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TREE SQUIRREL INTRODUCTION: A THEORETICAL APPROACH WITH POPULATION VIABILITY ANALYSIS

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Reintroduction efforts require knowledge of how many animals are needed for successful establishment. Population viability analysis can be used to predict trajectories of introduced populations and tree squirrels provide an ideal model system to investigate this challenge. Conservation action is needed because more than 80% of species of tree squirrels are of precarious conservation status in some portion of their range. We combined data from closely related species of tree squirrels and used VORTEX to determine how many squirrels are needed to successfully establish populations of 6 species (*Sciurus aberti*, *S. carolinensis*, *S. niger*, *S. granatensis*, *S. vulgaris*, and *Tamiasciurus hudsonicus*). We ran multiple simulations to account for between-patch differences in breeding success (resource availability) and variation between years in different habitats. In the best-case scenarios, populations could be successfully established with fewer than 35 individuals for all species and as few as 15 for a subset of species. Empirical evidence from introductions of tree squirrels supports our simulation results, with 93% of populations of greater than 10 squirrels surviving more than 50 years. With relatively few individuals needed for establishing new squirrel populations, reintroductions are feasible and useful as a buffer for imperiled species.

Key words: conservation tools, extinction, management, modeling, population viability analysis, reintroduction, Sciuridae, VORTEX

A fundamental concern of conservation biologists is the point at which a given population is at risk of extinction (Lacy 1992; Morris and Doak 2002; Shaffer 1981; Soulé 1987). Stochastic risks make small populations highly susceptible to extinction (Primack 2000; Pullin 2002); therefore, it is critical to assess the possibility of establishing new populations to buffer stochastic events or to increase the chance of recovery of species in decline (IUCN 1998; Morris 1986). In these reintroductions we are forced to speculate how many individuals are needed for successful establishment. The number of individuals needed can be examined through population viability analysis on small hypothetical populations established in large novel environments, simulating an introduction (Bustamante 1996; Howells and Edward-Jones 1997; Marshall and Edward-Jones 1998; South et al. 2000).

In small populations, where every animal is needed for persistence, experimentation is ill advised and theoretical techniques such as population viability analysis become even more useful. Population viability analysis can be repeated by other interested parties (Akçakaya and Sjögren-Gulve 2000), leaving results and conclusions open for multiple groups to discover and thereby reduce disagreement in decision making. Care should be taken with estimates because often very little is known about a species. However, useful and meaningful results can be generated by assuring the complexity of the question is on the same level as that of the data available (Caswell 2001).

Reintroductions create new populations that can serve as a buffer to extreme events that may cause the extinction of a species of a few or only a single population. Areas where a population has been extirpated and other habitable areas are candidates for such reintroductions, provided that disturbances have been removed and the area suitably recovered (IUCN 1998). Often populations of sufficient size to minimize risk of extinction due to demographic or environmental stochasticity are too large for a single reserve and require multiple sites and management of metapopulations to conserve species (Soulé 1987). Reintroduction is a valuable tool in establishing additional populations. With multiple small populations, species as a whole can have a greater chance at withstanding

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Table 1.—Summary of parameter estimates for VORTEX simulations of tree squirrel introductions. Worst-case scenario is a compilation of the lowest survival and reproductive output values across the 6 species.[a]

Parameter	*Sciurus aberti*	*S. carolinensis*	*S. granatensis*	*S. niger*	*S. vulgaris*	*Tamiasciurus hudsonicus*	Worst-case scenario
First breeding (years)	1	1	1	1	1	1	1
% females breeding (per season)							
Optimistic	90[b]	92	62[b]	65	90	77	
Average	62[b]	70	70[b]	55	90	85	25
Pessimistic	62[b]	70	62[b]	55	90	77	
Breedings (per year)							
Optimistic	2	2	3	2	2	2	
Average	2	2	2	2	2	1	1
Pessimistic	1	1	2	1	1	1	
Litter size (per female)							
Optimistic	3.5	3.2	2	3.1	2.5	3.7	
Average	3.4	2.8	2.2	2.8	2.2	4	2
Pessimistic	3.4	2.8	2	2.8	2.2	3.6	
Mortality 0/1+ years							
Female	60/28[b]	60/33.8	60/48	60[b]/28	62/32	67.8/36	75/58
Male	60/28[b]	60/33.8	60/48	60[b]/28	62/32	73/30	75/58

[a] Sources: Allen 1943; Allen 1982; Barkalow et al. 1970; Berteaux and Boutin 2000; Boutin and Larsen 1993; Brown 1984; Brown and Yeager 1945; Chesemore 1975; Dolbeer 1973; Emmons 1979; Farentinos 1972; Ferron and Prescott 1977; Glanz et al. 1982; Goodrum 1961; Gurnell 1994; Halvorson and Engeman 1983; Harnishfeger et al. 1978; Heaney and Thorington 1978; Herkert 1985; Jameson and Peeters 1988; Keith 1965; Kemp and Keith 1970; Koprowski 1985, 1994a, 1994b; Larsen and Boutin 1994; Layne 1954; Longley 1963; McAdam and Boutin 2003; McCloskey and Vohs 1971; Nash and Seaman 1977; Nitikman 1985; Shuttleworth 1999; Steele 1998; Stephenson and Brown 1980; Stuart-Smith and Boutin 1995; Thompson 1978; United States Fish and Wildlife Service 1993; Uphoff 1990; Verboom and Van Apeldoorn 1990; Wauters and Dhondt 1989, 1990, 1995; Whitehead 1976; Wood 1967.

[b] *Sciurus* mean value used.

environmental and demographic stochasticity, maintaining genetic variation through a large metapopulation that can withstand loss of individual populations to catastrophes and disturbance (Brown and Kodric-Brown 1977).

Arboreal rodents are excellent indicators of ecosystem health (Carey 2000; Steele and Koprowski 2001) and the same population processes that affect many other species also affect tree squirrel populations, making them an excellent model system for many studies in behavior, population ecology, and conservation biology (Steele and Koprowski 2001). Therefore, techniques generated in our study may be applicable to other species of precarious status. Furthermore, more than 80% of species of tree squirrels are in precarious conservation status in some portion of their range (Koprowski 2005a), indicating a need to examine viability of tree squirrel populations and feasibility of reintroductions to aid conservation efforts. Tree squirrels require mature forests in temperate and tropical regions (Gurnell 1987). Disturbance in old-growth forests is accelerated by anthropogenic forces, increased degradation, and fragmentation, and results in mortality of tree squirrels and reduced population sizes (Bendell 1974; DeBano et al. 1998; Hakala et al. 1971; Harris 1984; Koprowski 2005a, 2005b; Pyne 1982).

We used life-history data gleaned from the literature as input for a population viability model in order to examine the ability of introduced populations of tree squirrels to persist despite typical levels of environmental and demographic variability. We generated viable starting population estimates using these data and support our results with empirical evidence from actual introductions of tree squirrels.

MATERIALS AND METHODS

Life-history data.—We gathered life-history parameters (Table 1), including age of 1st breeding, maximum breeding age, sex ratio, litter size, female breeding percentage per breeding season, and mortality rates, from published sources for 6 species: Abert's squirrels (*Sciurus aberti*), eastern gray squirrels (*S. carolinensis*), red-tailed squirrels (*S. granatensis*), eastern fox squirrels (*S. niger*), Eurasian red squirrels (*S. vulgaris*), and red squirrels (*Tamiasciurus hudsonicus*). Species of tree squirrels considered at risk are poorly studied (Koprowski 2005a), so we combined data from multiple species to fill in the few gaps in life history. Reproductive output does not vary across species in the genus *Sciurus* (Heaney 1984), thereby allowing us to average across species with minimal error. We used the mean value for the 5 species of *Sciurus* to substitute for the few instances where values were unknown or uncertain (Table 1): *S. aberti* (mortality, breeding percentage), *S. niger* (juvenile mortality), and *S. granatensis* (breeding percentage). The life histories of the 5 species of *Sciurus* are remarkably similar. The notable exception, *T. hudsonicus*, is territorial in parts of its range (Steele 1998) but still maintains life-history tactics similar to those of other tree squirrels. We compiled sufficient information for *T. hudsonicus* such that we did not need to use across-species averages for any life-history parameters.

Simulations and scenarios.—We used VORTEX version 8.42 (Lacy 1993), to calculate viable starting population estimates. VORTEX is an individual-based Monte Carlo simulation package designed for population viability analysis of mammalian systems (Lacy 2000).

We made several necessary, biologically based assumptions to simplify simulations, while still allowing us to mimic most cases of tree squirrel introductions. The assumptions were: extinction occurred when only 1 sex remained; a single population without immigration was modeled to mimic decreased demographic linkages; squirrels reproduced until death; a promiscuous mating system, modeled as a polygynous system without monopolization of mates; no explicit addition of inbreeding depression to our models; no catastrophic events; and no density-dependent reproduction. An effect of inbreeding depression on survival and reproduction was not apparent in Eurasian red squirrels within recently fragmented populations of less than 30 individuals (Wauters et al. 1994), and no data exist on the effect of inbreeding specifically for tree squirrels. Therefore, we used a more general approach to examine theoretical effects of inbreeding (see "Discussion"). Clearly, catastrophes can have significant impacts on population persistence (Lande 1993). However, catastrophic events were not included in our simulations because our efforts were to assess the potential of introduced populations to establish from a few individuals despite typical ranges of environmental and demographic stochasticity. Eastern gray and Eurasian red squirrel populations only show density-dependent reproduction at high density, such as populations in highly fragmented environments (Sanderson and Berry 1973; Wauters and Lens 1995). Introductions for conservation purposes should occur in contiguous large areas that can maintain sustained growth rather than small woodlots (IUCN 1998), so a population large enough to realize negative density-dependence would be considered a successful introduction. Positive density-dependence (Allee effects) seems unlikely because females rear young individually and male squirrels maximize their chances of finding a receptive female, even expanding their home range beyond its already increased size during the breeding season when females are sparse (Steele and Koprowski 2001). Therefore, we did not model density-dependent reproduction.

Yearly changes in environmental variability do affect life-history parameters such as reproduction and mortality (Gurnell 1987). Such changes are incorporated in the stochastic nature of the model. However, adults can use other food sources in times of food shortage (Barkalow et al. 1970; Koprowski 1991) but may suppress reproduction, indicating bad years for reproduction may not necessarily be bad years for survival. Therefore, we did not model a direct link between survival and reproduction in our analyses. Large differences in juvenile recruitment are due to year-to-year variation within habitats that is incorporated through demographic and environmental variability in the stochastic model. However, overall resource availability (due to habitat quality) would result in different baseline parameter means for recruitment variables so we chose to model different scenarios to examine these factors. We used constant values for mortality, sex ratio, and breeding age values and generated 3 different reproductive scenarios using our compilation of life-history data: pessimistic, average, and optimistic, from the minimum study average, mean value across studies, and maximum study average (Table 1), reflecting baseline resource availability differences between potential habitats.

TABLE 2.—Yearly standard deviation values used as VORTEX parameters for habitat variability simulations of tree squirrel introductions (see references in Table 1).

Parameter	Low	High
Litter size	0.125	0.25
Female breeding %	5	10
Adult mortality %	4	7
Juvenile mortality %	5	10

We defined a successful introduction as the smallest starting population that has less than 1% chance of extinction (a 99% chance of survival) over the next 100 years, similar to a minimum viable population (Shaffer 1981). We used this definition to assign a binary score, viable or not, to different starting populations. We ran our population simulations for a 100-year period and repeated each set of initial conditions 500 times (Harris et al. 1987). We started initial populations with a stable age distribution of 10 squirrels and increased the starting population incrementally by 10 until 99% population persistence was reached. Then we reported a successful starting population as the population between the 1st trial with successful establishment (according to the above definition) and the preceding one. We generated minimum population for establishment estimates for 3 different scenarios (pessimistic, average, and optimistic reproduction) for each of the 6 squirrel species.

In addition to baseline resource differences, some potential habitats for introduction may have more variability between years, such as in edge habitat. To analyze how this affects viable starting population numbers we determined variation, representing variability in percentage of females breeding, litter size, and mortality from the literature. We gathered standard deviations from within studies (which also would include sampling error), to characterize the representative standard deviation for a particular system, and generated from these values a set of low and high standard deviations representing typical combinations of demographic and environmental stochasticity (Table 2). We ran each breeding scenario (pessimistic, average, and optimistic reproduction) at low and high variability, for a total of 6 starting population estimates for each species.

We ran an additional general test to evaluate the impact of a novel area on released individuals. Introduced squirrels would have to adjust to their new surroundings and during this initial learning period may be subject to higher rates of mortality and reduced fecundity. For this simulation we modeled the worst-case situation for survival and breeding by taking some of the lowest parameter estimates across species (Table 1) and combining them to see how many individuals would be needed to overcome an initial 2 years of extremely poor population performance. We ran 500 simulations at our high estimates of environmental and demographic stochasticity for starting populations of 0–200 squirrels by 20 squirrel

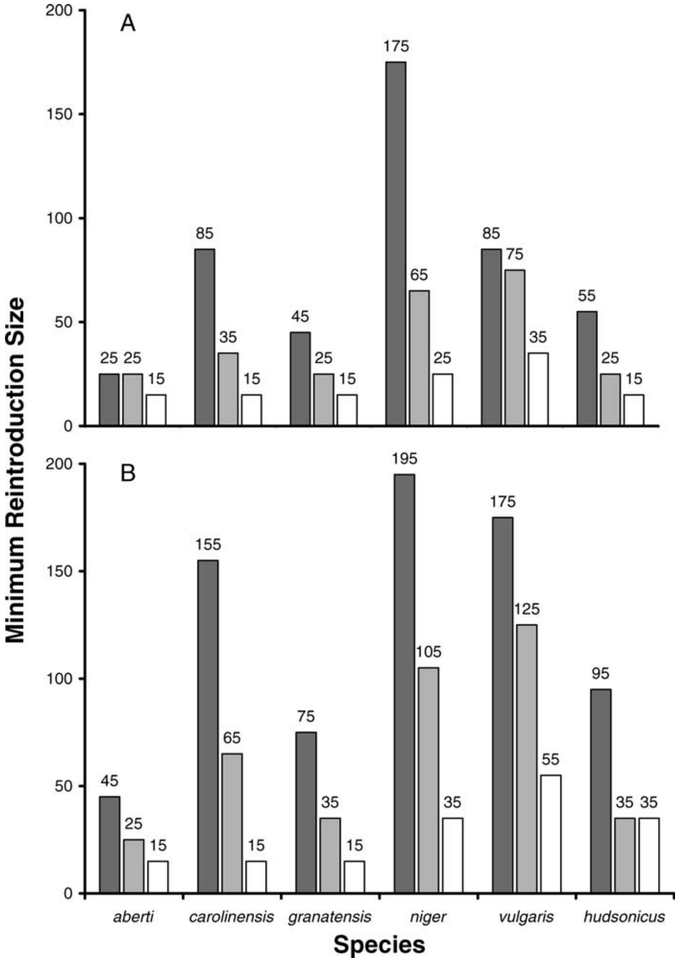

Fig. 1.—Simulated minimum starting populations of tree squirrels (*Sciurus* and *Tamiasciurus*) required for successful introduction at A) low and B) high resource variability for introduction into novel environments. Estimates are generated from VORTEX simulations. Reproduction values are from a literature review creating pessimistic (dark gray bars), average (light gray bars), and optimistic (white bars) scenarios (see Table 1).

increments and report the number of trials above 20 squirrels after 2 years.

Empirical data.—To assess the potential application of our estimates, we examined empirical evidence in the literature describing natural situations that were similar to those in our models (human introduction of squirrels into plentiful habitat). This situation most closely simulates introductions of non-native species because there are no long-term examples of squirrel reintroductions into forested ecosystems. We found very few introductions older than 100 years so we collected records of tree squirrel introductions older than 50 years, worldwide, to compare to our modeling results (Bertolino and Genovesi 2003; Cowan and Guiget 1965; Davis and Brown 1988; Huey 1964; Millar 1980; Payne 1976; Seebeck 1984; Verts and Carraway 1998; Yensen and Valdés-Alarcón 1999). By 50 years, the population will have gone through multiple generations and will have overcome many of the initial demographic challenges faced by introduced populations.

Results

Low habitat variability simulations.—Low habitat variability required only a few tens of individuals to establish a viable population in a novel habitat with optimistic reproduction (Fig. 1A). Only *S. vulgaris* required a starting population > 25 individuals. In the best scenarios, most species needed only a one-time introduction of 15 individuals to start a population that would persist for 100 years. As reproductive output decreased, estimates of successful starting populations increased, but large increases were only evidenced for a few species. *S. aberti*, *S. granatensis*, and *T. hudsonicus* required increases of only about 10 squirrels in starting populations when undergoing average reproduction and increases of fewer than 40 squirrels with pessimistic breeding scenarios (Fig. 1A). *S. carolinensis* and *S. vulgaris* required increases of more than 50 squirrels in the size of starting populations to produce viable populations from optimistic to pessimistic breeding scenarios. *S. niger* required large increases of 40 and 150 squirrels from optimistic to average and optimistic to pessimistic reproductive scenarios, respectively.

High habitat variability simulations.—High habitat variability increased required starting population sizes for viable reintroduction, but again successful reintroductions resulted from only a few squirrels with optimistic breeding scenarios (Fig. 1B). For the most optimistic breeding scenarios, only *S. vulgaris* required more than 35 squirrels in the starting population to yield a successful introduced population. For *S. aberti*, *S. granatensis*, and *T. hudsonicus*, even under pessimistic breeding scenarios at high habitat variability, we predicted that a population could be successfully established with an introduction of fewer than 100 individuals, and in most cases with fewer individuals. *S. carolinensis*, *S. niger*, and *S. vulgaris* required large (between 150 and 200 squirrels) starting populations for success under pessimistic reproductive scenarios. Under the poorest conditions, populations quickly declined and more than 160 squirrels were needed to have a $>95\%$ chance of a population being above 20 squirrels after 2 years (Fig. 2).

Empirical results.—We found 25 cases of tree squirrel introductions that occurred more than 50 years ago for *S. carolinensis*, *S. niger*, *S. aberti*, and *T. hudsonicus* (Table 3). Initial population sizes ranged from 4 to 111 squirrels ($\bar{X} = 30.7$, $SD = 33.7$) at locations in Canada, the United States, Mexico, Italy, Australia, and South Africa. Twenty-one (84%) of the introduced populations currently persist, whereas 13 (93%) of 14 introductions with more than 10 squirrels still persist. The smallest populations that persist stem from 4 individuals of *S. carolinensis* introduced to Turin, Italy (Bertolino and Genovesi 2003), and 4 individuals of *S. aberti* introduced to the Granite Dells of Arizona (Davis and Brown 1988). A population founded from a single pair of *S. carolinensis* went extinct after 36 years in Victoria, Australia (Seebeck 1984).

Discussion

Our findings suggest that tree squirrels can overcome typical ranges of environmental and demographic stochasticity and establish populations in novel habitats through introduction of relatively few squirrels under many achievable levels of habitat quality and demographic scenarios. Our use of generic values in 4 instances may reduce the accuracy of our results, but our pattern of small numbers of individuals required for successful introduction likely still holds. When more detailed data become available, more specific estimates can be generated. Habitat-specific information and spatially explicit processes can also be incorporated into site-specific models to improve specific estimates. For tree squirrel conservation in the present, our results are practical and likely indicative of widespread patterns.

The ability of most species in our models to establish from low numbers suggests managers should strive to conserve even the smallest populations because there is a strong likelihood that populations can recover with alleviation or amelioration of factors responsible for their decline. Small populations can persist, may recover from low numbers, and should not be immediately and universally discounted. We strongly caution that our numbers not be used as conservation targets because small populations face increased levels of the multiple threats of genetic, environmental, and demographic stochasticity and catastrophes that can lead to extinction (Shaffer 1981).

Although under ideal conditions a few animals can establish a population of tree squirrels, if conditions are not met, reintroductions may have a poor chance for success. Under the poorest conditions, possibly following an introduction, squirrel populations will decline. Increased environmental stochasticity accelerates extinction (Alvarez 2001); therefore, areas for reintroduction should be assessed for their ability to provide not only a large, but also a stable amount of food (Fornasari et al. 1997). Reintroduced individuals have to learn to cope in a new environment, and they may be subjected to increased mortality and lower reproduction in the 1st years after reintroduction. However, after a soft release, introduced tree squirrels exhibited a high degree of site fidelity and quickly acclimated to their new surroundings after a month-long period of higher mortality (Bendel and Therres 1994). Careful planning before the reintroduction, management (such as supplemental feeders and soft releases) during the initial few years of uncertainty, and reintroductions using translocation of wild stock, which are preferred over captive-bred populations (IUCN 1998), can minimize the chance repeated introductions will be needed to achieve a viable population. However, the possibility of catastrophes and unknown habitat quality or needs for a species may lessen chances for success.

Despite lack of evidence from squirrel populations suggesting significant effects of inbreeding depression (Wauters et al. 1994), populations that experience severe bottlenecks may be affected by inbreeding depression (Lynch et al. 1995). Mammals average 33% higher juvenile mortality due to inbreeding (Ralls et al. 1988). Although we did not explicitly include inbreeding in our model, one can use our model to predict its effects. Inbreeding depression is mostly realized in recruitment (Keller and Waller 2002); therefore, by using decreased reproductive success as a proxy for inbreeding depression (i.e., move to average from optimistic scenario), the potential change in the number of individuals required for successful reintroduction due to inbreeding depression can be estimated. Conservation efforts should consider the potential for inbreeding, be prepared for translocation of animals to maintain genetic diversity (Keller and Waller 2002), and maximize genetic variation in the founder population.

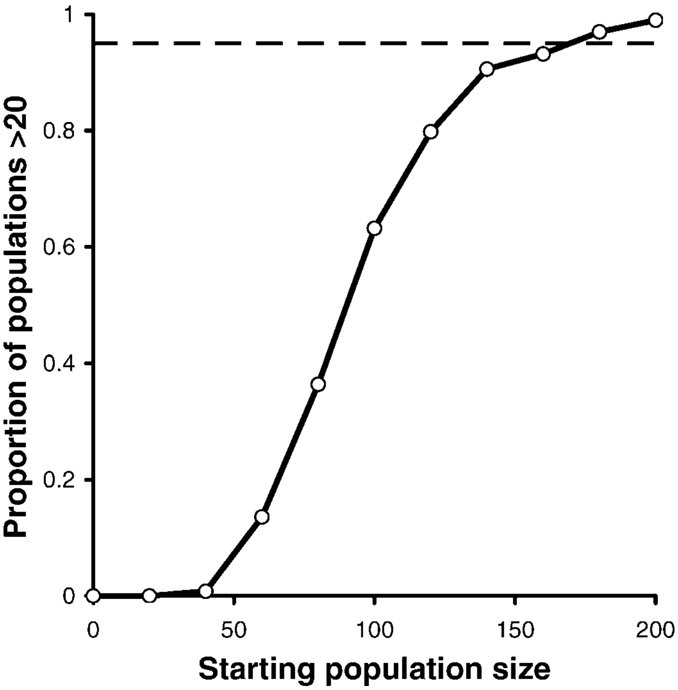

FIG. 2.—Proportion of populations with more than 20 squirrels after 2 years from different starting populations, generated from a VORTEX population viability analysis simulation. Life-history parameters were determined from one of the lowest reported parameter values for a single year for tree squirrels. Dashed line represents 95% cutoff.

Although failures may not be as widely reported as successes, the many successful introductions and small numbers used in those introductions support our results and illustrate that tree squirrels can quickly adapt to new areas after release. As few as 4 individuals have been introduced into a new area and survived for more than 50 years (Bertolino and Genovesi 2003; Davis and Brown 1988), introduced populations of Abert's squirrels have thrived and dispersed to nearby habitat patches (Lomolino et al. 1989), and despite efforts to remove eastern gray squirrels in Italy, many of these populations remain extant (Bertolino and Genovesi 2003). Many introduced populations are robust despite establishing from only a few founders, providing long-term hope for reintroduction efforts, which are becoming more common. Since 1978 the Delmarva fox squirrel (*Sciurus niger cinereus*) has been reintroduced (mean introduction size = 18.3, range 5–42) to Maryland, where 10 of 11 introduced populations persist (Therres and Willey 2002). Small reintroductions of Eurasian red squirrels persist in Belgium (Swinnen 1998; Wauters et al. 1997), the United Kingdom (Bertram and Moltu 1986), and Italy (Fornasari et al. 1997). Reintroductions of *Sciurus lis* into 60-ha (13 squirrels between 1984 and 1985) and 20-ha

Table 3.—Status of >50-year-old tree squirrel introductions reported in the literature. See text for references.

Genus	Species	Location	Number	Date	Persist	Extinct
Sciurus	*carolinensis*	Baja California, Mexico	8	1946	1964	
Sciurus	*carolinensis*	Baja California, Mexico	9	1946	1964	
Sciurus	*carolinensis*	Turin, Italy	4	1948	2003	
Sciurus	*carolinensis*	Genoa Nervi, Italy	5	1966	2003	
Sciurus	*carolinensis*	Novara, Italy	6	1994		1996
Sciurus	*carolinensis*	Oregon	<20	1919	2003	
Sciurus	*carolinensis*	British Columbia, Canada	8	1914	2003	
Sciurus	*carolinensis*	Victoria, Australia	2	1937		1973
Sciurus	*carolinensis*	South Africa	<20	1890s	2003	
Sciurus	*niger*	Maryland	20	1991	2003	
Tamiasciurus	*hudsonicus*	Newfoundland, Canada	6	1964	1976	
Sciurus	*aberti*	Arizona	100	1940–1943	1988	
Sciurus	*aberti*	Arizona	91	1940–1943	1988	
Sciurus	*aberti*	Arizona	42	1944	1988	
Sciurus	*aberti*	Arizona	8	1940–1941	1988	
Sciurus	*aberti*	Arizona	4	1944	1988	
Sciurus	*aberti*	Arizona	59	1940–1941	2003	
Sciurus	*aberti*	Arizona	111	1941, 1943–1945	1988	
Sciurus	*aberti*	Arizona	43	1944	1988	
Sciurus	*aberti*	Arizona	69	1941–1943	2003	
Sciurus	*aberti*	Arizona	21	1971–1977	1988	
Sciurus	*aberti*	New Mexico	16	1940	1988	
Sciurus	*aberti*	New Mexico	13	1929, 1940	1988	
Sciurus	*aberti*	New Mexico	12	1955, 1969		Unknown
Sciurus	*aberti*	Utah	?	1898–1908		After 1954?

(10 squirrels in 1986) city parks in Japan were unsuccessful, but an introduction into an 87-ha city park (5 squirrels in 1988) still persists (Yatake 2001).

What allows tree squirrels to establish from a small founding population? Gurnell (1987), in a review of tree squirrels, found that female tree squirrels are characterized by high reproductive output of 2 or 3 litters per year, litter sizes up to 8, and that each sex can reproduce at 1 year of age. Although survival to the 2nd year of life can be low (15%), adult survival is high (50–80%—Gurnell 1987; Heaney 1984), and in years with a good food supply, juvenile survival can increase to 60% and adult survival to 100% (Gurnell 1987). The high biotic potential of tree squirrels and lack of density-dependent reproduction at low population densities allows even a small population to increase during a year of good or modest food. Tree squirrels possess good dispersal capability, can colonize and use novel habitats, and can make their own nests (Gurnell 1987). Furthermore, adult tree squirrels eat many different foods, permitting persistence in a variety of forest types and enabling survival through poor seed years (Gurnell 1987; Steele and Koprowski 2001).

Additional modeling efforts have demonstrated that tens of animals are needed for successful reintroduction, not the larger numbers previously thought (Howells and Edward-Jones 1997; South et al. 2000). Reintroduction seems plausible for squirrel populations where a small founding population can be used to create additional populations to buffer against catastrophes such as hurricanes (Holler et al. 1989), disease (Rushton et al. 2000), wildfire (Koprowski et al. 2006), or insect infestations (Koprowski et al. 2005). Although reintroduction of tree squirrels is a practical use of the limited money available for conservation, ultimately, conservation of tree squirrels will depend on successful management of multiple reserves and maintenance of mature, connected old-growth forest that tree squirrels rely on for their survival.

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