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Journal
Proceedings of the Vertebrate Pest Conference, 30(30)

ISSN
0507-6773

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Publication Date
2022

Evidence for Irruptive Fluctuation in Axis Deer of Hawaiʻi

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ABSTRACT: Axis deer on the Hawaiian Islands of Maui, Lānaʻi, and Molokaʻi simultaneously experienced one of the most dramatic population crashes on record in 2020-2021, which coincided with extended drought conditions and prompted an emergency declaration for these islands. This phenomenon has been anecdotally documented during previous drought events in 2011-2012, but never formally studied. Newspaper articles document abundant deer becoming a nuisance to agriculture and natural resources, and then experiencing high mortality during droughts. This phenomenon fits Caughley's (1970) operational definition of eruptive (*sic*) fluctuation "…as an increase in numbers over at least two generations, followed by a marked decline." We examined available deer population and rainfall records over the time period of interest. Deer may have increased rapidly during favorable years with high survival and recruitment. During moderate drought, young of the year may experience high mortality, with little recruitment to populations. During severe drought, adults may experience noticeably high mortality. When populations are suppressed by large numbers of removals, fluctuations in mortality may be modulated. Abandonment of large-scale intensive agriculture in recent decades may complicate interpretation but understanding these population processes may lead to better management strategies for axis deer in Hawaiʻi.

KEY WORDS: *Axis axis*, Axis deer, drought, Hawaiʻi, Lānaʻi, Maui, Molokaʻi, population dynamics, ungulates

Proceedings, 30th Vertebrate Pest Conference (D. M. Woods, Ed.)
Paper No. 14. Published December 12, 2022. 4 pp.

INTRODUCTION

Axis deer (*Axis axis*) on three Hawaiian Islands (Maui, Lānaʻi, and Molokaʻi) simultaneously experienced one of the most dramatic mortality events on record in 2020-2021. This event occurred during a pandemic, and residents were aware that deer were capable of being infected with the SARS-CoV-2 virus (Chandler et al. 2021) and concerned that this mortality event might be disease-related. The mortality event coincided with extended drought conditions, and similar mortality events had been reported during droughts of 2011-2012 and during previous drought episodes (Honolulu Star Advertiser 2011). Many deer sought food and water at ranches, in agricultural crops, at resorts, and in residential areas, and had entered the perimeter fences at the Kahului, Maui airport, prompting an emergency declaration for these islands (Hawaii Emergency Management Agency 2022). Numerous deer died in the vicinity of residential areas, adding further concern about the sanitary disposal of carcasses.

A common phenomenon associated with similar mortality events is known as irruptive fluctuation (Caughley 1970), which is operationally defined as "…as an increase in numbers over at least two generations, followed by a marked decline." We hypothesize that deer may have increased rapidly during years with favorable climate, exhibiting high survival and recruitment. During moderate drought, young of the year may experience high mortality, with little recruitment to populations. During severe or extended drought, adults may experience noticeably high mortality. There are many examples of population increase followed by sharp decline in deer, elk, sheep, and goat relatives. Most examples are from New Zealand where there are no large predators. It was thought that populations should eventually equilibrate with the environment through a series of dampening oscillations. An often-idealized example from the early 20th century is that of blacktail deer on Kaibab Plateau of Arizona which Increased from 4,000 to more than 100,000 individuals in 18 years after predators were greatly reduced or eliminated altogether. Two harsh winters reportedly caused 60% mortality of the deer population after 1923. Caughley (1970) also cited other sources that claimed the probable capacity of 30,000 deer could have been maintained without excessive mortality if the herd had been reduced when range damage was first seen in 1918. Nonetheless, these previous examples were reported from seasonal temperate environments which may cause annual cold season mortality in sharp contrast to the relatively aseasonal environments of Hawaiʻi. However, like New Zealand, deer in the Hawaiian Islands had been introduced in the absence of large predators and increased to occupy most of the suitable habitat of these islands over many decades.

Axis deer were gifted to King Kamehameha V in late 1867 and first introduced to the island of Molokaʻi in 1868 (Hess 2008). Intermittent outbreaks of bovine tuberculosis led to the depopulation of deer, feral pigs (*Sus scrofa*), abandonment and reestablishment of commercial cattle ranching on the island. Although axis deer had been introduced to the island of Oʻahu before 1898, the population was apparently extirpated at an unknown later time. The introduction of axis deer to Lānaʻi in 1920 and

European mouflon sheep (*Ovis musimon*) in 1954 has made this island a popular sport hunting destination. A total of 14 individual deer were introduced to Maui in 1959-1960. Although the deer did not become apparent for more than a decade, hunting restrictions were lifted in the mid-1990s to alleviate overabundance of the species (Hess and Judge 2021). Axis deer were proposed to be introduced to Hawai'i Island in the late 1960s, but this action was opposed by ranchers and environmental groups. Nonetheless, four individuals were illegally introduced to the island in 2004, and a major effort was undertaken to locate and eradicate this incipient population (Hess et al. 2015).

The environment from which axis deer originate in tropical India has a strong and predictable annual monsoon season (Schaller 1967). In comparison, Hawai'i is relatively aseasonal, and climate variation between years is generally greater that variation within years. Axis deer are polygynous; only 27% of males breed starting at two years of age while 95% of females breed at one year of age. Gestation is approximately 235 days and twinning is rare, but some females give birth to two young within the span of a year. In their native range in India, tigers were a substantial contributor to early life mortality, depredating 48% of young of the year (Schaller 1967). In contrast the primary cause of mortality in Hawai'i is sport hunting, which primarily takes adult males. Consequently, predation in India acts on young age classes before deer have an opportunity to reproduce, whereas hunting in Hawai'i acts on the most mature age classes after these animals have had the opportunity to reproduce. The selective removal of adult males may also alter the sex ratio of the population (Hess and Judge 2021).

Case Events by Island

The island of Moloka'i (674 km^2) was the first to have experienced a drought-related mortality event in late 2020 and early 2021, primarily on the drier west end of the island. A veterinarian determined that the deer had reduced muscle and fat consistent with severe drought in December of 2020. The deer tested negative for tuberculosis, brucellosis, chronic wasting disease, and deer adenovirus. Toxicology tests did not identify toxicants or metals nor and significant parasite burdens (Hawaii Department of Agriculture 2021a). Nonetheless, in July of 2021, the Hawai'i Department of Agriculture reported that a cow on Moloka'i was infected with bovine tuberculosis for the first time in 25 years (Hawaii Department of Agriculture 2021b). Additional cases prompted the HDOA to issue a quarantine of all ungulates in April of 2022 (Hawaii Department of Agriculture 2022). Although there are no climate stations on the west end of Moloka'i, a weather station in the central part of the island recorded three successive years of decreasing rainfall 2018-2020. Unfortunately, no data were available for the previous drought period of interest in 2011-2012 (Figure 1).

Lāna'i (364 km^2) lies in the rainshadow of west Maui and is consequently uniformly drier than the other islands except for the summit of Lānaihale at 1,060 m asl. Deer and mouflon had both increased in numbers after major drought beginning in 2011-2012, reaching an estimated 17,600-19,500 axis deer and 5,800-7,800 mouflon in June of 2013. Malnourished deer and sheep came into residential areas and died in October 2021 and a storm that swept through several Hawaiian Islands on December 5, 2021, killed more than 100 deer in residential areas. Habitat suitability models have shown that afternoon cloud cover, mean annual precipitation, and vegetation greenness (NDVI) are all strong predictors of deer occurrence (Hess et al. 2020), suggesting that deer seek cooler areas with higher rainfall and succulent vegetation on Lāna'i. There was a generally decreasing rainfall over a 4-year period 2018-2021 and no recorded rainfall in 2012 (Figure 2).

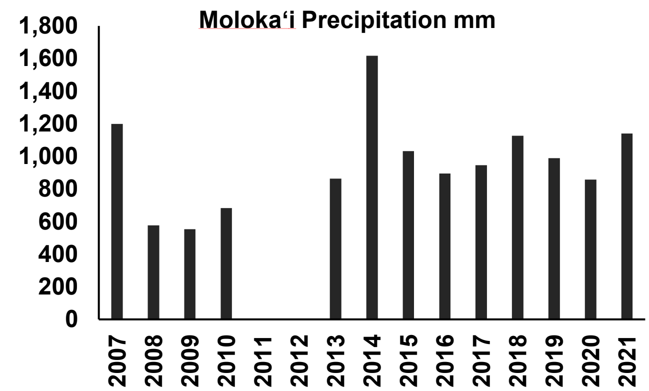

Figure 1. Rainfall from the island of Moloka'i during the period of 2007-2021. No data was available for the period of 2011-2012.

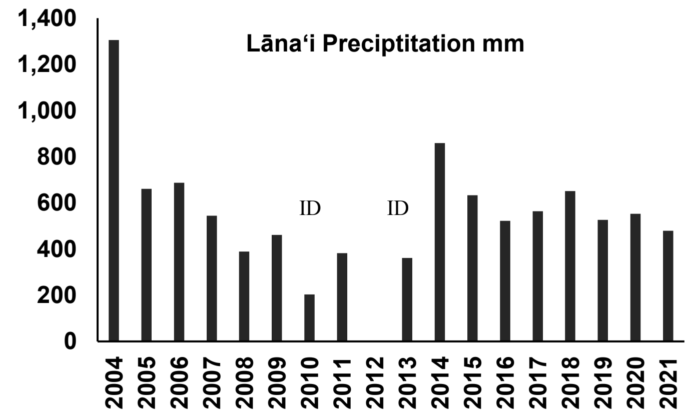

Figure 2. Rainfall from the island of Lāna'i during the period of 2004-2021. Data is incomplete (ID) for the years 2010 and 2013. No rainfall was recorded in 2012.

On the largest of three islands, Maui (1,883 km^2), drought conditions began in 2019, affecting ranches, agriculture, resorts, and residences. A strong pattern of increasing vehicle strikes occurred from 2018-2021: 20, 54, 83, and 173, respectively. An increasing number of deer occurred near the Kahului Airport, posing a strike risk to aircraft. Three emergency proclamations were issued in 2021-2022 to mobilize resources and mitigate the problems cause by encroaching deer (Hawaii Emergency Management Agency 2022). An aerial survey conducted in late 2021 through early 2022 recorded 46,743 deer on 32% of the island up to 2,150 m. Deer and drought conditions stripped vegetation from drier areas of the island,

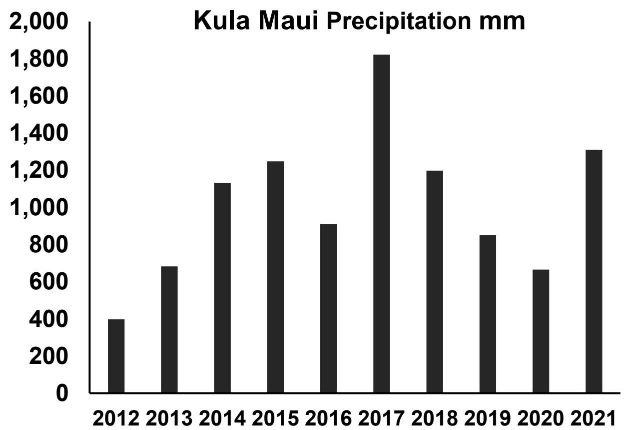

Figure 3. Rainfall from the island of Maui during the period of 2012-2021. Data is incomplete for the year 2011 and omitted.

and preliminary data analyses indicate that deer may have been seeking succulent vegetation near residential housing, resorts, and more recently established community gardens during droughts after forage on ranches and conservation lands was exhausted. Changes in land use such as the abandonment of intensive row crop agriculture may have also favored increased forage and cover for axis deer. Abandoned agricultural lands surrounding the Kahului (OGG) airport are therefore of concern for aviation safety. Climate station data from Kula, Maui recorded a pattern of decreasing rainfall over 2018-2020 after a year of above average precipitation in 2017 (Figure 3). Siltation of nearshore marine systems which is particularly detrimental to coral reefs is a problem common to all three islands and has been associated with erosion of upland areas as a consequence of overgrazing and trampling by invasive ungulates (Leopold and Hess 2017), which can be exacerbated by heavy rainfall following drought conditions.

Was This an Irruptive Fluctuation?

Although the recent drought does not appear to have been extraordinary, all three islands experienced a pattern of generally decreasing rainfall from 2018-2020. Moreover, populations may have been at high levels because of prior years with favorable rainfall conditions. Thus, deer may have outstripped forage due to overabundance and sought remaining succulent vegetation in and near residential and agricultural areas. However, it is important to note that disease has not been thoroughly investigated on all the islands and cannot be ruled out as a contributing or primary factor.

There are obvious strong differences between temperate and tropical climates, primarily little annual winter mortality in the tropics. Precipitation patterns in Hawai‘i generally follow multi-year oceanic climate cycles related to ENSO (Lu et al. 2020), consequently climate variability may be greater between years than within years in contrast to continental India which has a strong and predictable annual monsoon season. In the absence of strong annual seasonality in Hawai‘i, axis deer recruitment and abundance may follow multi-year climate cycles, periodically exhibiting drought-related mortality events. It remains to be seen if mortality events can be modulated by large-scale culling. For example, the extent of competition with other feral, wild, and domestic ungulate species such as goats (*Capra hircus*), pigs (*S. scrofa*), European mouflon sheep, and livestock remains poorly understood.

Few studies have examined population regulation mechanisms of ungulates in the tropics, especially in the absence of natural predators. Gaidet and Gaillard (2008) reported that food resource variation controls population dynamics of a tropical ungulate in a similar as temperate populations of large herbivores; however, with constant pressure from natural predators, unlike in Hawai‘i. Sinclair et al. (1985) also found an empirical relationship between population density, food supply, and dry season adult mortality rate for Serengeti wildebeest.

How Can We Learn More?

Axis deer and other non-native game species are rarely studied in Hawai‘i, consequently there is little reliable information on which to base management decisions (Lepczyk et al. 2011). Most of the basic life history of axis deer in Hawai‘i is known from Graf and Nichols (1966). Subsequent studies were motivated by problematic aspects of overabundance, detrimental effects on agriculture and the environment, and potential management strategies (Anderson 2003, Hess and Judge 2021, Rubino and Williams 2022). Consequently, aspects of life history such as adult sex ratio, recruitment, and survival are lacking, particularly differences in these parameters between drought and non-drought years. Several of these parameters such as age and sex composition can be determined by simple observational studies and monitored over time. Pregnancy by age class, sex ratio at birth, and the proportion of females bearing twins could be determined from necropsies of females harvested by hunters or by management removals. It would be informative if pregnancy or twinning changed as a result of climate, or management actions that reduced population density.

Abundance has been of perennial interest for many non-native game species in Hawai‘i. However, only one island has been surveyed for all species, and only on one occasion: Lāna‘i in 2013. Abundance is dynamic and changes rapidly, thus intensive surveys only provide an ephemeral perspective with little ability to make temporal comparisons. A remedy to this problem was outlined by Eberhardt (1982) by using the index-removal method. Costly abundance surveys would not be necessary if a repeatable, reliable index can be calibrated when there is data from substantial removals. In this manner, abundance can be estimated from apparent reduction to the population as measured by an index (Figure 4). Assumptions of the method are 1) the population is geographically closed, which can easily be met for most island systems; 2) demographic closure can be addressed with recruitment data previously mentioned; and 3) surveys have same detection probability which can be problematic if aerial shooting is used as a method of removal and aerial surveys are used as a method to index the same population. The method would be useful in this situation where relatively large numbers of deer are removed annually, providing insights into the effectiveness of these management actions for controlling deer populations in Hawai‘i.

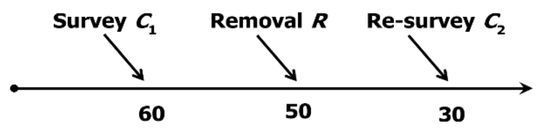

Figure 4. Application of a hypothetical index-removal scheme for monitoring a population undergoing substantial removals. Assuming a true but unknown population of N = 100 and a true but unknown detection probability of p̂ = 0.60, a first count should detect C1 ~ 60 animals. If R = 50 animals are then removed, a second count with the same detection probability should detect C2 ~ 30 animals if p̂ is roughly the same. Detection probability p̂ can be estimated as C2 / R (30 / 50 = 0.60) and the original population N can be estimated as C1 / p̂ (60 / 0.60 = 100).

ACKNOWLEDGEMENTS

The Maui Branch office of the Hawai‘i Division of Forestry and Wildlife, the Maui County Axis Deer Task Force, and the Maui Invasive Species Committee contributed valuable data to this manuscript. In memory of Fern Duvall II. This research was supported by the U.S. Department of Agriculture, National Wildlife Research Center (NWRC). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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