

Modeling Managed Monkey Populations: Sustainable Harvest of Longtailed Macaques on a Natural Habitat Island

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Computer simulation of population dynamics can be useful in managing harvested populations of monkeys on islands. Between 1988 and 1991, 420 adult female and 58 adult male simian retrovirus-free *Macaca fascicularis* were released onto Tinjil Island, Indonesia, to provide the nucleus for a free-ranging breeding colony. Natural habitat breeding facilities are excellent alternatives to wild trapping and compound breeding, maximizing the health and well-being of animals destined for essential biomedical research. To avoid a population crash, the number of offspring that can be harvested annually must be based on life table characteristics such as age-specific natality and mortality. We used a modified Leslie matrix to model changes in female population size over 26 years. First, we assumed that all 420 females were released simultaneously and varied the annual birth rate (50%, 60%, 70%), survival rate, and number of offspring harvested per year. Assuming high survival and birth rates vs. low rates, about four times as many female offspring could be harvested annually from a stable population (87 vs. 20 offspring). Terminal population size after 26 years did not differ much across rates modeled (568–696 females). Second, we modeled the number of females actually released (including the recent addition of 42 new female breeders) and harvested (averaging 49 annually 1991–1994), and projected the population through 2014. This indicated that threshold harvest rates and terminal population sizes increased considerably over the first model, assuming intermediate (78 harvested, 952 females) and high (152 harvested, 1,331 females) rates of survivorship and natality, but were unchanged assuming low rates (20 harvested, 559 females). A review of the literature and field observations on Tinjil suggest that actual birth and survival rates resemble the intermediate values modeled. If so, the present density on the island, projected to be ~215 males and females per square kilometer, is approaching carrying capacity. The high values are realistic upper limits. If actual survivorship and birth rates are at the high end of those modeled, the island's

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population may be on the verge of rapid expansion, requiring increased harvest and provisioning. © 1996 Wiley-Liss, Inc.

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INTRODUCTION

The use of nonhuman primates in biomedical research presents special challenges for conservation management. A few of the species that are critically important for biomedical research, such as chimpanzees (*Pan troglodytes*) [Erwin & Landon, 1992] and cotton-top tamarins (*Saguinus oedipus*) [Tardiff & Clapp, 1993], are threatened or endangered and are therefore bred in captivity. Most of the other species of research importance, however, are not currently vulnerable to extinction and some are still wild caught. Four of the species most frequently used in research—rhesus macaques (*Macaca mulatta*), longtailed macaques (*M. fascicularis*), savanna baboons (*Papio cynocephalus* subsp.), and vervet/green monkeys (*Cercopithecus aethiops* subsp.)—are still relatively common in the wild. In many areas these species have frequent contact with humans as the result of raiding crops or accepting handouts [Maples et al., 1976; Crockett & Wilson, 1980; Lee et al., 1986; Mittermeier & Cheney, 1987; Altmann & Muruthi, 1988; Horrocks & Baulu, 1988, 1994; Richard et al., 1989; Else, 1991; Southwick & Siddiqi, 1994b; Wheatley & Harya Putra, 1994, 1995]. This tendency toward commensalism contributes to their being among the easiest species to maintain and breed in captivity.

The challenge to conservation of these animals is to strike a balance between their preservation in the wild and their availability in the laboratory. Live capture and export of primates for biomedical research and the pet trade formerly contributed to declines of certain primate species [Kavanagh et al., 1987]. For example, excessive trapping, particularly of juveniles, was a major contributor toward a 90% reduction in the rhesus macaque population of India in the 1960s and 1970s [Southwick & Siddiqi, 1994a]. Primate exports declined markedly after the initiation of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) in 1973, and many countries soon banned exports of all native primates [Kavanagh et al., 1987; Mittermeier & Cheney, 1987; Held & Wolfle, 1994]. Most serious for biomedical research was India's 1978 ban on the export of rhesus macaques.

Faced with the reduced availability of their most common primate subject, the research community responded by establishing captive breeding programs for rhesus macaques and increasing use of longtailed macaques (*M. fascicularis*) [Vickers, 1986; Bowden & Smith, 1992]. Exports of longtailed macaques from Malaysia jumped by 40% in 1978, presumably in response to India's ban on the export of rhesus macaques [Bennett, 1991]. After Malaysia also banned primate exports in 1984, Indonesia and the Philippines became the principal exporters of longtailed macaques [MacKinnon, 1986; Kavanagh et al., 1987; Hobbs, 1989]. In 1989 (and again in 1996) an Ebola-like filovirus was found among longtailed macaques originating in the Philippines, making their long-term availability problematic [Bowden & Smith, 1992]. In April 1994, Indonesia joined the nations banning exports of wild-caught primates and restricted the use of indigenous primates to authorized research or breeding programs within Indonesia.

As a result of these measures, primate populations are on the increase. For example, the population of rhesus macaques in northern India has recovered by 50% since 1978, and the problem now is to manage the conflicts that often arise between humans and monkeys. "For species such as the rhesus, with high reprod-

ductive potentials but also high crop-raiding tendencies, some type of sustainable harvest and utilization will be necessary...The rhesus can become a serious local pest [Southwick & Siddiqi, 1994a:57]." Local agencies are charged with removal and translocation of problem monkeys, including trapping of rhesus macaques to be used for research within India [Malik & Johnson, 1991; Malik, 1992; Southwick & Siddiqi, 1994b]. In Barbados, humane trapping of introduced *C. aethiops* for research helps control agricultural pests and simultaneously provides some income to farmers [Horrocks & Baulu, 1988]. In Africa, the species most commonly exported for research, *C. aethiops* and the savanna baboons, are widespread and not apparently threatened by live trapping; the baboons are much more affected by pest-eradication programs [Kavanagh et al., 1987].

With continuing export restrictions, alternative approaches are needed to meet the demands of primate supply in a manner that is both economically advantageous and consistent with conservation objectives [Bowden & Smith, 1992; Held & Wolfle, 1994; Kyes et al., 1995]. Islands are especially suitable for establishing natural habitat breeding facilities (NHBFs) where the offspring can be "harvested" for use in important biomedical research.

Monkeys have been introduced onto various islands worldwide. Several populations derive from escaped pets that have multiplied over the centuries, such as the longtailed macaques of Palau and Mauritius [Poirier & Smith, 1974; Sussman & Tattersall, 1981], and the vervets of St. Kitts and Barbados [Denham, 1987; Horrocks & Baulu, 1988, 1994]. Other populations have been released intentionally onto small islands with the objective of breeding animals for research. Some of these islands are within the species' natural ranges [Kyes, 1993; Moya et al., 1993], whereas others are not [Pucak et al., 1982; Weed & Cheslak, 1984; Rawlins & Kessler, 1986b]. Using the natural vegetation and boundary provided by a small island within the natural range is convenient and economical, as at low population densities provisioning need not be extensive. Provisioning may be used as a management tool to facilitate capture as well as for nutritional supplement, but native food species provide much of the diet.

An NHBF within the normal range of longtailed macaques (*M. fascicularis*) has been established on Tinjil Island in Indonesia (7°0'S, 105°45'E). Between 1988 and 1991, 420 adult female and 58 adult male longtailed macaques that had been verified to be free of simian retroviruses and tuberculosis were released onto the uninhabited island to form the nucleus of a free-ranging breeding colony for AIDS-related research [Kyes, 1993; Pamungkas et al., 1994; Kyes et al., 1995; Morton et al., 1995]. These animals have spread throughout the 600 ha (~1 km × 6 km) island, forming approximately 18 troops. Tinjil's vegetation is predominantly lowland, secondary tropical rain forest and beach vegetation. More than 75 plant species have been identified, of which 28 produce fruits or foliage known to be eaten by the monkeys [Kyes et al., 1995]. In addition to their diet of native food species, the monkeys on the eastern and central portions of the island have daily access to bananas, corn, or sweet potatoes in nine feeder-capture cages, providing a modest portion of the diet, although the most dominant individuals eat the majority of this preferred food. Monkeys that moved to the western end of the island are subsisting entirely on native food species.

Now that the Tinjil Island NHBF is well established, a primary concern is to manage the harvest of offspring so that the population is self-sustaining. Ideally, once an island has reached its carrying capacity (which may be increased by provisioning), the number of monkeys removed should be balanced by the number of new animals born into the population. Owing to life table characteristics such as age-specific fecundity and mortality, only a proportion of younger animals should

be removed or the population will decline. However, determining the number that can be safely harvested to provide a sustainable-yield, renewable resource is not simple. The same environment that provides a free-ranging, largely unprovisioned existence makes determination of exact population size and demographic parameters difficult. For example, the monkeys that were released on Tinjil Island were tattooed on their chests and theoretically could be identified during censuses. However, those that spread to the western third of the island, farthest from the release site, are not habituated to humans and are difficult to observe [Kyes et al., 1995].

To provide more accurate estimates of the Tinjil population and to evaluate various management strategies, we modeled projected population growth varying survival schedules, birth rates, and numbers harvested. Such simulations allow projections of long-term population viability even when quantitative data are incomplete [Durant & Mace, 1994]. Similar models have been used to project growth and conservation status of provisioned and unprovisioned primate populations [Lyles & Dobson, 1988; Dobson & Lyles, 1989]. The parameter values used in modeling were derived from published information for macaques (see Methods) and birth rate data collected by R. Kyes from the habituated troops in eastern and central Tinjil Island. Births have been observed in every month of the year [Kyes et al., 1995]. The absence of strongly seasonal reproduction is consistent with other studies of *M. fascicularis* [Kavanagh & Laursen, 1984].

METHODS

Modeling Program

We modeled population growth of longtailed macaques using RAMAS/age, a commercially available computer program [Ferson & Akçakaya, 1993] based on a modified Leslie matrix [Leslie, 1945, 1949]. The program multiplies a vector (N), consisting of the initial number of individuals in each age class, by a sparse matrix (L), with fecundities (age-specific birth rates or natality) on the top row and age-specific proportions surviving along the subdiagonal (each row consisting of a proportion corresponding to one age class's survival and the remaining cells zero) [Batschelet, 1979; Ferson & Akçakaya, 1993]. The number (N) of initial animals in each age class at time t is multiplied by its corresponding birth rate and summed to comprise the 0 age class for the next time ($t + 1$) and by the corresponding survival probability to obtain the number of individuals in the next age class (age $+ 1$) at the next time ($t + 1$). Individuals can be added (modeling release of new breeders) or subtracted (modeling harvest or removal) from age classes in a vector called "migration."

Environmental stochasticity (variability in climate and other factors) is modeled using the coefficient of variation (CV) such that birth rate, survival, and migration are random variates from a lognormal distribution with mean values selected by the user. The CV for survival of the 0 age class (infants) can be different from that for age classes ≥ 1 ("adults"), since factors affecting infant survival might be distinct from those affecting adult survival. Age classes can be any equal duration. We chose 2 years because the largest age class allowed by the RAMAS/age program is 17, allowing projections to 34 years of age, a very old macaque [Ross, 1988]. However, the results are expressed as "per year" to be comparable to published data. Density dependence was excluded because our objective was to model a population that was sustained by harvesting to a level below carrying capacity. Every run of the simulation was for 250 replications, the maximum allowed by the program.

Our analysis had two components. First, we modeled population growth over

26 years (spanning the lease of Tinjil Island from the Indonesian government). For polygynous species like *Macaca fascicularis*, it is simpler and appropriate to model females only. If there are enough females, there will almost certainly be enough males to ensure breeding. For this model—simultaneous release with constant harvest—we assumed that all 420 female breeders were introduced at the same time. For nine possible combinations of three variations each of survival and birth rate, we determined the threshold harvest number, i.e., the largest number of 2-to-3-year-old females that could be removed annually without resulting in a declining population after 26 years. After determining this number, by examining graphs of projected abundance, the same number harvested was run a second time to verify the result and obtain a range of projected abundance.

Second, we modeled actual population growth by starting with initial numbers of females introduced each year from 1988 through 1991 and female offspring removed from 1991 through 1995 (in 2 year blocks). We modeled three combinations of survival and birth rate schedules to bracket a plausible range: high survivorship and high birth rate; intermediate survivorship and intermediate birth rate; and low survivorship and low birth rate. Then we modeled the consequences of the release of 42 new female breeders to the populations projected by the low, intermediate, and high models and modeled growth for 18 more years. Threshold harvest rates were estimated as in the first analysis.

In the following sections we describe and justify the values selected to plug into the program (see Appendix).

Initial Age Composition

The age structure of initial breeders was biased toward young adults, as these had been selected intentionally during screening. We assumed that the introduced breeding stock was composed of animals aged 4–11 years in proportion to the average stable age distribution for the demographic schedules modeled (0.36 aged 4–5, 0.28 aged 6–7, 0.21 aged 8–9, and 0.15 aged 10–11). The proportions were multiplied by 420 to obtain the initial numbers in each age class for the “simultaneous release and constant harvest” model, and by the 2 year totals actually introduced to obtain the numbers used in the “actual numbers released and removed” model.

Birth Rate

We modeled natality, or female births per year (FBY), as one-half the annual birth rate on the basis that macaques typically give birth to singleton offspring, about half of which are female. Figure 1 presents age-specific birth rates derived from the macaque literature and depicts the annual birth rates modeled. Based on the general pattern of age-specific natality, we modeled a constant birth rate for ages 5–19 years and assumed that only half of the 4-year-old females gave birth. Birth rate dropped at ages 20, 26, and 32 years to model patterns reported for macaques (Fig. 1). Fertility in macaques is reported to drop sharply at age 25–30 years [Hendrickx & Dukelow, 1995], although birth rates of rhesus macaques on Raccoon Key began to decline in middle age (Fig. 1) [Johnson & Kapsalis, 1995].

Provisioned macaques generally have higher birth rates than unprovisioned ones [Lyles & Dobson, 1988]. The “high” birth rate modeled was 0.70 for ages 5–19 years, simulating the 0.68 annual birth rate estimated for the most habituated and provisioned troops on Tinjil (R. Kyes, unpublished data from 1994 census period). We used 0.60 for ages 5–19 years as an “intermediate” birth rate, a plausible rate for the least provisioned troops on the island, based on data from wild longtailed macaques (see Fig. 1 caption). Average interbirth intervals for longtailed

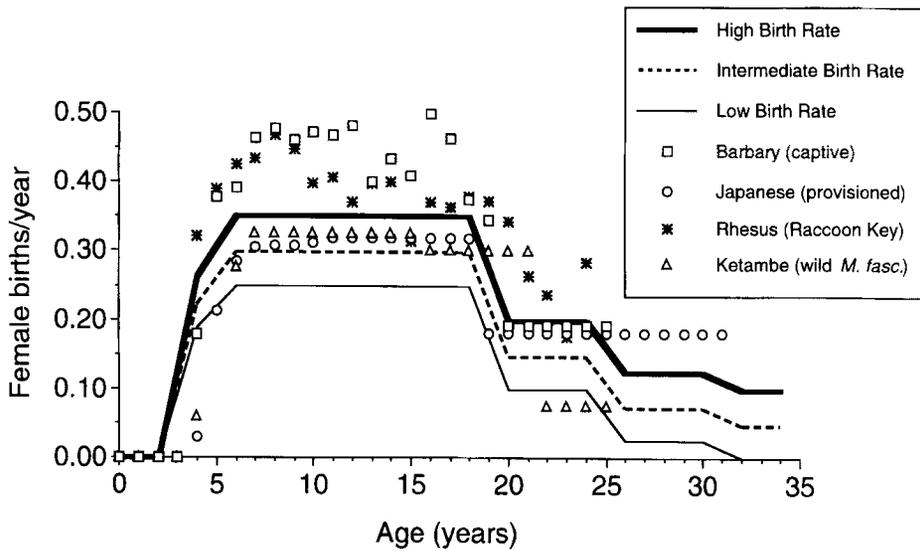


Fig. 1. Age-specific natality (female births per female year by age) in four macaque populations compared to the high, intermediate, and low birth rates modeled. Sources: a, captive Barbary macaques (*M. sylvanus*) in a 14.5 ha outdoor compound [Paul & Kuester, 1988]; b, provisioned Japanese macaques (*M. fuscata*), 79 females born between 1950 and 1967 in Japan in troop Arashiyama A, which was transported in entirety in 1972 to a 44 ha corral in Texas [Fedigan, 1991a,b]; c, provisioned rhesus macaques (*M. mulatta*) on Raccoon Key, an 81 ha mangrove island in the Gulf of Mexico [Johnson & Kapsalis, 1995]; d, approximate pattern for wild, unprovisioned longtailed macaques at Ketambe, Sumatra (van Noordwijk, personal communication).

macaques on Tinjil Island are unlikely to exceed 24 months, so a birth rate of 0.50 for ages 5–19 modeled the “low” birth rate.

Survival

We modeled three survivorship schedules on the basis of published data for other macaque species (Fig. 2). For the “high” survivorship model, we used reported age at death of the cohort of female Arashiyama macaques (*M. fuscata*) born between 1956 and 1967 [Fedigan, 1991a] to calculate age-specific survival (dynamic composite cohort life table) [Smith, 1980]. The result is very similar to the revised standard model life table for Old World monkeys [Gage & Dyke, 1993] (Fig. 2). The survival probability in the terminal age class, 17 (i.e., 34 years), was zero so that no females survived to age 36 years. The “low” survival model was derived from time-specific (or vertical life table) data for rhesus macaques (*M. mulatta*) on Cayo Santiago island during 1972–1973 [Sade et al., 1976], with all females dying by age 24 years. For the “intermediate” survival model, the survival proportions for each age class through 9 years were taken from dynamic composite cohort life table data from the same Cayo Santiago population from 1976 to 1983, and for ages 10–17 years were based on an average annual mortality of 6.8% [Rawlins & Kessler, 1986a]; the remaining survival proportions were adjusted so that all females were dead by age 30 years.

Coefficients of Variation

The CV (standard deviation/mean) used for infant survival probability was calculated as 0.04 on the basis of data on Cayo Santiago rhesus macaques for the

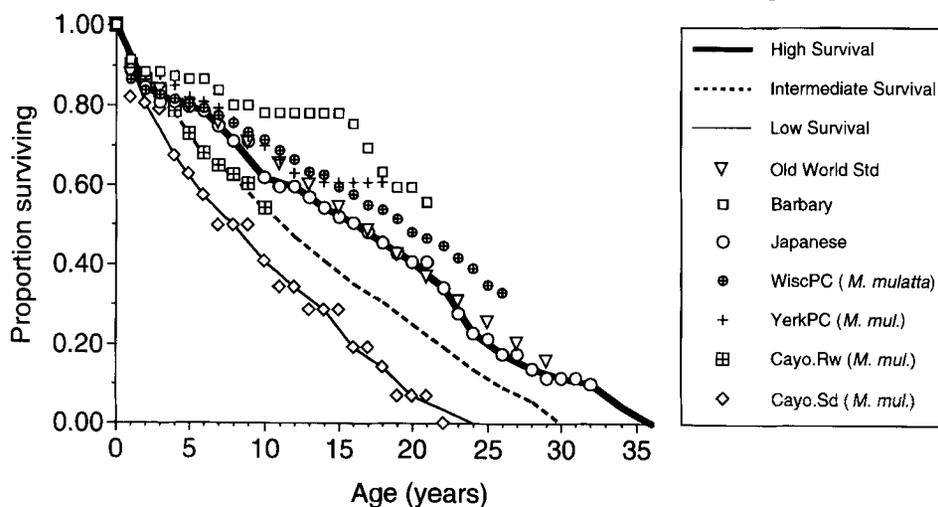


Fig. 2. Survivorship curves (proportion of females surviving to an age) generated by three survival probabilities modeled (High, Intermediate, Low), compared to published data for other macaque species. Sources (also see Fig. 1 caption): a, Old World Std, Old World monkey standard life table [Gage & Dyke, 1988]; b, captive Barbary [Paul & Kuester, 1988]; c, provisioned Japanese macaque females from Arashiyama A [Fedigan, 1991a]; d and e, WiscPC and YerkPC, rhesus (*M. mulatta*) born in Wisconsin Regional Primate Research Center [Dyke et al., 1986] and Yerkes Regional Primate Research Center [Tigges et al., 1988], both populations subject to culling of less healthy animals; f, Cayo.Rw, heavily provisioned Cayo Santiago Island rhesus, 1976–1983 dynamic composite cohort life table [Rawlins & Kessler, 1986a]; g, Cayo.Sd, Cayo Santiago rhesus, 1973–1974 time-specific life table [Sade et al., 1976].

years 1976–1983 [Rawlins & Kessler, 1986a]. In a preliminary simulation (Crockett & Kyes, unpublished data), we used a CV of 0.03, calculated for survival of Venezuelan red howler (*Alouatta seniculus*) infants [Crockett & Rudran, 1987]. Annual variation in infant mortality can be much higher, e.g., CVs of 0.67 and 0.77 calculated from data on Barbary macaques (*M. sylvanus*) in two strongly seasonal Algerian habitats [Ménard & Vallet, 1993].

For CV of adult female survival, we used 0.05, also calculated from red howler data. The CV of annual mortality for rhesus macaques was 0.10, but this included both sexes [Rawlins & Kessler, 1986a].

For CV of birth rate, we used a formula provided in the program's manual [Ferson & Akçakaya, 1993]. We tested this formula on seven sets of primate data from which CVs could be calculated directly, and found it to be very close (averaging 0.015 difference). We calculated the CV of birth rate to be 0.15, based on FBY of 0.25–0.45 (mean 0.34), and an N of 25 years. In our initial simulation, we used a CV of 0.24 based on red howler data. The latter value is very similar to the CV of 0.26 calculated for annual variation in birth rate reported for *Propithecus verreauxi* [Richard et al., 1991]. The CV calculated for Cayo Santiago rhesus macaques is much lower, 0.05, but the species breeds seasonally and the monkeys on Cayo Santiago are heavily provisioned. The CVs of birth rate calculated for Barbary macaques in two Algerian habitats were large, 0.40 and 0.35 [Ménard & Vallet, 1993].

The CV for harvesting (negative migration) was calculated to be 0.05, using a mean of 50 female offspring (range of 45–55) removed per year. The CVs for actual numbers introduced and removed were zero.

TABLE I. Annual Growth Rate (Instantaneous Rate of Increase, r), Threshold Harvest Rates (Female Juveniles Removed Per Annum), and Estimated Female Population Size After 8 and 26 Years

Survival	Model parameters				Simultaneous release with constant harvest rate ^d			Actual numbers released and removed, + 42 new ^e		
	Birth rate	Birth rate % ^a	Instant. r ^b	R_0 net repr. ^c	Harvest threshold ^f	After 8 years	After 26 years	Harvest threshold ^f	After 8 years	After 26 years
Low	Low	50%	0.036	1.49	20	588–598	591–623	20	536	559
Low	Intermediate	60%	0.054	1.80	34	622–622	605–624			
Low	High	70%	0.068	2.10	48	660–665	627–656			
Intermediate	Low	50%	0.063	2.11	40	618–620	617–622			
Intermediate	Intermediate	60%	0.080	2.59	57	648–651	636–639	78	795	952
Intermediate	High	70%	0.095	3.06	75	667–679	568–594			
High	Low	50%	0.078	2.62	50	648–652	657–675			
High	Intermediate	60%	0.096	3.26	68	673–679	672–696			
High	High	70%	0.110	3.90	87	697–698	665–689	152	1,052	1,331

^aPercentage of prime-age (5-19-year-old) females giving birth per year to infants of either sex.

^bInstantaneous rate of increase of population growth.

^cNet reproductive rate; average number of female offspring per female lifetime (replacement rate).

^dFour hundred and twenty females introduced simultaneously, population growth modeled for 26 years. Results for two runs with same birth rate, survival, and harvest values.

^eActual numbers released and harvested over 8 years; effects of release of 42 more breeders followed for 18 years with annual harvest at threshold value.

^fMaximum number of offspring females removed annually without setting population into decline.

RESULTS

Population Growth Over 26 Years Assuming Simultaneous Release and Constant Harvest

In the absence of density dependence, stochasticity, and harvesting, all combinations of survivorship and natality schedules projected population growth (4–11% annually; Table I).

Threshold harvest values varied considerably depending on which survival schedule and birth rate were used in the simulation (Fig. 3; Table I). The simulations generated approximately parallel lines for the three survival schedules. One can visually estimate a sustainable harvest rate for intermediate survival schedules and birth rates. The figure indicates that removing 50 female offspring annually can be sustained only if birth rate and survival are intermediate to high.

The terminal population size (approximate number of females of all ages after 26 years) ranges from 568 to 696 (Table I). These numbers indicate the approximately stable (sustainable) population size when the corresponding number of juveniles is harvested annually. The average terminal sizes are somewhat larger for all birth rates modeled with the high survival probabilities, but show no obvious relation to survival or birth rate for the other combinations modeled. In general, given that a sustainable number is harvested, the managed population size does not vary much across the various birth rates and survival schedules.

Modeling Actual Numbers Released and Removed

For modeling actual release and removal of animals, the simulation was run without stochasticity for one time period with numbers released or removed added or subtracted from the migration vector. This procedure was repeated four times, adding 42 new female breeders during the last period. Figure 4 depicts the projected numbers of females of all ages at the beginning of 1996 assuming three survival and natality schedules (high–high, intermediate–intermediate, and low–low). The lines show mean (\pm SD) population size over the next 18 years (with stochasticity) given a threshold harvest rate calculated as for the first analysis.

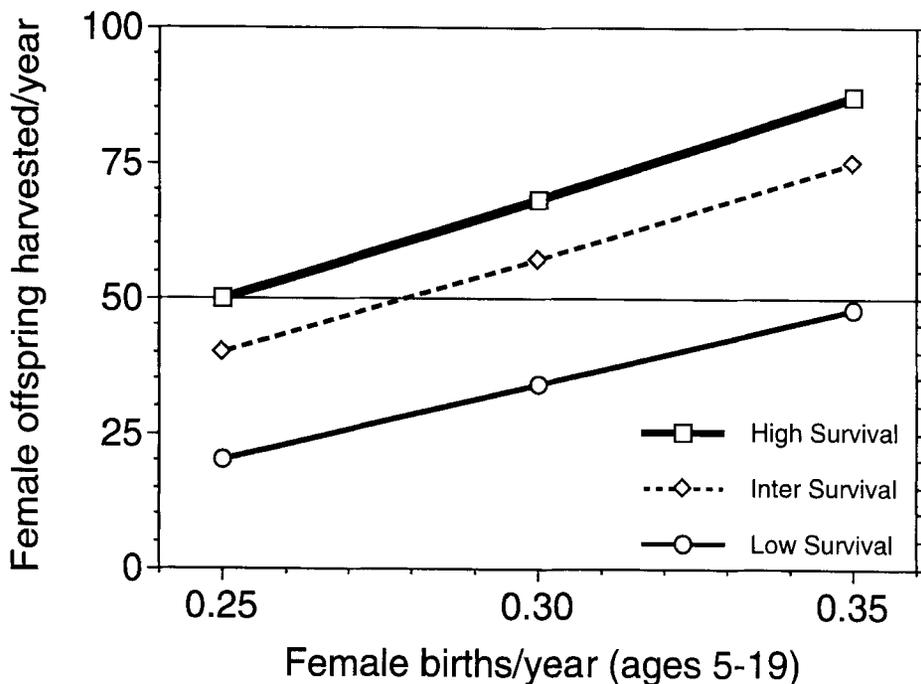


Fig. 3. Threshold harvest rates (maximum number of 2-to-3-year-old females removed annually without setting population into decline) vs. birth rate for three survival schedules. Horizontal line intersects survival and birth rates that must exist to sustain harvest averaging 50 females per year.

Projections indicate markedly different numbers of females on the island at the beginning of 1996: 536 assuming low parameter values, 795 assuming intermediate values, and 1,052 assuming high values. The sustainable (threshold) harvest rates also vary dramatically. The actual harvest rate, averaging 49 females per year (1991–1994), could not be sustained if the survival rate and birth rate are low (threshold harvest rate only 20 females/year), but is far below that needed to maintain a stable population if survival and birth rate are intermediate (78 females/year) or high (152 females/year) (Fig. 4; Table I).

DISCUSSION

Using Simulation Results to Guide Management of Harvested Primate Populations

Computer simulation of population dynamics can be useful in the management not only of threatened or endangered species but also of harvested populations. In both situations, a major objective is to identify the potential for population growth, maintenance, or extinction. Our goal was to provide realistic advice about how the population of Tinjil Island could be self-sustaining given that island-wide census data were unavailable.

We used the approach of modeling various parameter values and determining how many offspring could be harvested without setting the population into decline. The results of the modeling indicate that the outcome is strongly affected by assumptions about birth rate and survival (Figs. 3, 4), underscoring the importance of monitoring harvested populations to develop more accurate estimates of these

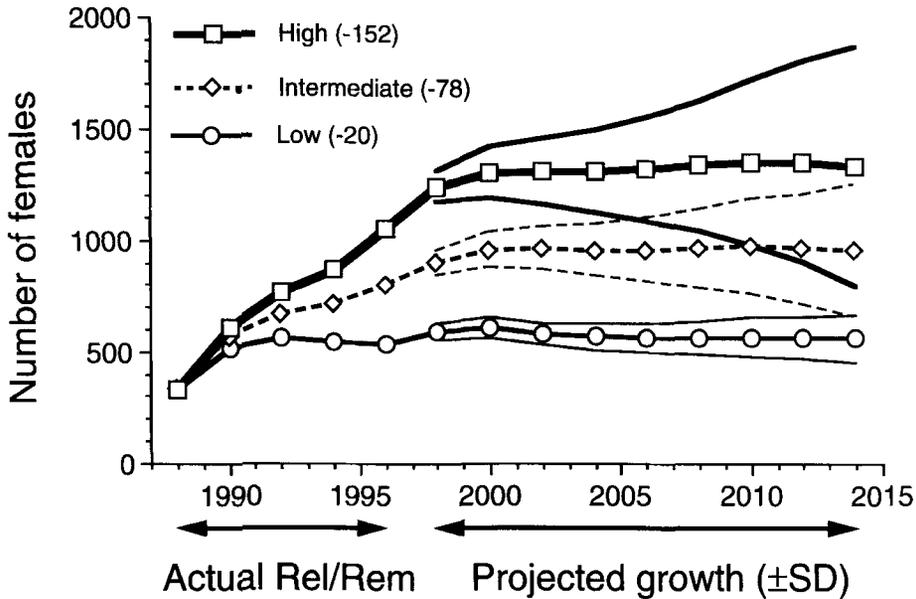


Fig. 4. Mean (\pm SD) number of females of all ages over years of expected island operation assuming three survival and natality schedules (high–high, intermediate–intermediate, and low–low). Actual Rel/Rem: modeling actual number of females released and removed, including 42 additional female breeders (see text). Projected growth (\pm SD): population size over time with annual harvest at threshold harvest rate, which varies for survival–natality schedules: high (152 female offspring/year), intermediate (78 female offspring/year), and low (20 female offspring/year).

parameters. Because age-specific natality and survival data are difficult to gather from free-living, long-lived monkeys which cannot be accurately aged as adults unless followed from infancy, at present we must draw upon comparative sources to evaluate our assumptions. In a later section, we discuss possible ways to differentiate between the various projections made by the simulations.

On the basis of data from wild longtailed macaques in Sumatra and provisioned Tinjil groups monitored by R. Kyes since 1990, the intermediate (0.60) to high (0.70) birth rate estimates seem to be a reasonable range for Tinjil Island macaques in their prime. A 0.70 birth rate is more representative of the provisioned groups, whereas 0.60 is more representative of unprovisioned groups at the west end of the island. The birth rate for provisioned Tinjil groups was 0.68 in 1994. For wild longtailed macaques at Ketambe, Sumatra, the overall birth rate was 0.53 infants per female year (M. van Noordwijk, personal communication, based on 349 adult female years and 184 infants born). Birth rate was a low 0.12 for 4-year-olds, rising to 0.55 for 6-year-olds, and 0.60–0.70 for 7-to-15-year-olds, leveling out at 0.60 for 16-to-21-year-olds, and declining to just 0.15 for females over 21 years (Fig. 1). These data from the wild are also consistent with our modeling of lower natality for the youngest and oldest females.

Intermediate to high survivorship values seem realistic for Tinjil Island. Sightings of tattooed individuals between 1991 and 1994 suggest a rough estimate of 7% annual mortality for the breeding females released (Kyes, in preparation). This is almost certainly an overestimate because animals missed in 1994 may have gone undetected or transferred to unhabituated groups. Intermediate survival val-

ues were derived from Cayo Santiago when one of the main causes of mortality was tetanus [Rawlins & Kessler, 1986a], which is presumably absent from Tinjil Island. Annual mortality on Cayo Santiago dropped from 6.8% to 3.7% after the eradication of tetanus [Rawlins, 1989]. Tinjil monkeys received intensive screening prior to release [Pamungkas et al., 1994] and were judged to be very healthy. Pythons may be the only significant predator on the island [Kyes et al., 1995; Morton et al., 1995]. Even with a full complement of predators, survivorship of wild longtailed macaques at Ketambe was around 0.70 from birth to age 5, but varied by rank thereafter: fewer than 0.50 of low-ranking females were still alive at age 12, dropping to 0.47 by age 16, whereas 0.64 of high-ranking females were still alive at age 12, and more than 0.50 survived to age 20 (van Noordwijk, personal communication) [Van Noordwijk & Van Schaik, 1987]). On the basis of the low, intermediate, and high survivorship schedules modeled for Tinjil, respective proportions of females surviving to a given age are 0.34, 0.47, and 0.60 for 12 years, 0.19, 0.36, and 0.51 for 16 years, and 0.07, 0.25, and 0.41 for age 20 years.

Group-housed female rhesus macaques reared at the Yerkes Regional Primate Research Center had high survival, about 0.61 at age 16; however, this value may be inflated if less healthy animals were removed from the group, and thus "censored" from the survival analysis [Tigges et al., 1988]. Survivorship of 192 female longtailed macaques monitored in a zoo colony for nearly three decades was just 0.22 at 20 years of age, the oldest attaining 26 and 28 years, but this may reflect increased mortality through aggression in a more confined setting [Luder, 1993]. However, wild Japanese macaque females, receiving partial provisioning on an island, did not survive beyond 23 years of age [Watanabe et al., 1992].

Overall, it seems that intermediate to high values for both birth rate and survival are reasonable estimates for the longtailed macaques on Tinjil Island. Intermediate values may be the most representative across the island, whereas the high values can be viewed as a realistic upper limit. Within this range of values, the actual harvest average of 49 juvenile females annually from 1991 through 1994 is sustainable until density-dependence factors, not modeled, come into play. If both survival and birth rates resemble the intermediate values modeled, by the beginning of 1996 there should have been ~1,280 females and males of all ages on the island, for a population density of ~215 individuals/sq km; this includes 42 new females that were released prior to 1996. If the survival and birth rates were high, we would estimate a population of ~1,750 for a density of ~290/sq km. Both density estimates are higher than the overall average of 55/sq km (range 11–143/sq km across habitats occupied) for wild longtailed macaques in various Sumatran habitats [Crockett & Wilson, 1980]. In the lowland primary forest of Sumatra, the total population density of six diurnal primate species, including *M. fascicularis*, was about 170 individuals/sq km [Crockett Wilson & Wilson, 1977]. Total primate biomass in Indonesia and Malaysia rarely exceeds 1,000 kg/sq km. For longtailed macaques, averaging about 3 kg in weight across age–sex classes, this translates to about 333 individuals/sq km. Partially provisioned rhesus macaques, the only nonhuman primates on a 10 sq km peninsula of Hainan Island, live at population densities of 150–250/sq km in the best, forested habitat; members of a smaller rhesus subspecies, they are close in weight to longtailed macaques [Jiang et al., 1991]. Japanese macaques, somewhat heavier than longtailed macaques, reached a stable density of about 333/sq km on a small (30 ha) island when given limited provisioning [Watanabe et al., 1992]. Thus, the current density on Tinjil Island may be approaching the upper limit of what can be supported by natural vegetation alone. The provisioning that does occur is primarily at a level to entice

individuals into the feeder-capture cages and does not currently affect the monkeys at the far, west end of the island.

The rhesus macaques on Cayo Santiago are maintained at much higher densities, 760/sq km, but are provisioned with monkey chow at a rate of 0.23 kg per monkey per day [Rawlins & Kessler, 1986a]. This works out to about 46 gm biscuit/kg body weight/monkey/day (assuming an average body weight of 5 kg), which is considerably more than the ~20 gm/kg/day consumed by individually housed rhesus [Henderson et al., 1993] and longtailed macaques (Crockett, unpublished data). Rhesus adults on Key Lois consume an average of 225 gm of food per day, or ~23 gm/kg for 10 kg adults [Pucak et al., 1982]. Such a high level of provisioning is not desirable on Tinjil because it would defeat the economic advantage of a natural habitat.

The modeling of the release of 42 new breeders provided some valuable insights about sustainable harvest rates and population size, and clearly indicates that no additional breeders should be released except for periodically introducing new genetic stock. Assuming intermediate to high survival and birth rates, the addition of new breeders increased the population size and the threshold harvest number over that projected by the 26 year model. The low model, in contrast, projected the same threshold harvest number, 20 female offspring, a quantity too low to justify the cost of maintaining the island. However, it is highly unlikely that birth rate and survival on Tinjil are in the range of the low values modeled. The intermediate to high models project that 78–152 female offspring must be removed annually to prevent the population from exploding beyond the capacity of the island. If 20% more males than females are to be removed, as in the past, the annual harvest quota must be 172–334 offspring. This is considerably more than the annual average of ~103 male and female offspring removed from 1991 through 1995. Clearly, it is essential to collect field data on Tinjil to determine whether the intermediate vs. high estimates of birth rate and survival are more appropriate.

Proposed Method for Distinguishing Estimates

We expect censuses over the next few years to enable us to distinguish among the population sizes projected by the simulations, and thereby differentiate among the low, intermediate, and high models. Between 1990 and 1994, the number of groups on Tinjil was stable at 17–18. In 1995, there was evidence of fissioning, with the number of groups appearing to increase. The 1996 field season will include a concentrated effort to verify the number of groups. Approximately 15 students in a summer training program will perform simultaneous transect censuses. In addition, all-day follows and habituation of the groups at the far west end of the island will begin. It is hoped that this will allow reasonable estimates of group sizes of the previously unhabituated groups as well as identification of some tattoos not seen since animals were released. The tattoo information will be added to the accumulating data set, simulating mark-recapture studies, which will allow more accurate estimates of adult survival. Any offspring captured that are not removed from the island are tattooed and released. Resightings of these individuals will permit survival estimates of younger individuals. However, we do not anticipate being able to collect complete life history information on the Tinjil monkeys.

With better estimates of number of groups and average group size, we will be able to calculate an estimate of the number of females on the island in 1996. We anticipate being able to distinguish among the female population sizes predicted by the low (536), intermediate (795), and high (1052) trajectories (Fig. 4; Table I). However, if birth rate is not relatively similar over the ages 5–19, as suggested by the data from wild longtailed macaques (van Noordwijk, personal communication;

Fig. 1 caption) and captive Barbary macaques [Kuester et al., 1995], but instead declines as suggested for rhesus macaques [Johnson and Kapsalis, 1995], then our projections will be overestimates. Birth rate data from aging females, released before 1991 and now at least 10–12 years old, will begin to resolve this question.

Conservation of Primate Species Used in Biomedical Research

All primate species, whether common or threatened with extinction, can benefit from some degree of conservation management. As reviewed in the Introduction, it is generally believed that the populations of most primate species still captured for research are not threatened by this practice [Kavanagh et al., 1987], although the details of their population status are not always known [Southwick & Siddiqi, 1994a]. One species of particular interest in AIDS-related research [Agy et al., 1992], the pigtailed macaque (*M. nemestrina*), is widespread but occurs at such low densities that it cannot sustain the same level of trapping as the much more common longtailed macaque [Crockett & Wilson, 1980; MacKinnon, 1986; Bennett, 1991]. However, for pigtailed macaques and virtually all nonhuman primates, habitat destruction and hunting have far greater effects on populations than live trapping [Erwin et al., 1995].

Habitat destruction is the major factor contributing to the decline of nonhuman primate populations, exacerbated by the fact that human population growth tends to be greatest in the same tropical regions where most nonhuman primates are found [Mittermeier & Cheney, 1987]. Hunting primates results in some species becoming locally rare even when their habitat is relatively intact [Ramirez, 1984; Redford & Robinson, 1985]. Sport hunting has virtually exterminated the otherwise adaptable *M. fascicularis* from parts of Sarawak, Malaysian Borneo [Bennett, 1991]. Although “weed” species such as rhesus and longtailed macaques are relatively unaffected by habitat disturbance [Richard et al., 1989; Bennett, 1991], they can be exterminated by pest eradication programs and habitat destruction. Rhesus macaques, for example, have been eliminated from most of China [Southwick & Siddiqi, 1994a].

In a move apparently motivated more by concerns for animal welfare than conservation, the government of the United Kingdom recently banned the use of wild-caught nonhuman primates in scientific studies [Anonymous, 1995]. This will surely have little effect on the well-being of wild primates, for in their native habitat they are often persecuted in ways that are seriously detrimental to their welfare. For example, in Sarawak, *M. fascicularis* are trapped and skinned alive, to be released as a deterrent to crop raiders [Bennett, 1991]. For species that are agricultural pests, live capture of primates is a means to reduce crop damage while providing local income and benefiting biomedical research [Horrocks & Baulu, 1988]. In Barbados, trapping has nearly replaced shooting as a means of pest control, and the vervets are now viewed by the local people as a valuable natural resource [Horrocks & Baulu, 1994]. It seems especially appropriate to harvest pest primates from islands such as Mauritius, St. Kitts, and Barbados, where they were introduced centuries ago and do great damage to local flora and fauna [Kavanagh et al., 1987]. In Peru, live capture of tamarins (*Saguinus spp.*) and owl monkeys (*Aotus spp.*) for research is viewed as a strong incentive to keep forests intact, as the monetary value of the primates and forest fruits harvested exceeds the value of the land when farmed [Moya et al., 1993]. Trapping of *S. mystax* and *A. nancy-mae* at several-year intervals was followed by population recovery [Glander et al., 1984; Ramirez, 1984; Moya et al., 1993]. Sustainable harvest of primates for use in biomedical research is a realistic objective for many species, if properly managed [Erwin et al., 1995]. Capture-related mortality can be reduced by the use of proper

methods and recognition that the primates are a valuable resource [MacKinnon, 1986; Kavanagh et al., 1987; Moya et al., 1993]. Since primates for trade are usually captured by skilled trappers employed by the major dealers, it is possible to encourage limitation of trapping activities to areas of intense habitat destruction, thus reducing pressure on populations in undisturbed habitat [MacKinnon, 1986].

NHBFs, such as the one on Tinjil Island, are alternatives for providing valuable research subjects while minimizing removal of animals from the wild. If only disease-free animals are released onto an island facility, their progeny are likely to be healthier than wild-caught animals in general. Free living, they experience the degree of environmental enrichment available to wild animals, and, if macaques, they form multimale, multifemale social units typical of the species. Such social units are not usually feasible in captive situations because, unless the captive enclosures are unusually large, male macaques often show unacceptable levels of aggression toward each other [Lindburg, 1991]. NHBFs can also benefit the local economy and provide conservation-education training for students, some of whom will be the future managers of the country's wildlife.

However, as we have illustrated in this analysis, such breeding facilities must be managed with population ecology concepts firmly in mind. Given that, under present staffing and observation conditions, individual life histories cannot be known for more than a small subset of the Tinjil macaques, modeling becomes a valuable management tool.

CONCLUSIONS

1. Computer simulation of population dynamics can be useful in managing harvested populations of monkeys on islands such as Tinjil Island, Indonesia. Assuming simultaneous release of 420 female breeders, simulations projected that about four times as many female offspring could be harvested annually from a stable population assuming high birth rate (70%) and survival rate compared to low rates (87 vs. 20 offspring harvested).

2. Modeling the number of females actually released (including the recent addition of 42 new female breeders) and harvested, and projecting the population through 2014, indicated that threshold harvest rates and terminal population sizes increased considerably over the first model, assuming intermediate (78 harvested, 952 females) and high (152 harvested, 1,331 females) rates of survivorship and natality, but were unchanged assuming low rates (20 harvested, 559 females).

3. A review of the literature and field observations on Tinjil Island suggest that actual rates resemble the intermediate values modeled. If so, the present density on the island is approaching carrying capacity (~215 males and females per square kilometer).

4. The high values are realistic upper limits. If actual survivorship and birth rates are at the high end of those modeled, the island's population may be exploding, requiring increased harvest and provisioning.

5. Natural habitat breeding facilities such as Tinjil Island are alternatives to wild trapping and compound breeding which maximize the health and well-being of animals destined for essential biomedical research while conserving wild macaque populations.

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APPENDIX. I Values Entered in RAMAS/age Simulation; 2 Year Age Classes*

Age in years	Proportions introduced	High			Intermediate			Low		
		Birth rate	Birth rate	Birth rate	Proportion surviving	Survival probability	Proportion surviving	Survival probability	Proportion surviving	Survival probability
0-1		0.00	0.00	0.00	1.00	0.85	1.00	0.87	1.00	0.80
2-3		0.00	0.00	0.00	0.85	0.96	0.87	0.91	0.80	0.83
4-5	0.36	0.52	0.45	0.37	0.81	0.97	0.78	0.87	0.67	0.85
6-7	0.28	0.70	0.60	0.50	0.78	0.90	0.68	0.92	0.57	0.87
8-9	0.21	0.70	0.60	0.50	0.71	0.88	0.63	0.87	0.50	0.81
10-11	0.15	0.70	0.60	0.50	0.62	0.96	0.54	0.87	0.41	0.85
12-13		0.70	0.60	0.50	0.59	0.91	0.47	0.87	0.34	0.83
14-15		0.70	0.60	0.50	0.54	0.93	0.41	0.87	0.29	0.66
16-17		0.70	0.60	0.50	0.51	0.90	0.36	0.87	0.19	0.75
18-19		0.70	0.60	0.50	0.46	0.89	0.31	0.82	0.14	0.50
20-21		0.40	0.30	0.20	0.41	0.84	0.25	0.77	0.07	0.50
22-23		0.40	0.30	0.20	0.34	0.67	0.19	0.72	0.04	0.00
24-25		0.40	0.30	0.20	0.23	0.78	0.14	0.67	0.00	
26-27		0.25	0.15	0.05	0.18	0.79	0.09	0.62		
28-29		0.25	0.15	0.05	0.14	0.82	0.06	0.00		
30-31		0.25	0.15	0.05	0.11	0.89	0.00			
32-33		0.20	0.10	0.00	0.10	0.44				
34-35		0.20	0.10	0.00	0.04	0.00				
36					0.00					

*The total number of animals introduced per 2 year time period was multiplied by "Proportions introduced" to obtain the number per age class. Birth rate is the number of female births per 2 year period. Survival probability is the probability of surviving through the 2 year interval. Proportion surviving is the proportion of those born that are still alive at the beginning of the interval, as projected by the corresponding survival probability.