult did not differ from survival of wild-reared juvenile prairie dogs (Shier and Owings, 2007). Although prairie dogs are more social than other ground squirrel species, these experiments provide evidence that anti-predator training can enhance post-release survival of captive-reared sciurids.

Literature reviews and meta-analyses suggest mixed results of anti-predator training of captive animals. Animals released from captivity were 1.7 times more likely to survive if they had been conditioned (which, in addition to anti-predator training, included environmental enrichment or soft release), with captive-bred juveniles having a higher likelihood of survival than captive-bred adults (Tetzlaff and others, 2019). However, only 53 percent of studies that measured post-release survival of trained versus untrained animals reported increased survival in the wild of trained individuals, with the remainder of studies reporting no increase in survival (Rowell and others, 2020). Although multiple factors can contribute to unsuccessful training programs, with success measured as increased post-release survival of trained individuals, one primary factor is the assumption that all training methods are appropriate for all species. Thus, protocols designed to meet the specific predator-avoidance requirements of the target species likely will maximize the chances of success of an anti-predator training program (Rowell and others, 2020).

Rowell and others (2020) suggested a series of steps to follow before initiating an anti-predator training program. These were:

1. identify predators at the release site;
2. identify behavioral characteristics of captive-bred animals that would make them susceptible to predators;
3. determine if anti-predator training is appropriate;

4. design training methods to address any behavioral deficits (for example, those induced by being bred in captivity for multiple generations);
5. compare behavior pre- and post-training, compared to untrained controls; and
6. post-release, compare survival of trained animals with controls (Rowell and others, 2020).

For steps 2 and 3, experiments with wild-reared individuals can provide baseline information on anti-predator behavior of the species, which then can be used to determine if anti-predator training is necessary for captive-born individuals. For example, wild-born Pacific pocket mice were exposed to predators after being brought into captivity, and their behaviors were documented (Shier, 2014). These test results were then used as a baseline to evaluate behaviors of captive-born mice to determine if anti-predator training was required and, if so, whether post-training behaviors were similar to those of the wild-born animals (Shier, 2014).

The final component of an anti-predator training program is assessing and measuring the effectiveness of the program (steps 5 and 6). A post-training assessment of anti-predator responses can determine whether an animal benefited from the training (Greggor and others, 2019). In addition to measuring behavioral change after training, evaluating post-release survival also will provide a clear understanding of the overall effectiveness of the training (Rowell and others, 2020).

Release

Release of captive-bred or translocated (see “Translocation” section below) animals is an important strategy for many species of conservation concern. Releases of most species generally have followed the guidelines published by the IUCN/SSC, which state that any release “must be justified, with development of clear objectives, identification and assessment of risks, and with measures of performance” (IUCN/SSC, 2013). Assessment of a proposed release can identify the potential benefits as well as the potential negative effects, including ecological, economic, and social impacts of the release. The guidelines further recommend having an exit strategy in place in case the release does not proceed according to plans (IUCN/SSC, 2013).

Several factors can increase the chance of having a successful release:

1. releasing 100 individuals or more (at once or over time);
2. removing the initial cause of decline at the release site; and
3. providing supportive measures before or after release (Fischer and Lindenmayer, 2000).

These supportive measures can include pre-release conditioning (discussed in the previous section), habitat modification, veterinary care, or provision of food, water, or shelter. Other factors to consider include, but are not limited to, genetics, inter-specific competition, and public education and outreach (Fischer and Lindenmayer, 2000).

A primary consideration for any release program is whether releases are “hard” or “soft.” A hard release is an immediate release of animals at a site with no enclosures or barriers and with no provisioning of resources by humans (Tetzlaff and others, 2019). A soft release is a gradual release of animals, first by placing animals in outdoor enclosures and providing supplementary resources, then releasing animals at the site. With a soft release, animals can acclimate to the new environment at the release site, and they may be less likely to immediately disperse upon release. Although some studies have found no effect of hard versus soft release on survival, others have reported reduced dispersal and increased survival associated with soft releases (Tetzlaff and others, 2019).

Several sciurid species, especially prairie dogs, have been reintroduced into previously extirpated areas using a soft-release method. Soft releases for prairie dogs typically involved acclimating the animals in artificial burrows (boxes or pots ranging from 30×30 cm cylinders to 30×45×30 cm boxes) placed in holes dug in the ground (ranging from 1 to 2 m deep; Long and others, 2006; Shier, 2006; Curtis and others, 2014; Davidson and others, 2014). Plastic corrugated tubing (10-cm diameter) connected the burrow to the surface. A cage (usually made from wire mesh and ranging from 50×50×25 cm to 40×90×90 cm) was then placed on the surface over the tube entrance to discourage dispersal and to deter predators (Long and others, 2006; Shier, 2006; Curtis and others, 2014; Davidson and others, 2014). In these releases, food was placed daily in the aboveground cages for up to 1 week, then the aboveground cages were removed (Long and others, 2006; Davidson and others, 2014). Other maintenance of release sites sometimes included mowing tall (greater than [$>$] 15 cm) vegetation to remove cover for predators (Dullum and others, 2005; Long and others, 2006), installing a temporary electric fence to exclude cattle that can damage aboveground cages (Long and others, 2006), and continuing to set out food for released animals after cages were removed (Davidson and others, 2014).

Southern Idaho ground squirrels (*U. endemicus*) were reintroduced in western Idaho in 2006–07 (Busscher, 2009). Some of these releases were hard, and some were soft. Squirrels that were hard-released were simply released at a site that contained no shelter or existing burrows. Squirrels that were soft-released were placed in aboveground cages (made from wire mesh and ranging from 0.6×0.6×0.46 m to 2.4×2.4×1.2 m) with no bottoms for 4–7 days. An artificial burrow made from plastic corrugated tubing (10-cm diameter) was buried in the ground below the cage, with one open end of the tube exposed at the surface. Both hard-released and soft-released squirrels were provided food for 1 week. More soft-released adults survived over winter than did

hard-released adults, but no differences in movement distances were observed between the two groups. Regardless of release type, survival was low, and these reintroductions failed to establish populations at the release sites (Busscher, 2009).

The environmental assessment for the Mount Graham red squirrel included protocols for the soft release of captive squirrels (USFWS, 2010). These protocols stipulated that candidates for release would be assessed to determine if they had the necessary behavioral skills to survive in the wild. Behavioral skills considered relevant included food recognition, food caching, predator avoidance, and finding shelter. Good candidates would then be placed in an outdoor enclosure (4.3×3.7×2.1 m) at a site on Mount Graham to allow the animals to experience the climate and elevation of their natural habitat. Protocols called for squirrels to be provided with resources by caretakers for 7–10 days and then released at sites within the species' current range. These sites would be selected to avoid conflicts with humans and to minimize impacts to wild squirrels. Each released individual would then be tracked with radiotelemetry to monitor their movements (USFWS, 2010). As of the time of writing this report, no Mount Graham red squirrels have been produced in captivity and, thus, have not yet been released (Phoenix Zoo, 2022).

The release program for the Key Largo woodrat was not successful (McCleery and others, 2013, 2014). Released woodrats suffered from high mortality rates from predation (see “Survival” section above; McCleery and others, 2013). Although the type of release, hard or soft, was not specified, apparently no anti-predator training was provided to animals pre-release. These authors suggested that an in situ captive breeding program, that is, breeding and raising captive animals in an outdoor facility at the Key Largo release site, might be a better option than the current ex situ program (at Lowry Park Zoo and Disney's Animal Kingdom in mainland Florida) because animals would be exposed to natural conditions their entire time in captivity (McCleery and others, 2013). The results from this program illustrate some of the difficulties with captive breeding and release programs and the importance of ensuring that captive animals are prepared for release.

Translocation

Translocation has been an important conservation strategy for several sciurid species. For the purposes of this report, we define a translocation as capturing animals from an existing site in the wild and releasing them at another wild site, either on the same day of capture or after a brief captive period. For sciurids, translocations have occurred primarily with prairie dogs, but also for southern Idaho ground squirrels (covered in the “Release” section above).

Prairie dogs have been released either the same day of capture (Davidson and others, 1999; Dullum and others, 2005; Curtis and others, 2014) or after a 1–2-week period in

an indoor facility (Long and others, 2006; Shier, 2006; New Mexico Department of Game and Fish, 2008; Davidson and others, 2014). The purpose of the holding period in captivity was to quarantine animals, examine them, and treat them for parasites that might cause disease at the release site. Success, defined as the establishment of a population at the release site, of these translocations was mixed. For black-tailed prairie dogs translocated to multiple sites in the western United States, adults were more likely than juveniles to survive, to reproduce the following year, and to dig new burrows (Long and others, 2006). In Montana, population growth was higher on colonies with more animals released (that is, 120 animals versus 60 animals), and survival was higher for animals released into large extant colonies than into small or extirpated colonies (Dullum and others, 2005). In Arizona, where black-tailed prairie dogs were released beginning in 2008, populations have grown, occupied acreage has increased, and most females have produced pups (Presler and Hicks, 2020, 2021). Gunnison's prairie dogs (*C. gunnisoni*) translocated in New Mexico had low survival (26 percent) over 8 years (Davidson and others, 2014). Precipitation was the primary driver of survival in this population, with < 12 percent survival during severe drought years (Davidson and others, 2014). Finally, translocated Utah prairie dogs (*C. parvidens*) in southern Utah that were heavier at the time of capture at their origin site were more likely to remain at the release site than were lighter animals (Curtis and others, 2014).

Based on these and other studies, a suite of factors have been identified as essential to consider before beginning a translocation program for sciurids. These are:

1. gather baseline biological or ecological knowledge about the species (Novak and others, 2021);
2. decide if novel conditions at a release site should be
 - a. avoided by selecting areas similar to the habitat of the source animals, which removes opportunities for adaptation to new conditions, or
 - b. allowed so that animals can experience and adapt to the novelty of the release site, potentially resulting in higher post-release mortality (Hunter-Ayad and others, 2021);
3. eliminate the original cause of the decline at the proposed release site (Novak and others, 2021);
4. choose release sites with existing burrows (from previously extirpated populations of the same species or from other burrowing species, so that released animals can spend less time excavating new burrows) and with high-quality habitat that includes native grasses, forbs, and shrubs (Busscher, 2009; Novak and others, 2021);
5. consider the size of the release cohort (more individuals may have a greater chance of success; Dullum and others, 2005);

6. consider releasing animals in multiple releases (Davidson and others, 2014);
7. for social species, release individuals in known family groups, as survival and reproductive success may be higher than they might be if family groups are not released together (Shier, 2006);
8. release a mixture of adults and juveniles, but more adults than juveniles, and more females than males (Long and others, 2006);
9. capture and release large, heavy adults if translocating animals early in the season, or wait until later in the season to capture juveniles and lactating females (Shier, 2006; Curtis and others, 2014);
10. consider implementing habitat management or a supplemental feeding program, either short-term or long-term (Presler and Hicks, 2020, 2021); and
11. implement a comprehensive post-release monitoring program, preferably for several years after release (Novak and others, 2021).

Additionally, social support for the release from the community and other stakeholders, as well as a consistent funding source for each step of the program, are vital components of a successful translocation program (Novak and others, 2021).

Common difficulties in translocation programs have been identified (Berger-Tal and others, 2020). Many of these are related to animal behavior, especially dispersal and movement of animals post-release, and to a lesser degree, animal learning, foraging deficiencies, and intra-specific competition. Dispersal can be reduced by implementing soft releases (described in the "Release" section above), by providing supplemental food, or by choosing sites with good-quality habitat. Other common problems identified in translocation programs are lack of, or difficulty with, post-release monitoring, quality of habitat at release sites, lack of baseline knowledge, and lack of funding and public support (Berger-Tal and others, 2020), all of which are noted above as essential factors to consider.

Literature reviews of translocation programs have shown mixed results. Translocations of threatened and endangered species were less successful than those for native game species, but numbers of the former group were small (Griffith and others, 1989). By contrast, translocations were found to have been important to the recovery of 30 percent of United States species that were delisted, and they were a part of the recovery actions for 70 percent of listed species (Novak and others, 2021). However, this same study determined that > 50 percent of all translocation releases did not result in establishment of populations, and that successful programs required multiple releases (Novak and others, 2021). Successful translocations were associated with increased habitat quality at release sites, releasing wild-captured animals rather than captive-bred animals, larger release cohort sizes,

releasing animals into the core of historical ranges (rather than on the periphery or outside historical ranges), release sites without competitor species, and stable or increasing source populations (Griffith and others, 1989). Overall, translocations for conservation purposes tended to generate the intended ecological benefits without resulting in unintended harm (Novak and others, 2021).

Evaluating a Captive Breeding and Release or Translocation Program

For any captive breeding and release or translocation program, international guidelines suggest that the need for, and suitability of, such a program must be carefully evaluated as part of an overall conservation strategy for the target species (IUCN/SSC, 2014). The IUCN/SSC has outlined a 5-step decision-making process that can be followed when deciding whether a program is appropriate for, and will provide conservation benefit to, a species:

1. compile a status review of the species, including a threat analysis;
2. define the role that the program will play in the overall conservation of the species;
3. determine the characteristics of the captive or translocated population needed to achieve the conservation role;
4. define the resources and expertise needed for the program to meet the role and assess the risks; and
5. make an informed and transparent decision (IUCN/SSC, 2014).

Some form of population modeling can be implemented to evaluate a captive breeding and release or translocation program, both before initiating the program and after releases have been made (Seddon and others, 2007; McCleery and others, 2014). Matrix population models can evaluate the effects of alternative management strategies on population dynamics (McCleery and others, 2014) and assess long-term viability of a released population (Seddon and others, 2007). For a new program, modeling can be used to identify demographic targets needed to make the program successful, such as number of animals from the wild, recruitment rate in captivity, and survival of released animals (McCleery and others, 2014).

Finally, as mentioned in the “Translocation” section above, implementing long-term monitoring protocols is important for any captive breeding and release or translocation program. Such protocols include gathering information on key parameters, such as number of animals, sex and age ratios, changes in the released population, and a continuing assessment of threats (Fischer and Lindenmayer, 2000). The

establishment of a viable self-sustaining population at the release site is usually considered to be the ultimate measure of a successful release (Fischer and Lindenmayer, 2000).

Summary

The purpose of this review was to examine protocols for captive breeding and release programs for sciurid species and, in some cases, non-sciurid rodent species. We also discussed wild-to-wild translocations for sciurid species. We anticipate that this review can provide detailed information on these programs to wildlife managers responsible for the conservation and management of Mohave ground squirrels.

Some possible next steps for the Mohave ground squirrel program are to evaluate each of the above sections to determine how each described protocol would apply to the species, identify appropriate resources and funding sources, establish an experimental captive population to refine specific approaches for the species, and outline a protocol for determining when a full-scale captive breeding and release program, or a translocation program, will be necessary. Although some of the protocols outlined in this report may not fully apply to Mohave ground squirrels (for example, some of the methods for prairie dogs, which are social species, may not be entirely relevant to Mohave ground squirrels, which are not as social), each protocol can be considered and evaluated for this species. Comprehensive, thoughtful planning for a captive breeding and release program, or a translocation program, for Mohave ground squirrels will increase the probability of success for that program and may contribute to the continued conservation of the species. As such, a number of questions may be relevant to consider as this process is conducted. Although not an exhaustive list, the following questions, listed by section as described in this report, may be considered in this evaluation:

Capture of Founder Animals

1. What will be the source population for the founders of a captive colony of Mohave ground squirrels? Is this population likely to be displaced by new development? Will there be more than one source population?
2. If a population is not being displaced, what proportion of that local population will be removed?
3. What will be the age and sex ratios of founders?
4. When will trapping take place, which is dependent on the age class of animals to be captured?
5. What will be done if animals are unable to be captured from the source population? Will an alternative site be available for trapping?

Housing

1. What facilities would be willing and able to implement a captive breeding program for Mohave ground squirrels?
2. Should enclosures be indoor or outdoor?
3. If enclosures are outdoor, how should predators and parasites be excluded?
4. If enclosures are indoor, how should light, temperature, and photoperiod be adjusted?
5. How should enclosures and ambient conditions be changed for breeding and hibernation seasons?
6. How should season-specific enclosures be designed, including size, materials, and vertical versus horizontal burrowing structure?
7. What type of nesting material should be placed in the cages?

Diet

1. What foods should be provided to Mohave ground squirrels?
2. Should amounts of food be increased for lactating females?
3. How should food and water be provided, that is, dish, bottle, or provide water only through food?

Environmental Enrichment

1. What types of enrichment should be provided to Mohave ground squirrels?

Sociality

1. Should Mohave ground squirrels be housed singly in enclosures, except during the breeding season, or in groups?

Health

1. How long should Mohave ground squirrels captured from the wild be quarantined before being placed into the captive colony?
2. How should parasites be treated in wild-captured animals?

3. Should any, and what type of, vaccinations should be given to wild-captured animals?
4. How often should captive animals be given health examinations, including physical exams, infectious disease testing, and vaccinations?
5. How long should captive animals be quarantined before release into the wild?

Survival

1. What are acceptable survival rates of Mohave ground squirrels, both in captivity and after release into the wild? This question can be informed by population modeling, as described in the “Evaluating a Captive Breeding and Release or Translocation Program” section above.
2. What type of monitoring program will be implemented to calculate survival rates, especially post-release?

Reproduction

1. How will Mohave ground squirrels be paired, that is, one male:one female, one male:multiple females, etc.?
2. When will pairings begin, and when will males and females be separated? Will this decision be based on time of year or on behavioral observations?
3. Should males and females be placed in the same cage, or in separate cages connected with a tunnel?
4. Should the program have an AZA Studbook, and who will be responsible for maintenance of the Studbook?
5. How will genetics be used in pairing decisions?
6. If females do not hibernate, how will breeding readiness, that is, estrus, be determined?
7. Will double-littering be attempted?
8. At what age will pups be provided solid food, and at what age will they be separated from their mothers?

Hibernation

1. Will there be a separate hibernation room for Mohave ground squirrels, kept dark and at cold temperatures?
2. How will hibernation readiness be determined?
3. Will food be withheld from animals to encourage hibernation?

4. What will be the protocols for animals that do not hibernate?
5. Will all males, and separately females, be aroused from hibernation at the same time to synchronize breeding, as in the 13-lined ground squirrel colony?

Pre-Release Conditioning

1. If captive Mohave ground squirrels are found to have behavioral characteristics that make them susceptible to predators, will anti-predator training be provided to them before release?
2. If anti-predator training will be given, what type will be provided? Will live or model predators be used? Will a recording of a conspecific alarm call be used, or a live adult conspecific?
3. What type of monitoring or experiments will be implemented to compare behavior pre- and post-training, and to compare with untrained controls?
4. What type of monitoring or experiments will be implemented to compare post-release survival of trained animals with controls?

Release

1. How will release sites be chosen? Will they be currently occupied by Mohave ground squirrels, or will they be sites that were previously extirpated? Will the cause of previous extirpation be known, and if so, will that cause no longer be relevant?
2. Will animals only be released in years with sufficient precipitation to ensure an adequate food supply?
3. Will only juveniles be released, or will some breeding adults be released as well?
4. How many squirrels will be released at one time, and how many releases will be made in one season?
5. What time of year will animals be released, which will be dependent on age and sex classes of released animals, and on the timing of anticipated hibernation?
6. Will animals be released in a hard or soft release?
7. If soft release, what type of burrows will be constructed, and what other supportive measures will be provided and for how long?
8. Will released animals be tracked with radiotelemetry to monitor both survival and movements?

9. What type of public education and outreach, if any, will be done before and after releases?

Translocation

1. Will translocations of Mohave ground squirrels take place in addition to, or instead of, a captive breeding and release program?
2. How will source population sites and release sites be chosen?
3. When will translocations take place?
4. Will captured animals be released on the same day or after a short quarantine period?
5. Will family groups, such as a female with weaned pups, be identified at the source site and released together at the release site?
6. What will be the age and sex ratios of captured and released animals?
7. Will habitat management or supplemental feeding at the release site be implemented and, if so, for how long?

Evaluating a Captive Breeding and Release or Translocation Program

1. Before pursuing either program, have the five steps outlined by the IUCN/SSC been followed?
2. Will population modeling be conducted to identify demographic targets needed for a successful program?
3. What long-term monitoring protocols are needed to evaluate the program?
4. Is an exit strategy in place if the program is found to be unsuccessful?

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Glossary

Pre-release conditioning A training program that teaches captive-born animals sufficient survival skills for life in the wild, post-release. One example is anti-predator training, which has the potential to increase the expression of anti-predator behaviors by animals post-release.

Translocation Capturing animals from an existing site in the wild and releasing them at another wild site, either on the same day of capture or after a brief captive period.

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