# Status of the Introduced Mule Deer Population on Catalina Island, California, Based on Annual Spotlight Counts

**Paul Stapp**
Department of Biological Science, California State University, Fullerton, California
**Emily Hamblen**, **Calvin L. Duncan**, and **Julie L. King**
Catalina Island Conservancy, Avalon, California

**ABSTRACT:** Mule deer were first introduced to Santa Catalina Island, California, in the early 1930s and persist today. Other feral, non-native ungulates have been eradicated (goats, pigs) or significantly reduced in numbers (bison) over the past two decades. Effective management of the deer population is necessary to protect the island's biodiversity but is dependent upon reliable estimates of population density and demography. We used annual summer spotlight counts, conducted in eight of the past ten years, to estimate deer densities in the island interior. In 2021, we also surveyed transects in the area around Avalon, the largest town on the island. Distance sampling (Program DISTANCE) was used to model density based on line transect data. Island-wide densities varied from 6.3 to 16.9 deer per km$^2$, with an average of 10.2 per km$^2$, and were positively correlated with July-June rainfall during the preceding year. Most (77-96%) of the identifiable deer were adults and most adults were does (58-75%). Deer were spotted most frequently in island chaparral and coastal sage scrub vegetation, the most common vegetation cover types along transects, whereas the use of grasslands and man-made and non-native habitats varied among years. The estimated deer density in Avalon (65.7 per km$^2$) was six to nine times higher than estimates for the interior transects in 2021. The high density of deer near Avalon suggests that gardens, landscaping, golf courses, and intentional feeding subsidize deer numbers in town that have the potential to spill over into the more natural areas of the island.

**KEY WORDS**: California, distance sampling, introduced herbivores, mule deer, *Odocoileus hemionus*, overabundance, population density, Santa Catalina Island

**Proceedings, 30th Vertebrate Pest Conference** (D. M. Woods, Ed.)
Paper No. 22. Published December 27, 2022. 8 pp.

## INTRODUCTION

Introduced herbivores threaten ecosystems and native plant and animal communities on islands, especially in the absence of predators (Donlan et al. 2002). Multiple species of large mammalian herbivores were introduced to Santa Catalina Island (hereafter, Catalina), in the California Channel Islands, during the past two centuries, including bovids [cattle (*Bos taurus*); sheep (*Ovis aries*); goats (*Capra hircus*); American bison (*Bison bison*)] and feral pigs (*Sus scrofa*) (McEachern et al. 2016). Mule deer (*Odocoileus hemionus*) were first introduced between 1928 and 1932 (Longhurst et al. 1952) and quickly became established island-wide. Concern for the native biota led to the removal of all large, introduced feral mammals on Catalina by 2005, except for a small (<120) herd of bison (Duncan et al. 2017) and the deer. With the eradication of elk (*Cervus elaphus*) and mule deer on Santa Rosa Island in 2011, Catalina is now the only Channel Island with wild populations of non-native mammalian herbivores.

Nonetheless, there is evidence that deer, and to some extent, bison, continue to damage native vegetation and pose a threat to endemic plants on Catalina (Figure 1). Deer browsing was the most common source of disturbance and damage to planted seedlings of island scrub oak (*Quercus pacifica*), with approximately 2.3-5.4% of seedlings browsed by deer during a 14-month study (Manuwal and Sweitzer 2008). Ramirez et al. (2012) reported that deer browsing reduced growth, increased mortality, and reduced canopy cover of *Heteromeles arbutifolia* and other common woody shrubs as they recovered from fire. Dvorak and Catalano (2016) found that browsing by deer significantly reduced growth and seed production of *Crocanthemum greenei*, a federally threatened sub-shrub. At present, populations of rare and endemic plants, including the critically endangered *Cercocarpus traskiae*, which is found in a single gully on the island, are protected by fencing. However, fences can be damaged and breached, especially in a system prone to wildfire and erosion, which would have catastrophic consequences for these plant populations.

In addition to excluding deer by fencing and caging, the Catalina Island Conservancy, whose mission includes conservation of natural resources on the island, also attempts to manage the mule deer population by hunting. Hunting is permitted through the Private Lands Management (PLM) program with the California Department of Fish and Wildlife (CDFW). The details of the program on Catalina have varied across the decades since it was established, but in general, it is characterized by a prolonged hunting season (July - December) that permits harvest of both sexes by residents, non-resident guests, and non-residents guided by a contracted outfitter (currently, Wildlife West, Inc.). Approximately 70%, on average, of the 300-400 tags issued per year are filled, and most (66%) of these are filled by guided hunters (Catalina Island Conservancy, unpubl. report). Evaluating the utility of public hunting as an approach for keeping the population below a desired ecological carrying capacity requires reliable estimates of population size and demographic structure over time.

The aim of our study was to estimate population

**Figure 1.**
**Left panel: Group of mule deer near Descanso Beach on Catalina Island.** Photo by J. L. King

**Right panel: Fence-line contrast associated with a large deer exclosure in the southeastern portion of Catalina Island. Bison are not present on either side of the fence.** Photo by A. E. Catalano.

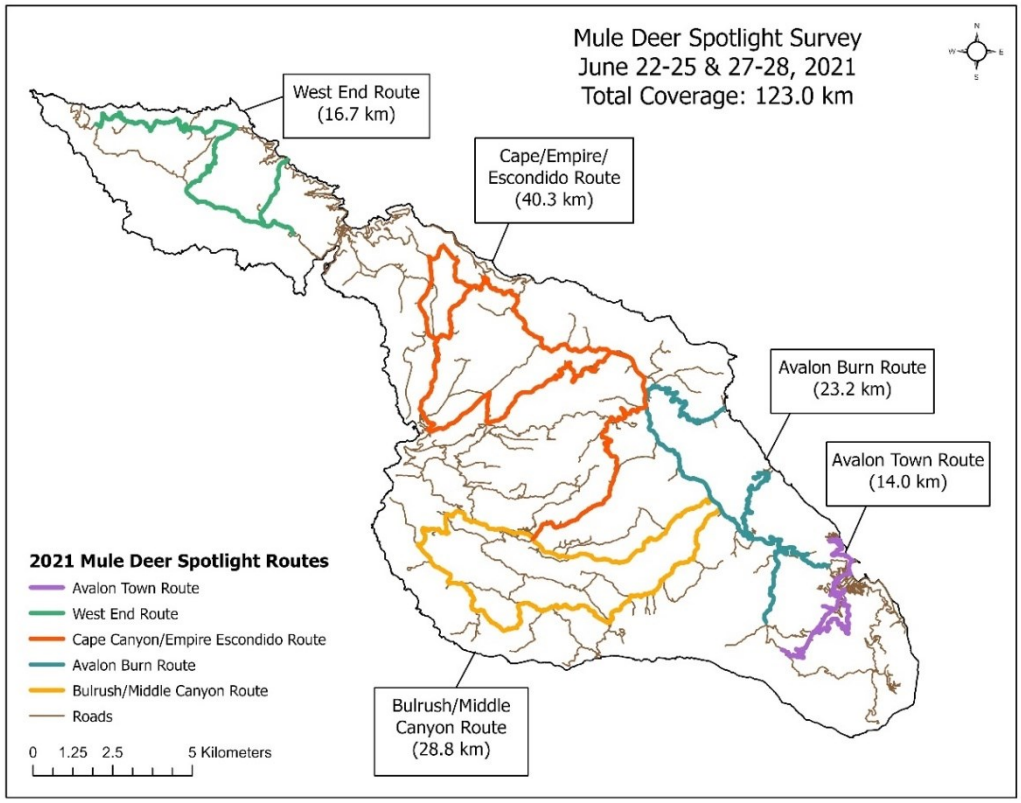


**Figure 2. Map of Santa Catalina Island, California, showing the locations and lengths of the four interior spotlighting transects in 2021. Similar routes were driven twice in late June or July each year to estimate mule deer densities. The Avalon Town Route transect was only surveyed in 2021.**

density of mule deer on Catalina annually using spotlighting and distance sampling. Spotlight surveys, which were conducted on transects distributed across the island, also provided an opportunity to collect demographic information about the deer population.

## METHODS

### Study Site

At 194.4 km$^2$, Catalina Island is third-largest of the California Channel Islands and is located just west of Los Angeles, California, USA. The climate is Mediterranean, with mild temperatures year-round (8-23ºC) and most (93%) of the 235 mm of annual rain typically falling between November and May. The vegetation is composed primarily of coastal sage scrub (38%), island chaparral/woodland (30%) and annual grassland (20%), with several small riparian areas (Stapp and Guttilla 2006). Much of the terrain is steep, rugged, and inaccessible, except along a network of unpaved roads. Avalon, the largest town, has a population of approximately 3,600 people, with smaller communities in Two Harbors and in camps along the coast. Catalina receives more than 1 million visitors annually.

### Field Survey Methods

Mule deer were spotlighted on four transects (Avalon Burn, Bulrush/Middle Canyon, Cape/Empire/Escondido, West End) that followed mostly unimproved roads distributed across the island (Figure 2). Surveys were conducted annually in late June or early July from 2012 to 2021, except for 2017 and 2020, when no surveys were conducted. Surveys were timed to be completed prior to the onset of the hunting season; they could not be routinely done after the season because roads were often inaccessible or wet and dangerous in winter. Each transect was sampled on two occasions (nights) within one week of each other, although in a few instances the two surveys had to be completed across three different nights to account for fog, rain, spotlight failures, inaccessible roads, and insufficient nighttime. Spotlighting vehicles were driven at a relatively slow speed, with the number of observers varying from two to four (two spotlights per vehicle). Crews used a digital rangefinder to estimate the perpendicular distance to each individual or cluster of deer spotted and a compass to determine the bearing. They used binoculars to attempt to determine the age and sex of each individual, and in the case of adult males (bucks), the number of antler points. Vegetation cover type and topographic position were also noted for each location to characterize habitat characteristics at deer locations.

To estimate deer density in the vicinity of Avalon, in June 2021 crews surveyed for deer along a 14-km route in and around town. This route was also driven twice by the same crew that conducted surveys in the island interior that year.

### Data Analysis

We calculated two indices of relative abundance, the number of deer spotted per night and the number spotted per km driven, to examine temporal trends in relative abundance. Stretches of the transects that could not be driven or where fog significantly reduced visibility were omitted from transect lengths. Population density was modeled using Program DISTANCE (versions 6.0.3 to 7.3; Buckland et al. 1993). Because substantial fractions of the individuals spotted were of unknown sex (43.1%; range = 36.3-57.2%) and age (13.3%; range = 4.4-23.8%), and to facilitate comparisons across years, we combined all sex and age classes to estimate density. To calculate adult male to adult female demographic ratios (i.e., buck:100 does ratio, an index of habitat productivity or range condition; juveniles to adult females, i.e., fawn:100 does ratio, an index of recruitment), we used the number of non-male adults (females plus unknowns) to estimate the number of does.

We followed the general approach described by Stapp and Guttilla (2006) to model population densities for the island interior transects. Following exploratory visual inspection of the frequency distribution of distances and the extent to which they fit the recommended shape criteria, data were right- and left-truncated or grouped into bins. We used conventional distance sampling to fit a global detection function model using all of the data, and then used this model to estimate density for each night/transect, as well as a pooled estimate weighted by transect length. A uniform detection function, with one cosine expansion parameter, was the model chosen most often as providing the best fit to the transect data, based on goodness-of-fit tests, AIC values, and coefficients of variation (%CV) of sample and pooled density estimates. Means are expressed ±1 standard deviation (SD) unless otherwise noted.

## RESULTS

Combining across all transects and both spotlighting occasions, the total distance surveyed in the island interior varied across the eight years from 196 km to 227 km. The total number of deer seen varied from 374 to 1,056 (605.5 ±234.2). Most deer (63.2 ±5.5%) were alone when detected, with a mean group size of 1.6 ±0.1 (n = 8 years).

Deer were usually spotted in island chaparral or coastal sage scrub vegetation, which collectively comprised an average of 74.3% (SD = 5.1) of locations in any given year (Table 1). Detections in grassland habitat varied greatly across years. Detections in human-developed areas and non-native vegetation have generally increased since the start of surveys.

Deer were most abundant in 2012 and 2016 and least abundant in 2015 and 2019 (Figure 3). Ratios of adult males to 100 females ranged from 23.2 to 43.2 (34.1 ±7.3), whereas the ratio of juveniles to 100 adult females ranged from 6.3 to 44.4 (21.6 ±13.6; Figure 4). Both the number of males and the number of large males (three antler points or more) have tended to decline since 2012 (Figure 5).

Population density varied among transects and across years (Figure 6). Density was usually highest on the Avalon Burn transect and lowest on the West End transect, with the other two transects intermediate. Over time, densities were highest in 2012 and 2016, and lowest in 2015 and 2019. This variation occurred during periods

**Table 1. Vegetation type at locations of mule deer, expressed as the proportion of locations in each type, which was recorded during spotlight surveys on four interior transects. Values sum to slightly less than 100% in any given year because rarer categories such as bare ground were omitted.**

| Year | Island Chaparral* | Coastal Sage Scrub | Grassland | Developed | Non-native |
|---|---|---|---|---|---|
| 2021 | 32.8 | 38.3 | 6.4 | 10.3 | 8.7 |
| 2019 | 44.7 | 26.4 | 17.3 | 2.2 | 5.7 |
| 2018 | 32.2 | 34.4 | 6.8 | 5.7 | 17.4 |
| 2016 | 50.3 | 23.4 | 11.6 | 5.8 | 3.2 |
| 2015 | 51.7 | 21.2 | 13.6 | 9.7 | 2.6 |
| 2014 | 59.4 | 22.7 | 14.1 | 2.4 | 0.4 |
| 2013 | 39.6 | 36.9 | 14.1 | 6.3 | 0.8 |
| 2012 | 53.5 | 26.6 | 9.8 | 6.0 | 1.6 |
| *Mean* | *45.53* | *28.74* | *11.71* | *6.05* | *5.05* |
| *SD* | *9.94* | *6.78* | *3.82* | *2.92* | *5.70* |

*Includes areas characterized as woodland in Stapp and Guttilla (2006).

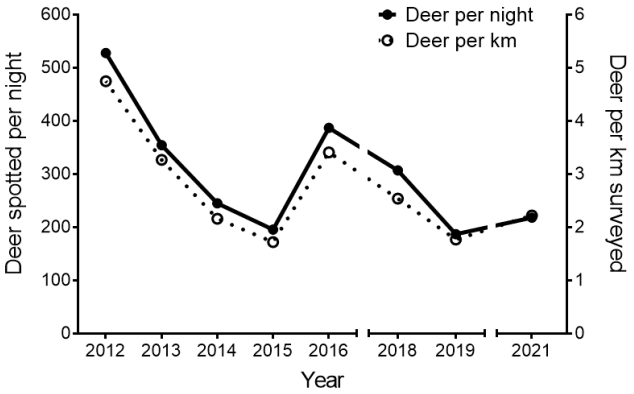


**Figure 3. Changes from 2012-21 in two indices of relative abundance of mule deer on Catalina Island, California, based on counts along four spotlight transects in the island interior, driven on two nights each in late June or July.**

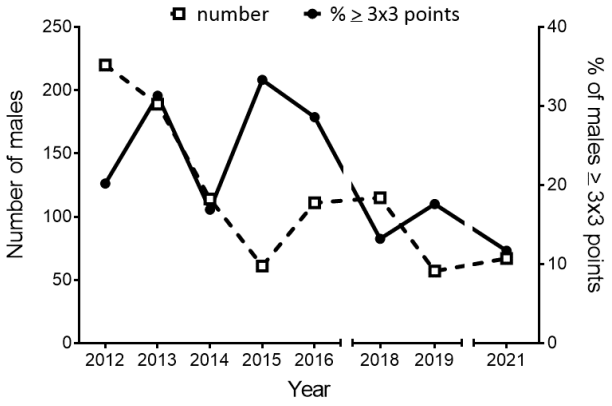


**Figure 5. Number of adult males seen and the representation of large individuals (3×3 or more antler points) among identified adult males along spotlight survey routes on Catalina Island, California, in late June or July each year from 2012-2021.**

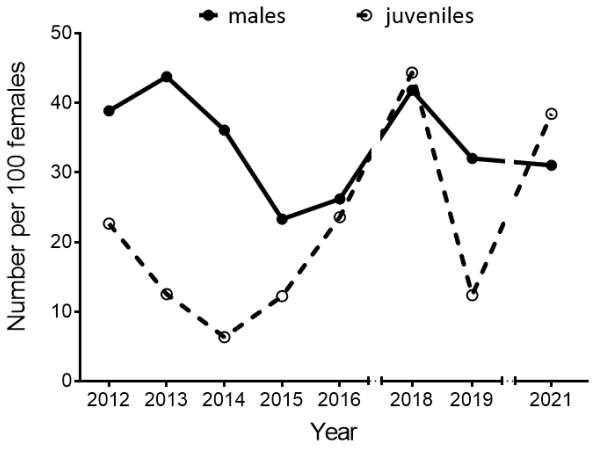


**Figure 4. Demographic representation of mule deer during spotlight surveys in late June or July on Catalina Island, California. Values are expressed as a fraction of the number of females, defined here as the number of non-male adults seen across both survey nights each year.**

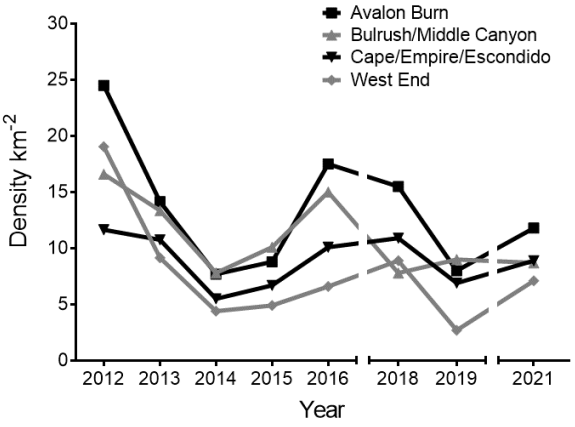


**Figure 6. Variation in population density (deer per km$^2$) of mule deer from 2012-2021 along four interior spotlight transects sampled for two nights each in late June or July on Catalina Island, California. Values are the means of DISTANCE-modeled density estimates for the 2 nights of surveys of each transect in each year.**

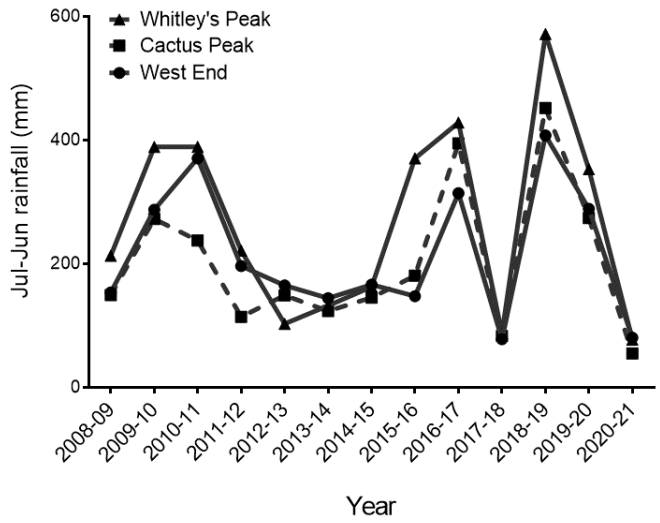


**Figure 7. Annual precipitation (July-June) at three weather stations on Catalina Island, California. Whitley's Peak and Cactus Peak stations are located in the middle of the eastern part of the island, roughly in the vicinity of the AB, BMC, and CEE transects, whereas the West End station is on the western part of the island (WE transect). For 2014-15 and 2015-16, data from the nearby Dakin Peak station were used in place of Whitley's Peak because of an instrument error at the Whitley's Peak station. Data from the nearby Wild Boar Gully station were used for Cactus Peak for Nov 2018, Dec 2018, and Jan 2019 because no rainfall data were available for the Cactus Peak station for more than a third of the days (32/92 days).** Data source: http://www.wrcc.dri.edu/catalina/.

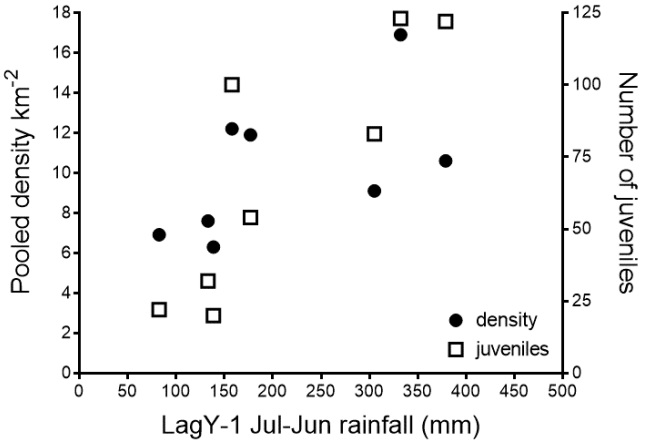


**Figure 8. Population density (per km$^2$) and number of juvenile mule deer were positively correlated with July-June precipitation during the previous year (average across three weather stations). For example, density and juvenile numbers from July 2019 are plotted against annual precipitation between July 2017 to June 2018. Spearman correlations: density (r = 0.64, P = 0.096), number of juveniles (r = 0.83, P = 0.015).**

of drought punctuated by wet conditions in 2016-17 and 2018-19 (Figure 7), which may have affected the deer population. Both island-wide deer density and the number of juveniles seen were positively related to rainfall amounts two years prior (Figure 8).

A total of 284 deer were seen on the 27.2 km of transect driven in and around the town of Avalon in 2021, for an average of 142 deer per night. Deer were seen in much larger herds in town: mean group size was 5.2, with groups of 50, 27, 22, 17, and 12 recorded, exceeding the size of the largest group ever seen on interior transects (10) during any previous survey. Large groups are regularly seen near youth camps in the interior, where they have access to water and are fed. Only 29.1% of town deer were seen alone. Unlike the interior transects, deer were only seen up to 150 m from the transect due to more visual obstructions (e.g., buildings, dense plantings) and steep canyon walls, so data were right-truncated at 130 m. Using the same approach as for the interior transects, the estimated population density in Avalon was 65.7 per km$^2$ (Figure 9). Modeling density as clusters, which treats these urban deer as loose aggregations rather than fixed social units and using the untruncated data set to include the large group of 50 directly on the transect on Night 1, the pooled density of clusters was 11.8 per km$^2$ (95%CI: 8.7-16.0; %CV = 15.4%), with a mean cluster size of 5.2 (95%CI: 3.4-7.8 deer), resulting in an average density of 61.4 per km$^2$.

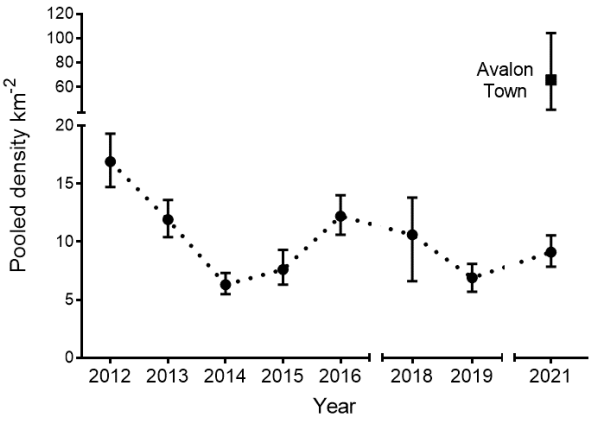


**Figure 9. Island-wide mule deer density (deer km$^{-2}$) from 2012-2021 along four spotlight transects sampled for a total of two nights each in late June or July on Catalina Island, California. Values are the point estimates and 95% confidence intervals of the pooled, DISTANCE-modeled densities for each year. The Avalon Town Route transect was only sampled in 2021.**

## DISCUSSION

Understanding and mitigating the ongoing impacts of introduced mule deer on the native biota of Catalina Island depends upon reliable information on demographic structure and population density. Although our transects covered a large area of the island, we caution that our surveys were only conducted once per year, in summer, and used spotlighting and distance sampling instead of more traditional methods of studying deer populations

(harvests, aerial counts), which are usually conducted in winter, after the usual fall hunting season. The rugged and steep terrain of the island and dense vegetation made some areas with deer inaccessible and required us to survey non-randomly, along existing roads. Crews varied from year to year and differed in the amount of experience and training. Spotlighting may underestimate the number of fawns (Kie and Boroski 1995), many of which would still be quite young in June and July and therefore may have remained hidden from sight. Although our estimates of fawn:doe and buck:doe ratios (21.6 and 34.1, respectively) may not be directly comparable to estimates derived from winter counts, they did tend to fall at the low end of ranges reported recently for deer populations sampled during summer and early fall elsewhere in California (Brazeal et al. 2017, Furnas et al. 2018, Furnas et al. 2020, Macauley et al. 2020).

We estimated that, in the island interior, densities ranged from 6.9 per km$^2$ to 16.9 per km$^2$ across the eight years of our surveys, with a mean of 10.2 per km$^2$. Assuming the areas we sampled are roughly representative of the 194.4 km$^2$ of the island as a whole, we estimate that the island-wide deer population ranged in size from 1,225 deer in 2015 to 3,285 in 2012, with a mean of 1,981 deer (±681). Both island-wide density and the number of juveniles detected were positively related to rainfall amounts not during the preceding 12 months but during the year prior, suggesting residual effects of forage production on body condition that influence recruitment. Marshal et al. (2008) described similar lagged effects of precipitation on body condition in mule deer populations in the Sonoran Desert in southeastern California.

By comparison, estimated population density in Avalon in 2021 was 65.7 per km$^2$, some six to nine times higher than densities on the interior transects in the same year. Assuming a town footprint of about 2.3 km$^2$, the herd in Avalon would number approximately 151 deer. From the time they were first introduced, deer have been numerous in town; media reports from the 1940s describe extensive damage to gardens and landscape plantings and public nuisance complaints caused by thousands of deer (Daily 2022). Although deer are described as moving from the dry interior into town to feed on irrigated plants and handouts, the extent to which deer move from Avalon to the island interior, or vice versa, is currently unknown. The Avalon Burn transect, which is closest to town (Figure 2), consistently had the highest densities of the interior transects, suggesting that there may be some demographic connection.

**Management Implications**

The population density of mule deer on Catalina, both island-wide and especially in Avalon, tends to be considerably higher than elsewhere in California (Table 2). The highest population densities in the state have typically been reported on the coast or in suburban areas. Furnas et al. (2020) proposed that, at densities exceeding 10 per km$^2$, deer should be considered overabundant from the standpoint of causing ecological damage to natural areas. Although Catalina densities have been lower recently, perhaps reflecting years of drought, the interior population, on average, is at this threshold (exceeding 10 per km$^2$ on the three main transects in four of the eight years; Figure 6) and the Avalon herd exceeds it six-fold. Given that deer are not native to Catalina, that they have no natural predators, and that they pose a threat to rare and endemic plants, they arguably should be considered overabundant on Catalina and managed as such.

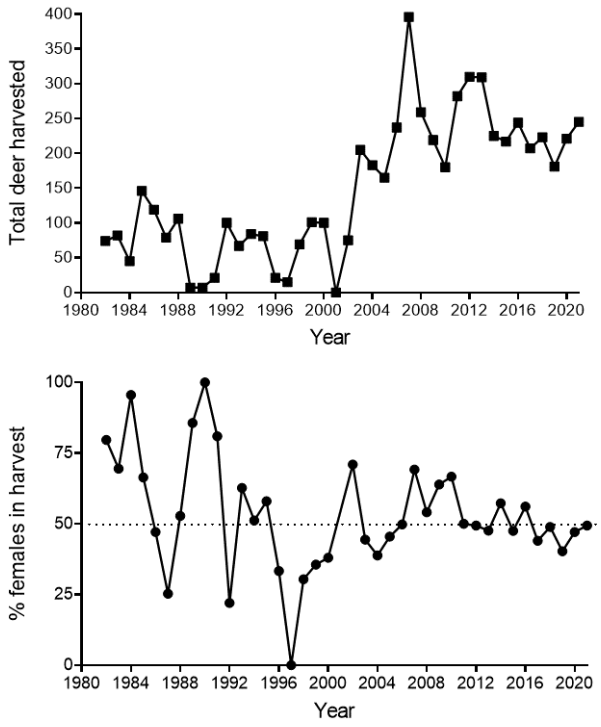


**Figure 10. Annual hunter harvest of mule deer on Catalina Island, California. Top panel: Total number of deer harvested of both sexes per year. The large number of deer harvested in 2007 was the result of a dedicated and expensive effort in 2007 and 2008 to bring hunters to Catalina, yet still only removed ~400 deer (16% of the estimated population). Bottom panel: Percentage of females in the harvest each year. Since 2003, when the total harvest increased markedly, on average, 51% (SD = 8%) of the deer taken have been does but does comprised more than 50% of the harvest in only six of the past 19 years. Data source: Catalina Island Conservancy and CDFW PLM reports.**

Aside from fencing, the main approach to control the deer population is through public hunting. As implemented, the current PLM program allows for the harvest of up to 300-400 deer each year, and hunters, mostly guided non-residents, have removed more deer from the island recently than during earlier decades of the program (Figure 10). However, because guided hunters usually prefer large or trophy bucks, a larger fraction of those taken since 2010 have tended to be males (Figure 10), and the harvest sex ratio has favored males in all but two years of the past decade. A hunter preference for bucks may, in part, explain the declines in the number of males and, especially, large males in our spotlight surveys (Figure 5), although effects of persistent drought on forage quality could have also reduced buck condition.

**Table 2. Estimates of population densities of mule (*Odocoileus hemionus*) and black-tailed deer (*O. h. columbianus*) in California. fDNA = fecal DNA.**

| Location | Density ($km^{-2}$) | Method | Source |
|---|---|---|---|
| Statewide | 5.0 (4.2 - 7.3) | harvest | Longhurst et al. (1952) |
| Southern Sierras | 3 - 5 | spotlight | Kie and Boroski (1995)[a] |
| Central Sierras | 5.0 - 5.1 | fDNA | Brazeal et al. (2017) |
| Southern Cascades | 5.2 | fDNA, cameras, telemetry | Furnas et al. (2018) |
| San Benito County | 7.7 - 8.6 | cameras | Macauley et al. (2020) |
| Mendocino County | 7.2 - 11.3 | fDNA, telemetry | Lounsberry et al. (2015)[a] |
| Marin County | 18.3 (5 - 44) | fDNA, cameras | Furnas et al. (2020) |
| Point Reyes | 30 | unknown | Gogan and Barrett (1995) |
| Lake County | 35 - 56 | direct counts | Dasmann and Taber (1956) |
| Angel Island | 92 | removal trapping | O'Bryan and McCullough (1985) |
| **Catalina Island** | | | |
| 1987 (Aug-Sep) | 10.5 | spotlight | Garcelon (1988) |
| 2004 (Jan-Jul) | 5.4 (3.1 - 7.8) | spotlight | Stapp and Gutilla (2004) |
| 2006 (Jul-Aug) | 12.3 | spotlight | Manuwal (2007) |
| 2007 (Dec) | 12.4 | spotlight | Guttilla (2009) |
| 2009 (Jan) | 3.1 | spotlight | Guttilla (2009) |
| 2012 - 2021 (Jun-Jul) | 10.2 (6.3 - 16.9) | spotlight | This study (interior) |
| 2021 (Jun) | 65.7 | spotlight | This study (Avalon Town Route) |

[a] Density as re-calculated by Furnas et al. (2020)

Because deer have remained abundant on the island over the past three decades (Table 2), it does not appear that the PLM program has a meaningful effect on the deer population. By harvesting an average of 244.3 deer annually (SD = 44.9) over the past 10 years, hunters have taken only 13.0% (SD = 2.9) of the estimated interior population in a given year. A much higher level of annual removal (e.g., 60% or more) is considered necessary to curtail deer population growth (Association of Fish and Wildlife Agencies 2018). Manuwal (2007) modeled deer population trajectories on Catalina under different harvest intensities and estimated that reducing and maintaining the population at 50% of current levels would require the removal of half of the fawns and antler-less adults and 10% of adult males each year for two consecutive years, followed by annual removals of 15% of each group. To date such harvest levels have not been attained by hunting, despite significant efforts to recruit hunters to the island. Given 1) the costs associated with guided hunts, the challenge of convincing these hunters to focus their efforts on does (which would have the greatest impact; Manuwal 2007), especially as hunter success rates decline with decreasing density; and 2) the logistical constraints imposed by the island's inaccessible terrain and need to ferry gear to and from the island, it is not clear that public hunting will ever be sufficient to control the deer population. Other alternatives are currently impractical even if they were permitted legally (contraception) or are unacceptable due to capture myopathy and low survival (translocation). Given the continuing threats to the island's natural resources posed by the deer, and the Conservancy's mission to preserve and restore the environment, a concerted eradication effort involving sharpshooting (e.g., DeNicola et al. 1997) should be re-considered.

## ACKNOWLEDGEMENTS

We thank the Catalina Island Conservancy for its support of these annual surveys. We are indebted to the dozens of individuals who helped with spotlighting over the years, as well as the particular contributions of Lara Brenner, Tyler Dvorak, Amy Catalano, Darcee Guttilla, and Peter Sharpe. The Department of Biological Science at California State University Fullerton provided additional logistical support.

## LITERATURE CITED

Association of Fish and Wildlife Agencies 2018. Methods for managing deer in populated areas. A product of the Human-Wildlife Conflicts Working Group. Accessed 14 May 2022 at https://www.fishwildlife.org/application/files/7315/3745/9637/AFWA_Deer_Mngmt_Pop_Areas_August_31_2018_version.pdf .

Brazeal, J. L., T. Weist, and B. N. Sacks. 2017. Noninvasive genetic spatial capture-recapture for estimating deer population abundance. Journal of Wildlife Management 81:629-640.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating the abundance of populations. Chapman and Hall, London, UK.

Daily, M. 2022. Deer: Santa Catalina Island. Santa Cruz Island Foundation. Accessed 14 May 2022 at https://www.islapedia.com/index.php?title=*_Deer:_Santa_Catalina_Island.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143-164.

DeNicola, A. J., S. J. Weber, C. A. Bridges, and J. L. Stokes. 1997. Nontraditional techniques for management of overabundant deer populations. Wildlife Society Bulletin 25:496-499.

Donlan, C. J., B. R. Tershy, and D. A. Croll. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. Journal of Applied Ecology 39:235-246.

Duncan, C. L., J. L. King, and P. Stapp. 2017. Effects of prolonged immunocontraception on the breeding behavior of American bison. Journal of Mammalogy 98:1272-1287.

Dvorak, T. M., and A. E. Catalano. 2016. Exclusion of introduced deer increases size and seed production success in an island-endemic plant species. Ecology and Evolution 6:544-551.

Furnas, B. J., R. H. Landers, S. Hill, S. S. Itoga, and B. N. Sacks. 2018. Integrated modeling to estimate population size and composition of mule deer. Journal of Wildlife Management 82:1429-1441.

Furnas, B. J., R. H. Landers, R. G. Paiste, and B. N. Sacks. 2020. Overabundance of black-tailed deer in urbanized coastal California. Journal of Wildlife Management 84:979-988.

Garcelon, D. K. 1988. A census and evaluation of deer in select areas of Santa Catalina Island. Unpublished report prepared for the Santa Catalina Island Conservancy, Avalon, CA.

Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. Journal of Range Management 48:327-335.

Guttilla, D. A. 2009. 2009 Catalina Island mule deer spotlight survey. Unpublished report prepared for the Santa Catalina Island Conservancy, Avalon, CA.

Kie, J. G., and B. B. Boroski. 1995. Using spotlight counts to estimate mule deer population size and trends. California Fish and Game 81:55-70.

Longhurst, W. M., A. S. Leopold, and R. F. Dasmann. 1952. A survey of California deer herds: their ranges and management problems. California Department of Fish and Game Bulletin 6, Sacramento, CA.

Lounsberry, Z. T., T. D. Forrester, M. T. Olegario, J. L. Brazeal, H. U. Wittmer, and B. N. Sacks. 2015. Estimating sex-specific abundance in fawning areas of a high-density Columbian black-tailed deer population using fecal DNA. Journal of Wildlife Management 9:39-49.

Macaulay, L. T., R. Sollmann, and R. H. Barrett. 2020. Estimating deer populations using camera traps and natural marks. Journal of Wildlife Management 84:301-310.

Manuwal, T. A. 2007. Implications of introduced mule deer on Santa Catalina Island, California: their impacts, population ecology, and management. M.S. thesis, University of North Dakota, Grand Forks, ND.

Manuwal, T. A., and R. A. Sweitzer. 2008. Effects of mule deer and bison on regeneration of island scrub oak on Santa Catalina Island, California. Pages 529-540 *in* A. Merenlender, D. McCreary, and K. L. Purcell, editors. Proceedings of the sixth California Oak symposium: today's challenges, tomorrow's opportunities. General Technical Report PSW-GTR-217. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2008. Body condition of mule deer in the Sonoran Desert is related to rainfall. Southwestern Naturalist 53:311-318.

McEachern, K., T. Atwater, P. W. Collins, K. Faulkner, and D. V. Richards. 2016. Managed island ecosystems. Pages 755-778 *in* H. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, CA.

O'Bryan, M. K., and D. R. McCullough. 1985. Survival of black-tailed deer following relocation in California. Journal of Wildlife Management 49:115-119.

Ramirez, A. R., R. B. Pratt, A. L. Jacobsen, and S. D. Davis. 2012. Exotic deer diminish post-fire resilience of native shrub communities on Santa Catalina Island, southern California. Plant Ecology 213:1037-1047.

Stapp, P., and D. A. Guttilla. 2006. Population density and habitat use of mule deer (*Odocoileus hemionus*) on Santa Catalina Island, California. Southwestern Naturalist 51:576-582.