Introduced Axis deer (*Axis axis*) on Maui, Hawaii: History, Current Status, Home Range, Grouping Patterns, and a Species Account

By

STEVEN BRADLEY ANDERSON

B.S. (University of California, San Diego) 1992

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Committee in Charge

2003

UMI Number: 3097417

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

Table of Contents

List of Figures

List of Tables

Introduced Axis deer (*Axis axis*) on Maui, Hawaii: History, Current Status, Home Range, Grouping Patterns, and a Species Account

Abstract

In the 40 years since their introduction to the island of Maui, Hawaii, axis deer numbers and their range have increased dramatically to the point where they have become a problematic exotic species. **Chapter one** presents findings on axis deer distribution, range expansion, and management options. Deer on Maui are now common and widespread, impacting a variety of island residents. Impacts include public safety (deer-vehicle collisions, disease spread, and unregulated hunting), economic (crop loss, grazing competition, and golf course damage), cultural (archeological site damage) and environmental impacts (watershed and native species impacts, fence damage). Axis deer cannot be contained or excluded with 100 percent success, so axis deer management requires short-term and longer-term strategies at both local and regional scales. Cooperative management will be essential, since deer are widely distributed throughout the island's suburban areas. **Chapter two** presents findings from a 30-month radio-telemetry study of 23 adult axis deer on Maui. Annual home ranges of this introduced population were 4 to 10 times larger than those found in their native range. Group sizes of axis deer increase during the spring and decrease during summer. Overall group size for axis deer on Maui was nearly 16 individuals, versus an average of 8 in native areas of Nepal and India. Seasonal grouping patterns were similar to native lands, with the largest

numbers of deer, the most groups, and the largest groups encountered from February to May. Intensive hunting activity appears to decrease home range size and movement for both sexes, and may cause deer to disperse rather than cluster. **Chapter three** is a "mammalian species account" detailing the current state of knowledge on all aspects of axis deer biology. The chapter reviews axis deer systematics, worldwide distribution, reproduction, ecology, behavior, genetics and related species.

Acknowledgements

This research would not have happened without the financial assistance of The United States Fish & Wildlife Service, The Nature Conservancy, Haleakala National Park and Ulupalakua Ranch. Dr. Alan Kaufman, formerly of Aardvarks to Zebras Inc., also provided vital field assistance. Haleakala Ranch, Maui Land & Pineapple, Hawaii's Department of Land & Natural Resources and the Makena Resort provided additional land access. Public information meetings on deer were facilitated with help from the Maui County Farm Bureau, Don Reeser, Maui Rotary Clubs, Grady Timmons and Tim Hurley of the Maui News. Special thanks also to Mayor Apana for attending our largest public deer forum in August, 2000.

This research also would not have happened without the support, advice, and guidance of my dissertation committee. So, a special mahalo my major advisor, Dr. Christine Schonewald, my two additional dissertation advisors, Dr. Shawn Smallwood and Dr. Dirk Van Vuren and my two additional examiners, Dr. Mike Johnson and Dr. Debbie Elliot-Fisk. I want to extend a thank you as well to my other advisor that left early on for a new position, Dr. Sharon Collinge.

Finally, I would like to thank the following individuals for their important assistance on this project: Sumner and Pardee Erdman, Ted Rodrigues, Ron Nagata, Eric Nishibayashi, Mark White, Anders Lyons, Zadoc Brown, Don Shearer, Howard Takashita, Chris and Peter Baldwin, Cal Shinyama, Donald Dudoit, Art Medeiros, Wendell Wong, Dan Dorfman, Pat Bily, Dave Barnes, Chuck Chimera, Bill Evanson, Graham Nugent, Doug McClure, Grady Timmons, Clayton Matchett and "skeeter", Cindy Lawrence, Buck Joiner, Ed Tanji and, of course, "the other Steve Anderson", Stephen J. Anderson. Thanks also to the people of Maui for providing critical data through interviews, and by phoning sightings into the axis deer hotline.

My final thanks is reserved for my family, including my new nephew Leo! It is their love and encouragement that has allowed me to complete this journey. A childhood full of PBS nature programs and early outdoor experiences served as my inspiration. This manuscript is dedicated with all my love to my mother, Shirley Smith Anderson, who passed away September 14, 2000. She taught me to never be afraid of a challenge...

Chapter 1: The axis deer on Maui

Introduction

The human-assisted introduction of exotic species, both purposeful and accidental, has left a noticeable mark on global biodiversity (Jewel, O'Dowd et al. 1999). Ecological effects of exotic introductions have long been recognized as one of the most important challenges facing conservation biologists (Coblentz 1990; Soule 1990). Today, many believe we are in the early stages of a global homogenization process that will lead to decreased biodiversity and the widespread distribution of competitively dominant 'weedy' species (Cox 1999). Generally, continental biotas and species-rich communities have proven less invasible by introduced species (e.g. Smallwood 1994), whereas islands have proven particularly fragile, especially in the Pacific (Howarth 1985; Mlot 1995; Cox 1999).

Having evolved in isolation (Stone 1985), 2,400 miles from the California coast and 3,800 miles from Japan (Figure 1), the Hawaiian Islands have had very little natural immigration of species. An estimated 2,000 colonizing species naturally established in Hawaii over ca. 70 million years, indicating a natural arrival rate of roughly one species per 35,000 years (Loope 1998). The isolation of the Hawaiian Islands and their resultant evolutionary history has made them particularly vulnerable to the impacts of non-native species (Vitousek, Loope et al. 1987). Isolation enhanced speciation and sub-speciation in Hawaii (Brockie et al. 1988), allowing for intricate specialization among the native flora and fauna (Carlquist 1980). It is this fragility, produced in isolation, that makes invasive species one of the top threats to Hawaii's ancestral biodiversity (Loope and Juvik 1998).

Not only are the Hawaiian Islands uniquely diverse owing to their extreme isolation, but the islands also host wide arrays of climatic and topographic conditions.

The Hawaiian island cluster (Figure 2), with mountains extending from sea level to more than 4000 m, hosted a higher degree of endemism than most Pacific islands (Loope 1998). Today, following human colonization and extensive land conversion for agriculture, Hawaii is an unrivaled hotspot of endangerment for plants and birds (Dobson, Rodriguez et al. 1996; Rutledge, Lepczyk et al. 2001). Loope and Juvik (1998) cite more than 30% of the U.S. Endangered Species list belonging to Hawaii, with 363 of the then listed 1104 species (Mlot 1995). Thus far, alien species have been responsible for the extinction of more Hawaiian species than all other human activities combined (Loope 1998; Mehrhoff 1998).

Exotic species impacts are numerous, varied, and often unpredictable. A suite of literature chronicles how introduced cats (*Felis cattus*) (Hu 1998; Smucker, Lindsey et al. 2000), pigs (*Sus scrofa*) (Diong 1982; Foote, Stone et al. 1992; Katahira, Finnegan et al. 1993), goats (*Capra hircus*) (Baker and Reeser 1972; Cuddihy and Stone 1990), rabbits (*Oryctolagus cuniculus*) (Loope, Medeiros et al. 1991), rats (*Rattus rattus*) (Atkinson 1977; Amarasekare 1993) and other rodents (Cole, Loope et al. 2000) have left, and continue to leave, their mark on Hawaii. A similar story is told in the Galapagos (Schofield 1989).

Separately from their biological impacts, introductions can also pose direct threats to humans, including the transmission of disease (dengue fever, yellow fever, encephalitis) (Cox 1999), animal-vehicle collisions (red deer, *Cervus elaphus*, in Scotland) (Bruinderink and Hazebroek 1996), crop damage (glassy-winged sharpshooter, *Homalodisca coagulata*, as vector for Pierce's disease in California vineyards) (Anonymous 2000), declines in fishery production (Mills, Leach et al. 1995), and even electrical power disruption (Guam- brown tree snake, *Boiga irregularis*; Pimentel et al. 1999). Generally, those species with the highest, or most apparent, direct economic costs receive the earliest attention (Mills et al. 1995).

Nine axis deer (*Axis axis*) (Simpson 1945), were introduced to Maui in 1959 and 1960. Today, several thousand deer occur island-wide (Figure 3) and substantial biological, economic and public health impacts of deer are occurring. My goal was to chart historical range expansion of axis deer on Maui, determine their current distribution, and document the extent and degree of deer impacts on the island in order to establish a foundation for the development of local and regional deer management strategies.

Study Species

Axis deer are a mid-sized deer species with an average shoulder height of 90 cm. Adults have a rich russet brown coat, flecked with white spots running from head to rump in nearly linear rows along each flank (Figure 4). In season, males have a pair of lyre-shaped (Lydekker 1898) 3-tine antlers (Figure 5) that are shed annually. Male axis deer are larger than female axis deer worldwide (Figure 6), with bucks in India weighing 65-90 kg and does averaging 45-60 kg (Schaller 1967).

Axis deer are widely introduced to many parts of the world, including Europe (Evtushevskii 1977; Fadeev 1986), Australia, Java (Bentley 1967), New Guinea (Groves & Grubb 1987), New Zealand, Brazil, Argentina, Uruguay (Grubb 1992), and the United States [Hawaii, Texas, Florida, Georgia, California] (Whitehead 1972). In Hawaii, they are currently on Maui, Molokai and Lanai (Figure 2).

Methods

To gather distributional data, a series of interviews were conducted with long-time residents concerning their 'first encounters' with deer on Maui. These data formed the basis for a preliminary range expansion map. A telephone "hotline" for public deer sightings was also established and publicized to examine contemporary distribution (1997-2000). As part of the radio-telemetry study, five helicopter over-flights and 2 nighttime censuses provided additional estimates of deer numbers across a large region supporting many of Maui's deer. A coalition of interested agencies and individuals known as MADG (Maui Axis Deer Group) also co-ordinated several public axis deer forums. Simple, brief (1 page), multiple choice surveys were occasionally taken on pertinent issues, including sightings, deer damage, and the need for and methods of control.

Several sources of deer-vehicle collision data were compiled. 'Game salvage' records from the State Department of Land and Natural Resources (DLNR), along with deer-vehicle collision data from police and major auto insurance agencies on Maui were examined. DLNR frequently received calls from the public when dead deer were found along Maui's roadways, or live animals were trapped or in danger, and filed an incident report. For recovered carcasses, DLNR recorded the animal species, sex, date, time, location and likely cause of death. Anecdotal collision reports, based on informal discussions with locals over three years, were also collected. Potential impacts of this species were determined from a comprehensive worldwide literature review and discussions with locals from all three Hawaiian Islands currently supporting axis deer (Maui, Molokai, and Lanai).

Results

Arrival & Establishment

Maui, at 1884 km^2 (Juvik, Juvik et al. 1998), is the second largest island of the Hawaiian chain. Deer first arrived on Maui by legislative mandate in 1959, based on management assurances that the deer would not penetrate native forests and would eat largely non-native plant species (Tomich 1986). Deer were also considered free of dangerous diseases and parasites and thought to be easily controlled by hunting (Tomich 1986). A more detailed history of axis deer in Hawaii is found in Appendix I.

Several factors were important in the establishment and range expansion of axis deer on Maui. First, establishment was greatly aided by the lack of any naturally occurring competitors on the island. All potential free-ranging competitors on Maui [pigs (*Sus scrofa*), goats (*Capra hircus*)] were actively managed, reducing competition. Cattle (*Bos taurus*) and horses (*Equus caballus*) were the only numerous domestic competitors. A second advantage the deer had was a complete lack of natural predators on Maui, leaving humans and free-ranging packs of dogs (*Canis familiaris*) as the only threat.

Combining these two advantages with a benign, moderate environment provided an ideal stage for establishment (Cox 1999). Maui is a perfect setting for successful invasion by a grazing ungulate, and the deer meet the majority of Ehrlich's (1989) criteria for successful vertebrate invasions. They are abundant in their native lands (and were widespread prior to habitat loss), consume a wide variety of foods, and persist in a variety of plant communities(Ehrlich 1989) . They also survive well in proximity to humans (Lyon 1950). Axis deer establishment on Maui was further facilitated by exceptionally high rainfall following introduction. The decade following their release was the wettest of the past 75 years (Figure 7), so stimulation of plant growth might have aided the deer's establishment and subsequent spread.

Range Expansion

The introduction of axis deer to Maui involved two separate releases. Five axis deer were released on the grounds of Pu'u O Kali in September, 1959 (2 bucks, 3 does), followed by a second release of 4 deer (1 buck, 3 does) at nearby Ka'onoulu Ranch in July, 1960 (Kramer 1971). Based on interviews, the first sightings of axis deer came 7 years after the release of the second group. In the next 8 years, two additional sightings were documented. All three of these were near the original release points (Figure 8) and, up until 1974, were north and west of the release sites. Still, deer range was expanding south as well. In 1976, a worker at Haleakala National Park encountered two deer (doe and fawn) above 2000 m elevation along the Park's fence.

Thereafter, deer began being seen more regularly on Maui. Several sightings throughout the early and mid-1980s confirm that deer had spread widely across the southern flank of Haleakala. Some sightings were 20-30 km from the original release sites (Figure 9). By the early 1980s, deer had successfully colonized the majority of grazed pastureland on the western flank of Haleakala and had dispersed well onto the southern flank. On the much drier southern flank, dominated by sparsely vegetated lava flows and a lack of agricultural activities, surveys reveal fewer deer. It is only recently (1990, based on interviews) that a population of several hundred animals has developed on Haleakala's southern flank (Figure 10). The population on Maui grew most quickly in and around the original release site and today this remains the heart of Maui's deer population.

Current Distribution

Over a 26 month period, 127 hotline sightings were received. Results show that deer are widespread on Maui (Figure 3), and that a number of smaller 'satellite' populations are well established throughout the island (i.e. Haiku, Hana, Auwahi, Kahikinui, Maalaea, Waihee, Ukumehame, Lahaina, and Kapalua). There is also a small population of deer in downtown Kahului (Keopuolani Park), probably consisting of animals escaped from the former Maui Zoo (Alan Kaufman. Pers. comm.) rather than deer colonizing from elsewhere.

Discussion

In 1996, The Nature Conservancy drafted a map of potential habitat for axis deer based solely on the deer's preference for drier forests and pastureland (Figure 11). This habitat-based prediction was on target. Regional population estimates (based on spotlight censuses, interviews, and reported sightings of herds) indicate that in the 43 years since introduction, a population of several thousand deer has emerged from this founding propagule of 9. Axis deer remain undocumented only in the wettest forest areas of Maui (Figure 3). Given the thickness of the vegetation in these areas, the absence of detections does not demonstrate that no animals occur there. Maui's eastern half is estimated to hold the majority of the deer population, with 90% of deer sightings and vehicle collision reports coming from this region.

Given the heavy rains following introduction, food and cover may have been readily available to colonizing deer throughout their establishment phase on Maui. Early on, with few colonists hidden among thick vegetation, deer were rarely encountered. Normal rainfall years bring a thick, green, shrubby layer to this area, making deer detection extremely difficult, as it does in their native lands during the monsoon (Dinerstein 1979). Deer are much more easily seen under drought conditions.

My study of axis deer occurred during the driest 3-year period of record for this portion of Maui, and two patterns were observed. First, public sightings of deer and deer-vehicle collisions became more frequent (with few to no vehicle collision records prior to 1996, based on police records). Second, reports of crop and golf course damage increased substantially, even in areas where deer were formerly not a problem (based on hotline data). These reports suggest that deer might be ranging over larger areas under the influence of drought. If drought causes deer to range more widely, deer-vehicle collisions should decrease substantially during years of more normal rainfall. A review of other home range studies (Anderson 2003) indicates that generous forage availability acts to restrict home range area in axis deer, resulting in more sedentary (Eisenberg and Lockhart 1972) behavior.

Radio-collar data supports this finding. Under drought conditions, deer abandoned established home range areas and traveled more than 3 km to crop or golf course margins (unpublished data). During a peak period of drought (September 1999), nearly 1000 deer and more than 80% of the radio-collared animals moved to golf course margins, remaining there for ≥ 1 month (Anderson 2003). These findings suggest predispositions for range shifts and expansions that are similar to other deer, particularly the more phenotypically and behaviorally 'plastic' genera (i.e. *Cervus, Dama, Capreolus*).

This observed spatial response to drought on Maui suggests that a similar situation might have been operative in the 3-year drought of 1975-1977. The rainfall pattern is similar during this period (3 consecutive years well below average), and wherever axis deer are found in the world they have been seen to shift ranging areas in order to meet food needs (Moe and Wegge 1997). Range shifts in the early 1970s might have led to the establishment of new or expanded home ranges, spreading deer throughout the island. A number of sightings during the drier years of 1982 to 1986 occurred in new areas.

Deer Impacts

Axis deer on Maui present concerns to a broad range of individuals and agencies (Table I).

Table I: Spectrum of Concerns Presented by Axis Deer on Maui

Public Safety	Deer-vehicle collisions Disease transmission Poaching/un-regulated hunting
Economic	Crop Damage Grazing competition Ornamental/Nursery/Golf course damage
Environmental & Cultural	Native species & Watersheds Cultural: sacred sites (heiaus), walls Fence damage

Table I data are based on interviews, hotline data, and personal observation.

Deer Vehicle Collisions

A notable human health issue that axis deer pose throughout Maui County (includes Maui, Molokai and Lanai) is the threat of deer-vehicle collisions on roads and highways. These collisions have occurred regularly on Molokai for years, but the generally slower speed of automobiles there has limited the potential for damage. Cars on the higher speed roadways of Maui are increasingly encountering axis deer, and collisions are on the rise over the past few years (Maui Police Dept., pers. comm.). Insurance claims remain rare, but State Farm did receive its first-ever deer claims (five total) on Maui between January 1999 and May 2000 (Wayne Yamamura pers. comm.).

Sixty-six deer-vehicle collisions were documented throughout Maui County from 1998-2000 (Figure 12). In Maui County, where collision times were known, 80% (28 of 35) of all collisions with axis deer occurred in darkness from 7pm to 7am. Sixty one percent (40 of 66) occurred from January-April. In 1999, 60% (23 of 40), and through April 2000 75% (12 of 16), of the County's collisions occurred on Maui.

The pattern echoes that of moose (*Alces alces*) in Newfoundland (Joyce and Mahoney 2001), as there is a significantly higher collision rate under the cover of darkness, and the collisions are clustered seasonally and spatially, generating 'hotspots' (Bruinderink and Hazebroek 1996). On Maui, vehicle collisions peak during the fawning season (Jan-April). At this time of year does appear to wander more widely, possibly looking for secluded fawning grounds (Anderson 2003). This likely increases their chances of being hit, as it does for roe deer (*Capreolus capreolus*) and hogs (*Sus scrofa*) in Europe (Bruinderink and Hazebroek 1996). Collision data seem to support this, as 65% of deer killed by cars were adult does.

Collision data on Maui reveal similar patterns in 1999 to 2000 (Figure 13), but both were drought years and this may be a factor. During the last 'normal' years of rainfall (1996 and 1997), DLNR recorded only one deer-vehicle collision. During the subsequent dry years, the numbers were noticeably higher. DLNR salvaged 5 deer in 1998, 11 deer in 1999, and 9 in the first 4 months of 2000. This increase is unlikely solely attributable to an increasing deer population.

Disease Transmission

In Hawaii, disease is an area of significant concern regarding axis deer. A list of diseases and parasites is found in Appendix II. From India, we know that these deer are susceptible to rinderpest (Gupta & Verma 1949, c.f. Schaller 1967) and its role in significant reductions of axis deer populations in Uttar Pradesh has been documented (Singh 1958; Srivastava 1957, c.f. Schaller 1967). The only other disease that has led to significant reductions in deer populations (in both India and Texas) is malignant catarrhal fever (Clark, Robinson et al. 1970; Clark, Robinson et al. 1972).

The disease challenges axis deer present are not entirely straightforward. While it is true that deer are likely to carry common animal-borne human illnesses such as *Giardia*, *Leptospirosis*, *Cryptosporidiosis*, and harmful strains of *E. coli.* this is not necessarily the biggest concern. There is also the potential for deer to act as reservoirs of diseases such as bovine tuberculosis (Fahimudden 1963) and anthrax (Lyon 1950). Axis deer are known carriers of these diseases in both India (Schaller 1967) and Texas, yet they remain highly resistant to their effects (Robinson, Galvin et al. 1977), enhancing the deer's reservoir potential.

On Molokai, three axis deer have been documented with bovine tuberculosis (Tomich 1986), most recently in 1995 (Dept. of Agric., pers. comm.). Removal of all cattle from the island is the standard solution, and this has been done more than once on Molokai (Tomich 1986). Harold Lyon (1950) notes that four separate outbreaks of anthrax have occurred in Hawaiian cattle from 1910 through 1950. The establishment of axis deer populations in Maui County has likely introduced a permanent reservoir for livestock diseases, as it has on Point Reyes, California (Rieman, Ruppanner et al. 1979).

Crops, Pastures & Golf Courses

Axis deer frequently cause crop damage throughout their native range, especially when available forage is scarce in the cool-dry season (Dinerstein 1980). Heavy crop damage is attributed to axis deer near the Karnali-Bardia and Chitawan areas of Nepal (Dinerstein 1979; Mishra 1982). Axis deer are also responsible for damage to nursery plantings in India (Sushil, Thakur et al. 1993) and severe bark damage in Sri Lanka (Santiapillai, Chambers et al. 1981). With unfettered access to crops, axis deer diets can constitute a larger percentage intake of crops than naturally occurring forage species (Dinerstein 1979). Crop damage is most severe where thick vegetation occurs nearby (Nepal: Dinerstein 1979; Hawaii: Graf & Nichols 1967, Anderson 2003; India: Sekhar 1998). Specific crops consumed by axis deer in Nepal include lentils, wheat and mustard (Dinerstein 1979). On Maui, they frequently consume strawberries, lettuce, corn, sweet potatoes, eggplant, pineapples, avocados, onions and tomatoes (unpublished data).

Axis deer include agricultural environments as preferred aspects of their habitat. Specifically, it is the juxtaposition of open areas (e.g. glades, pastures, agricultural fields) and nearby forest cover that promotes axis deer occupancy (Seidensticker 1976; Dinerstein 1980; Mishra 1982). It has been argued that the presence of grazing actually increases the carrying capacity of an area for axis deer (as it does for most cervids and bovids) by promoting continued fresh growth of new leaves, and inhibiting the development of mature, less palatable, grasses (Elliott 1973; Elliott 1983). Axis deer have a well documented preference for young new shoots (Mishra 1982), so cattle grazing acts to continually replenish the axis deer's preferred forage. The deer's spatulate first incisors also allow it to graze closer to the ground than cattle (Elliott 1973). On Maui, the deer's preference for grazing short and newly sprouting grasses (Dinerstein 1979; Tak and

Lamba 1984) attracts large herds of deer (at times exceeding 100 animals) to several of the island's golf courses.

Axis deer are already causing substantial crop damage on the island. In the year 2000, Maui Land & Pineapple Company, Inc. reported a minimum of $35,000 (and up to $60,000) in deer-related damages, and a single corn farmer estimated $20,000 in crop losses and fence damage (Kubota 2001). A survey from our largest public axis deer forum (~150 people) revealed crop damage as the number one concern of the majority of those responding (53%). Diseases and deer-vehicle collisions came next, followed by poaching/trespassing.

Environmental & Watershed Impacts

Currently, the top two threats to Hawaii's rarest plant species remain alien weeds and alien ungulates (Mehrhoff 1998), particularly goats and pigs (Stone & Loope 1987). The fragile Hawaiian ecosystem developed over 25 million years (Juvik, Juvik et al. 1998) in the absence of any browsing mammal species, leaving an endemic flora without standard herbivore defenses such as thorns or toxic secondary metabolites (Bryant, Provenza et al. 1991; Lamoreaux 1998). Today, 89% of Hawaii's 1023 plant species are endemic to the islands (Mauchamp 1997; Cox 1999). The preferred habitat of axis deer in Hawaii is lowland dry forest, a fragile plant community that has already been reduced by more than 90% (Bruegmann 1996). Yet, deer are also penetrating the edges of wet forests (as they have on Molokai), posing a direct and immediate threat to the Nature Conservancy's Waikamoi Preserve, Haleakala National Park and the entire East Maui Watershed.

Axis deer preferentially graze grass, but have been shown to consume a wide range of forage items in native and introduced areas (Schaller 1967; Elliott 1973; Ables

1977; Elliott 1983). They also eat the full spectrum of plant parts, including leaves, stems, fruits, seeds, flowers and bark (Johnsingh 1981; Schaller 1967). Worldwide, axis deer consume a minimum of 513 plant species from 86 plant families and 344 genera (unpublished data). The number of species consumed worldwide by study site appears in Figure 14. The plant families containing the majority of these species are listed in Figure 15.

The only rumen content data for axis deer in Hawaii comes from an unpublished report to the U.S. Fish & Wildlife Service (Swedberg 1978) (Appendices III and IV). Data show that axis deer consume a wide variety of native and exotic species in Hawaii, those of particular concern appear in Tables II and III. Ignoring crop species, axis deer are documented eating 68 species of plants in Hawaii, 30 of which (44%) are native species. Many of the remaining species are problematic weeds. Sixty six percent (25 of 38) of plant species identified from samples collected on Lanai were exotic versus 87% (33 of 38) of those species identified on Molokai. In the upper wet forests of Lanai, two alien grass species (*Panicum maximum, Melinis minutiflora*) comprised nearly 40% of axis deer rumen volume. In the upper wet forests of Molokai, the weeds *Drymaria cordata and Paspalum conjugatum* made up 85% of the rumen. The latter species is Hilo grass which, equipped with barbed awns, is particularly well adapted to animal dispersal (S. Anderson, pers. comm.).

Table II: Native Species Known Consumed by Axis Deer in Hawaii

Native Species:	Island
Styphelia tameiameiae	L
Osmantus sandwicensis	L
Panicum torridum	L
Osteomeles anthyllidifolia	L
Santalum ellipticum	L
Diospyros sandwicensis	L/MA
Chamaecyse loriflora	L/MA
Achyranthes splendens	MA
Nototrichium sandwicense	MA
Lipochaeta rockii dissecta	MA
Acacia koaia	MA
Geranium multiflorum	MA
Abutilon menziesii	MA
Gouldia spp.	MO
Fimbristylis diphylla	MO
Heteropogon contortus	MO
Sida fallax	MO/MA

Table II summarizes the documented consumption of native plant species in the Hawaiian Islands. The following abbreviations are used: L- Lanai; MA- Maui; MO- Molokai. Data are from Swedberg 1978 and Medeiros, in prep.

Table III: Exotic Species Known Consumed by Axis Deer in Hawaii

Exotic Species:	Island
Melinis minutiflora	L/MA
Glycine wrightii	MA
Bidens pilosa	MO
Cenchrus echinatus	MO
Waltheria indica	MO
Eupatorium adenophorum	MO/L
Hypochaeris radicata	MO/L
Acacia farnesiana	MO/L
Panicum maximum	MO/L
Portulaca oleracea	MO/L
Leucaena glauca	MO/L/MA
Solanum sodomeum	MO/L/MA
Lantana camera	MO/L/MA

Table III summarizes the documented consumption of exotic plant species in the Hawaiian Islands. The following abbreviations are used: L- Lanai; MA- Maui; MO- Molokai. Data are from Swedberg 1978 and Medeiros, in prep.

Natural area managers are also concerned with the consequences of axis deer frugivory as a potential dispersal agent for a variety of invasive plant taxa. Species such as miconia (*Miconia calvescens*), ginger (*Costus* spp.), guava (*Psidium cattleianum*), koa haole (*Leucaena leucocephala*), gorse (*Ulex europaeus*) and *Rubus* spp. as well as fire-adapted grasses (e.g. *Andropogon virginicus*) are of particular concern (P. Bily and S. Anderson pers. comm.). Axis deer clearly compound the challenge of protecting native ecosystems and watersheds on Maui from invasive weeds. Managers must also consider the potential for various weed species to increase following deer management, as deer in certain areas may currently be suppressing the growth of species such as kiawe (*Prosopis chilensis*) and lantana (*Lantana camera*).

In the upper wet forests of Lanai, two native plant species (*Osteomeles anthyllidifolia* and *Styphelia tameiameiae*) comprised more than 30% of axis deer rumen volume (Swedberg 1978). The native species *Nototrichium sandwicense* is also a preferred food on the dry leeward slopes of Maui's Haleakala Volcano (Medeiros in prep.). Axis deer eat its leaves, stems, and bark and bucks rub their antlers on, and damage, this tree. In contrast, several native species might benefit from axis deer transport. These include two native grasses (*Heteropogon contortus*, *Deschampsia nubigensis*) and Ohelo (*Vaccinium reticulatum*).

On Maui, axis deer possess a suite of traits that are cause for concern (Table IV). Deer diets worldwide are characterized by high variability and seasonal diet shifts. Axis deer diet breadth is comparable to that of goats (*Capra hircus*). The deer also forage on ground cover like rabbits (*Oryctolagus cuniculus*) or sheep (*Ovis aries*) and move in large herds on fixed trails like cattle (*Bos Taurus*) and goats (*Capra hircus*), causing erosion (Figure 16). The deer, like pigs (*Sus scrofa*), are also a vector transporting seeds (both internally and externally), facilitating weed spread and establishment. Seasonal antler rubbing by bucks can also kill small trees (Figure 17). The deer's direct elimination of plants, its impact on plant recruitment, and the potential to disturb soil and transport weeds (particularly grasses) underlie this species' challenges to managers. At one time, six of the top ten weed threats to Haleakala National Park were grass species (Brockie, Loope et al. 1988).

Table IVExotic Herbivore Impacts on islands

IMPACT		*Species*	
	Axis Deer (*Axis axis*)	**Pig (*Sus scrofa*)**	**Goat (*Capra hircus*)**
Preferential foraging on young plants, inhibiting plant regeneration	X	X	X
Plant community alteration; successional disruption; under story elimination	X	X	X
Trampling, trailing, soil compaction (increased erosion)	X	X	X
Soil disturbance favoring exotic plant colonization; soil fertilization	X	X	X
Transportation of viable exotic weeds (internal/external) esp. grasses and fruits	X	X	X
Carry, transmit or harbor diseases of concern to humans, livestock or wildlife	X	X	X

Table IV summarizes a number of common impacts of exotic herbivores on Pacific islands. Data are from Yocom 1967, Diong 1982, Lever 1985, and Anderson 2003.

Like rabbits, the axis deer's strong preference for new shoots and emerging seedlings of plants and trees implies a substantial impact on plant regeneration. On Santa

Barbara Island, the smallest of the Channel Islands, disturbance from intense rabbit grazing facilitated invasion of exotic ice plant (*Gasoul crystallinum*) (Brockie, Loope et al. 1988). The island of Laysan is also famous for being nearly entirely denuded of all vegetation by rabbits (Carlquist 1980). In watershed areas on Maui, elimination of low growing vegetation by deer can increase erosion and decrease the soil's water holding capacity.

Following native plant species elimination, exotic plant species often establish, driving community change and greatly confounding restoration efforts (Loope 1998). The combination of axis deer foraging preferences and weed transport potential make it possible for this animal to substantially alter vegetation communities on Maui. Community shifts resulting from deer impacts have already occurred on the Kalaupapa peninsula of Molokai where grass elimination by intensive deer grazing allowed non-native lantana (*Lantana camera*) and Christmas berry (*Schinus terebethifolius*) to colonize large areas, forming impenetrable swaths (D. Goltz and A. Yost, pers. comm.). On Maui, the Pu'u o' Kali dry forest is also rapidly losing native plant species to axis deer and the vegetation community is transforming, with native *Sida fallax* and exotic *Bidens pilulosa* becoming the new dominant species (Medeiros pers. comm.).

Axis deer, like goats, exhibit trailing behavior and this has previously been shown to increase erosion and facilitate exotic plant dispersal and establishment in Hawaii (Brockie, Loope et al. 1988). As the numbers of axis deer grow, 'trailing' behavior increases, creating dirt pathways through the thickest of vegetation. Many alien plant species in Hawaii require this type of soil disturbance in order to competitively displace native species (Loope and Scowcroft 1985). A longer-term concern of axis deer is that it is much easier to rid an area of invasive animals than invasive plants (Brockie, Loope et al. 1988).

Deer trailing behavior has also caused damage to a variety of culturally and archaeologically significant sites on Maui (hotline and pers. obs.). Damage to Hawaiian stone walls occurs as deer herds numbering in the hundreds habitually pass through (Figure 16). Archaeological impacts of axis deer will increase as numbers grow, especially along the leeward slopes of southern and western Haleakala, a region that historically contained numerous dwellings and supported more than 2000 residents (Sterling 1998).

Management Situation

Scope

Axis deer on Maui currently pose a significant and increasing threat to a variety of landowners island-wide. The deer are of direct concern to:

- Small (individual) and large (corporate) agricultural interests who may suffer significant crop damage and direct economic impacts
- All island residents concerned about human and animal disease transmission and spread
- All individuals who have insulated areas through fencing and now face the prospect of direct structural damage by axis deer
- Water supply boards and agencies aiming to safeguard watersheds from erosion, animal waste and disease
- The police and public safety agencies aiming to curb animal-vehicle collisions and resultant injuries
- Residents who face potential injury from poaching and un-regulated hunting in suburban areas where deer are becoming more and more common
- Golf course and resort owners who aim to maintain their courses and ornamental plantings

This broad spectrum of individuals needs to be incorporated into the planning process regarding axis deer. It is critical to remember that 'deer problems' are fundamentally 'people problems' (Caughley 1983), stemming from varied value systems. Eliminating any interest group from the negotiations is the first step towards collapse of the process (McShea and Rappole 1997).

Vertebrate abundance has been a subject of much debate and discussion, since variations in cultural values act to polarize the issue, and anthropogenic impacts introduce a suite of human values. Answers typically depend entirely on the circumstances. Contexts vary widely (urban, sub-urban, native species, non-native species) and specific decisions hinge on the degree to which impacts affect livelihood (crop damage), lifestyle (deer-vehicle collisions), health (disease spread, transmission), aesthetics (endangered species, trespassing) and other aspects of day-to-day life (Caughley 1981; Goodrich and Buskirk 1995; Healy, deCalesta et al. 1997).

Evidently, axis deer management on Maui will need to operate at both local and regional scales. Immediate local action is required to prevent any incursions of axis deer into specific areas of concern. Figure 3 makes it clear that deer are past the point of containment, so some type of island-wide action will also be necessary. Goals of regional action should be to limit population spread and prevent the establishment of satellite populations. A regional plan might best emerge from a series of local management strategies. This will facilitate accommodating varied landowner interests, improving both cooperation with, and effectiveness of, the plans.

Fencing

Although fencing has been the stock solution to limit feral ungulate impacts in Hawaii, axis deer are difficult to effectively fence out of areas they seek to inhabit. On Maui, these tend to be agricultural areas (crops & pastureland) and edges of thick, infrequently disturbed forests. This problem therefore affects crop farmers, water supply agencies aiming to protect the watersheds, and natural area managers striving to protect native Hawaiian ecosystems. New Zealand's management challenges with red deer (*Cervus elaphus*) were greatly magnified by inaccessible backcountry terrain (Caughley 1983; Mungall and Sheffield 1994). Backcountry concerns are paramount on Maui, since fencing axis deer out remains a prohibitively expensive and insecure solution for most concerned.

Axis deer readily jump 2-meter fences (Mungall & Sheffield 1994) and it is not economically feasible to build 3-meter fences in most areas of the island, particularly in backcountry areas. Axis deer fencing requires fixed, tight-lock, vertical wires with no more than a 15 cm spacing to be effective. If the fence's vertical strands can slide on the horizontal wires, axis deer will quickly open gaps.

Axis deer regularly pace newly constructed fence lines, searching for ways through or under (Graf & Nichols 1967) and taking advantage of any weak points. Over time, deer help to further weaken fences. When startled, deer commonly charge straight into a fence, breaking strands and bending posts. These weaknesses in the fence become further opened up and exploited over time. Generally, axis deer on Maui cause the most damage to fences within 50 cm of the ground (S. Erdman, pers. comm.), as deer try to slip under, rather than jump over, a fence (pers. obs.).

From a practical standpoint (costs, bird strikes, human sabotage, etc...), fencing against axis deer throughout Maui County can never be considered 100% effective at preventing deer incursion. Yet, fencing remains an important management tool regardless of this substantial limitation. Fences do act to deter free passage into protected areas, and when fencing is combined with other techniques it has proven itself a consistently valuable management tool (Stone and Loope 1987).

Private Property

Figure 10 shows a map of deer distribution on the Eastern portion of Maui, as of May 2000. Since the majority of the deer population on Maui occurs on a relatively small number of large privately owned parcels, it is essential that managers work with private landowners to devise cooperative management strategies. Hunting is essentially the only mortality factor axis deer face on the island, so it is fortunate that many of the larger landowners are willing to carry out significant 'population control' through hunting programs on their lands.

Deer are currently present on lands bordering nature reserves and watersheds, so it is critical to disrupt population establishment and any further 'trickle' of deer into these areas. Such actions need to be carried out immediately and can only occur with the cooperation of adjacent landowners. The direction of any hunting also needs to be carefully considered to avoid driving animals further into protected areas.

The deer population on the western slope of Haleakala (Figure 10) is well established and numbers more than 1500 animals, based on census estimates. This area should therefore be targeted for deer population control. Landowners, through hunting, should manage this area to prevent any further increase in the population while ensuring that many more females than males are harvested. In contrast to the 'sacred doe' hunting paradigm (Williams 2002), an 'earn-a-buck' program is encouraged, whereby a buck may be sought only after 3-5 does have been harvested.

The western slope should be censused annually. Censuses conducted from April through June on Maui would follow the peak birth season (November through March), allowing landowners to monitor both fawn production and, since most adult bucks will have hard antlers at this time, the potential for trophy-class bucks in the coming season. Landowners should also accompany managers during censusing of their lands (nighttime spotlight surveys, hiking transects, helicopter). It is well recognized that landowners underestimate populations of game on their lands, especially following hunting or management action (Rollins and Higginbotham 1997). Involving property owners in the process allows all parties to work from the same 'image' of animal numbers in a region. Deer harvest targets can then be assessed.

Regional & Long-term

Although a population of more than 1500 deer is estimated (via census) to occur throughout the western slope, this area also receives heavy hunting pressure throughout most of the year. Nearly one-third of ca. 1500 deer are harvested each year (based on interviews). Discussions with landowners indicate that as many as 200 animals are shot annually by family and friends, with poaching accounting for another 200 animals per year (a minimum of 4/week, as it is nearly a daily occurrence). The combined take from several golf course 'damage control' operations is approximately 150, based on informal discussions with managers. Though this certainly will hinder population growth, it is not clear what influence this hunting might have on spreading the axis deer population.

The northwest slope of Haleakala (Figure 10) is a suburban region that requires immediate management action geared towards significantly reducing the resident deer population. Interviews, hotline sightings, and surveys indicate that as many as 400 deer occupy the region from Haiku to Kula. The principle challenge throughout this region is the suburban nature of the landscape, among the most complex of management realms owing to the concentration of homes and varied land ownership. Firearm use is also limited, so bow hunting will need to be employed and perhaps snaring. Bow hunting partnerships throughout this region should be encouraged, since this is an effective method for axis deer hunting and bows greatly decrease landowner liability. Landowners are encouraged to partner with private 'game management' or 'fee hunting' operations to aid in deer control. For practical reasons, 'population control' of this sort should begin on the largest parcels owned by amenable landowners. There is still a chance to suppress these populations before they grow out of control.

Helicopter surveys and discussions with locals indicate that the southern slope of Haleakala holds at least 300 deer (Figure 10). If landowners are willing, an effort to limit this population to no more than 200 animals should be made [National Park Service does this for Axis deer in Pt. Reyes, CA- held at 400 for the last 20+ years (Elliott 1983; Gogan, Barrett et al. 2001)]. This region's proximity to Haleakala National Park makes it an especially important part of any management program.

One challenge facing the development of a regional plan centers on the lack of understanding the public has for this issue. Owing to the axis deer's secretive habits, unless one is currently experiencing deer damage, most people remain unaware of deer on Maui. It is particularly hard to demonstrate an overpopulation issue when there is little public evidence of the animal on the island.

Despite this limitation, work must begin on a longer-term island-wide management plan that will address the future of deer on Maui. A set of regional deer 'management' options has emerged from deer conflicts elsewhere (Stout, Knuth et al. 1997), though only a subset of these tools is appropriate for consideration on Maui (Table V). As a first step, individual working groups should form to address critical issues that axis deer present on Maui. The groups should individually address the aforementioned areas: human health and safety, economic impacts, and impacts to cultural sites, environmentally sensitive areas, and watersheds. A long-term plan is needed, since deer will continue to expand and increase in number with no action.

Table V: Management Options Available

Fencing
Contraceptives/Sterilization (research)
Rifle hunting by qualified volunteers
Archery hunting
Tranquilize/Euthanasia
Culling at bait stations/tree stands
Trap and kill/eat
Spotlight hunting
Dog-assisted hunting
Helicopter hunting
Poisoning
Snaring
Combination of methods

Trap & Relocate (deer farms)
Let Nature take its Course
(re-)Introduce Predators

Table V presents an overview of common deer management options. Italicized options are included to be comprehensive, though they are unlikely to be applied in an island situation. Data are from Stout et al. 1997 and Anderson 2003.

Local & Immediate

Managers will most likely need to employ current management practices (fencing and shooting) for some years into the future, at least until an island-wide or regional plan is devised and implemented. Given the proximity of deer to protected areas (Figure 3), it is essential that managers work especially hard at the local scale. 'Zero-tolerance' areas need to be established throughout Maui and monitored to keep deer clear of these parcels.

Hired hunters may need to be employed for deer control, as they have historically in Maui County (Tomich 1986) (Appendix I).

Though it will be a subject of much debate on Maui, immediate, lethal control at specific sites adjacent to protected natural areas will be required to protect native species. This local control of deer near protected areas will serve as a critical short-term measure (Goodrich and Buskirk 1995), inhibiting the continued spread of deer into these much less accessible backcountry areas. For these boundary areas, a 'zero-tolerance' policy for deer should be adopted. Local population reduction and elimination should be the goals.

Axis deer are creatures of habit where undisturbed by hunters (Graf & Nichols 1967), so hunting may be more successful when conducted periodically (e.g. once per week), rather than continuously (e.g. 3 or more days per week). Remote camera use is also encouraged (Jacobson, Kroll et al. 1997; Cutler and Swann 1999) since camera sightings can be used as an activity 'index' to combine with management 'take' data. Careful camera monitoring can also help estimate population size (Karanth and Nichols 1998), rate of ingress, sex and age ratios, and other data on axis deer activity, breeding biology and social behavior.

Since the goal is 'local eradication' in these boundary areas, management must be targeted to be most effective. Every advantage should be taken to exploit seasonal vulnerability of axis deer to population control (Goodrich and Buskirk 1995), meaning pregnant does should be targeted throughout their peak period of pregnancy from November through February (Appendix V: Management Calendar). Timing management in order to have the greatest impact on population recruitment aided the control of feral pigs (*Sus scrofa*) on the Island of Hawaii (Katahira, Finnegan et al. 1993).

In season (April-August), buck bellowing can also be monitored to help locate mixed-sex herds of animals. If a 'judas' animal is attempted, it appears as though radio-collaring a resident adult female deer might be best in this species. Socially, pregnant and fawning females in Hawaii will lead a hunter to other pregnant and fawning females from December to April (Anderson 2003). Bucks will also be encountered once mixed sex/age groups form again in spring. Local management at a variety of reserves in Hawaii might benefit from these suggestions, including Kanaio, Kahikinui, Auwahi, and Pu'u o' Kali on Maui, as well as the Nature Conservancy's Kanepu'u reserve on Lanai and Pelekunu reserve on Molokai.

Exotic herbivores represent a real challenge for managers charged with protecting 'natural areas' throughout Hawaii. A long history documents the serious negative impacts of introduced herbivores, and 'active management' is frequently necessary to prevent extinction (Cole, Medeiros et al. 1992). This is the situation with axis deer on Maui, as it has been previously with both pigs (*Sus scrofa*) and goats (*Capra hircus*). Ungulate management in Hawaii is a thorny issue (Baker and Reeser 1972) since, on islands, drastic actions are commonly taken to protect the system.

On San Clemente Island, the goat was considered the most damaging ungulate. As a result, from 1972 through 1989, 29,000 goats were killed or relocated to the mainland (Cox 1999). On Maui, goats were largely responsible for a vast reduction in the endangered Haleakala silversword (*Argyroxiphium sandwicense*) through trampling and foraging (Yocom 1967; Carlquist 1980; Loope and Medeiros 1995). With management (goat removal, fencing), the plants returned from 4,000 in the 1930's to number more than 60,000 today (Loope and Medeiros 1995). Hawaii and the Channel Islands have also both utilized a 'Judas goat' technique to ensure near zero population levels within National Park boundaries (Taylor and Katahira 1988; Keegan, Coblentz et al. 1994). In Hawaii, the eradication or exclusion of exotic herbivores has generally resulted in substantial regeneration of native plant species (Hamann 1979; Loope and Scowcroft 1985; Brockie, Loope et al. 1988; Cabin, Weller et al. 2000). Nearly 20 years ago, researchers called for the eradication of axis deer on Maui (Stone and Scott 1985).

Conclusions

In the absence of human management action, axis deer pose an ever increasing threat to a variety of landowners on Maui. The economic, environmental and cultural costs of maintaining this species on the island are already substantial, and these costs will increase rapidly. A careful assessment of both management and damage costs is urgently needed to better understand the costs and benefits of maintaining this species. A survey of crop losses to deer depredation on Maui is also needed.

It is clear from data on Point Reyes, CA that the recurring costs of managing this species in perpetuity are substantial (Gogan, Barrett et al. 2001). It is also frequently argued that the elimination of ungulate populations on islands is an essential first step towards the protection of native ecosystems (Coblentz 1990; Coblentz 1997; Rainbolt and Coblentz 1997; Cabin, Weller et al. 2000). This may well be the case for axis deer. Public meetings should proceed to assess the current situation and begin charting a future for Maui's axis deer population. The situation, both regionally and locally, demands urgent attention as Maui's deer population continues to spread and increase in number.

Chapter 2: Home Range and Group Size

Introduction

Following the introduction of exotic axis deer (*Axis axis*) to private lands in the late 1950s, a population of several thousand animals is now established on the island of Maui. At current population levels, deer adversely affect farmers, motorists, and ranchers. They also affect public agencies charged with protecting the island's water supply and natural areas (Anderson 2003). Only limited information exists on this species' habits in Hawaii (Graf and Nichols 1967; Swedberg and Walker 1978; Waring 1996), but worldwide data indicate that opportunism and adaptability enhance this deer's success in new areas (Mungall and Sheffield 1994).

Introduced deer on Maui face a very different environment from that in Asia, principally owing to a reversed seasonal structure (dry summers, wet winters) and a lack of natural predators. These changes in local conditions amount to the relaxation of selective pressures, resulting in adaptive behavioral responses. Introduced goats (*Capra hircus*), pigs (*Sus scrofa*), and a number of other species exhibit altered seasonal reproductive behavior, movement patterns, and fecundity following establishment in new areas (Yocom 1967; Diong 1982; Lever 1985; Stone and Keith 1990; Mungall and Sheffield 1994).

Given the unpredictable nature, a basic understanding of local behavior is essential to the development of effective management plans. Management prescriptions founded exclusively on research conducted 'elsewhere' may fail to account for the full range of potential variation exhibited locally under specific conditions. Cervids particularly, and South Asian ungulates as a group (Dinerstein 1980), exhibit considerable phenotypic flexibility; responding quickly to local conditions (Geist 1998).

The axis deer's resiliency and opportunism (Mungall and Sheffield 1994) has been likened to several ungulates from seasonally arid parts of Africa (McKay and Eisenberg 1974).

Prior work indicates that axis deer home ranges are small (Moe and Wegge 1994) and that they are relatively sedentary animals (Eisenberg and Lockhart 1972). Since these deer are introduced, and closely related to other phenotypically variable cervids, is it safe to assume that native patterns will hold for this population? This study aims to: a) determine basic home range and grouping patterns for axis deer on Maui, b) compare these findings with prior work on axis deer in their native range, Nepal, c) interpret these data in the context of Hawaiian introduction and establishment of axis deer and, d) examine the effects of intensive hunting on axis deer social behavior and movement.

Study Site

Axis deer field observations were conducted on a ranch on the southwestern and western slopes of Haleakala volcano on Maui. The ranch, at 65 km^2, is among the largest privately owned parcels in the Hawaiian Islands (Juvik, Juvik et al. 1998). Haleakala is the most massive mountain on the island, rising steadily from sea level to 3055 meters over 20 km. The principle study site covers 50 km^2 (Figure 18) and is located directly in the rain shadow of the mountain slope. The average annual rainfall is 83 cm (ranch rainfall data archives, since 1925). Approximately 1000 deer currently occupy (May, 2000) the lower portions of the ranch at elevations ranging from sea level to 800 m. The dominant ecosystem is a "lowland dry shrubland", following the classification of Pratt (1998).

The study area was bounded at the upper elevations to the East (ca. 600 m) by a paved road, with a cattle fence serving as a significant yet permeable barrier to deer passage. Above the road, open pastureland provides little cover for deer and holds few animals. A narrow 2-3 km strip of residential development combined with golf courses lies to the west, between the study area and the ocean. To the south, the most recent lava flows from Haleakala (1792) cover broad sparsely vegetated areas. To the north, the study ranch abuts another cattle ranch with similar vegetation and ranching activity.

Climate & Rainfall

On Maui, axis deer experience a much more moderate climate than in Nepal, with both temperature and rainfall being significantly lower year-round. Maui's annual average rainfall, at 83 cm, is a fraction of Nepal's 230 cm. High temperatures and monsoonal rainfall characterize Nepal's highly seasonal climate, with temperatures exceeding 35° C for three months prior to summer monsoons that deliver up to 90% of the annual rainfall (Seidensticker 1976). In contrast, Maui's rainy season lasts twice as long, with 75% falling between October and April.

Radio-collars were first deployed on the ranch in January 1998. That month, the ranch experienced what would be its worst rainfall season in 75 years. Following that, the ranch received just one year's average annual rainfall (83 cm) throughout the 29-month study period (January, 1998 through June, 2000). The 1998-2000 period was the driest 3 year stretch since rainfall records began in 1925, and included the first (1998), seventh (1999) and sixth (2000) driest years of the last 75. In contrast, the two years prior to the study (1996-1997) received above average annual rainfall, 1996 by 25% and 1997 by 19%.

Methods

Mapping

A one-person mapping system produced by Condor Earth Technologies, Inc. (Sonora, CA; 209-532-0361) was used to map the study area. A Trimble Pro-XR GPS receiving unit with real-time differential correction was interfaced directly with a Kalidor K2500 weatherproof, portable, pen-based, field computer running Windows 95 and Condor's proprietary 'Penmap' software. These tools allowed real-time mapping and correction of data in the field. As a basis for the deer radio-telemetry study, essential landscape and topographic elements of the 50 km^2 study site were mapped.

The ranch's roads were particularly important since they provided my access to a variety of prominent points necessary for collecting telemetry bearings. Both were mapped. New 'fix points' were added as needed. All points were located at the most prominent points, improving study area coverage and accuracy while decreasing signal reflection (White & Garrott 1990). Overall, 106 km of roads, 81 telemetry fix points and 51 km of pasture fences were mapped.

Home Range

Deer were radio-collared with the aid of Dr. Alan Kaufman, D.V.M., a specialist with his own practice as an exotic animal veterinarian (Aardvarks to Zebras, Inc. Kula, HI). We used radio-telemetry darts and equipment from Pneu-Dart, Inc. (Williamsport, PA) (Kilpatrick, Denicola et al. 1996), and experimented with the new application of a combination of drugs to deer: medatomidine + ketamine. Previously, this combination was used to sedate black-footed ferrets (*Mustella nigripes*) in Wyoming and fishers (*Martes pennanti*) in New Hampshire (Kreeger, Vargas et al. 1998; Dzialak, Serfass et al.

2001). Dr. Kaufman was conducting trials using medatomidine on a *special-use permit* held by Wildlife Pharmaceuticals (Ft. Collins, CO), to test the drug's efficacy as a sedative for axis deer under field conditions.

A combination of 10 mg medatomidine and 100 mg ketamine delivered in a 1 ml transmitter dart was a safe, effective and reliable method for sedation of wild axis deer. To revive collared deer, we reversed the drugs' effects with an intra-muscular injection of 25 mg atipamezole (5mg/ml). The collaring procedure rarely took more than 1 hour including the initial darting, reversal, and mobilization. The drug combination never proved lethal. Collars were placed only on adult animals, estimated at least 2 years of age.

Axis deer are less timid and tend to move out into open pastureland after nightfall. Given the difficulty of hunting axis deer on foot by day, and a longstanding island-wide ban on hunting from a vehicle, initial darting attempts were made nocturnally from a vehicle using 1 million candlepower spotlights. However, trespassers (poachers) had recently begun illegal, nocturnal, spotlight-assisted hunting. Over time, this hindered our darting attempts as the deer became adversely conditioned to lights at night. Darting attempts were hindered further as the 1998 drought settled in, and cover vegetation receded. Light acclimation and combined landscape change doubled our average darting distance, from 30 to 60m, in the course of one year. In the second year, helicopters and daytime darting on foot were employed to compensate and increase sample size.

Two bearings were obtained at least once a week for each deer, using a hand-held Yagi antenna. The average interval between collection of consecutive bearings was 10 minutes. Distance between adjacent fix points rarely exceeded 500 m, and the distance to target animals averaged 361 m. Angular error averaged 2% per bearing. We tested the accuracy of the telemetry equipment early in the study by sneaking in on radio-collared deer during the heat of the day, when they were least likely to respond to our presence. The locations of animals found lying down were recorded and registered as 'known' locations. Heavy nocturnal poaching activity limited telemetry monitoring to daylight hours (0600-1800 hrs), for safety reasons.

Bearings of individual sightings were entered into Penmap Software (Condor Earth Technologies, Inc. Sonora, CA) and locations were plotted using the 'bearing and distance' function for triangulation. All maps were exported to ArcView software (Environmental Systems Research Institute) for GIS use. Home range analyses were conducted on a PC using a free, downloadable, ArcView extension (Hooge and Eichenlaub 2000). Statistical analyses used Microsoft Excel. MCP and Fixed kernel home range estimates (95% and 50%) are applied for comparative purposes where appropriate. Low sample sizes require that theses kernel estimates be interpreted cautiously. Least squares cross validation helped to improve accuracy (Seaman and Powell 1996). For seasonal analyses, sample sizes were equalized prior to comparison using a bootstrap procedure to generate 100 replicate seasonal MCP home ranges using n from the season with fewest fixes.

Group Size

Group size data were collected during regular radio-telemetry monitoring drives throughout the ranch. Drives were conducted from 0600 to 1800 hrs, 3 to 5 days per week, and averaged 30-50 km each. The routing and direction of these drives was purposely varied, and a record was kept of all deer seen during the latter 18 months of the study. Deer were occasionally illegally hunted from trucks and flushed by vehicles, so encounter time with groups rarely exceeded 15 seconds, making estimates of herd composition difficult. Consequently, it was not always feasible to obtain exact counts, so estimated group sizes were tabulated separately from exact counts. Group size and encounter rate data were tabulated by season and month for analysis. Five helicopter over-flights (100 km^2) and 2 nighttime censuses (same route, 13 linear km road loop, estimated visual coverage of 3.9 km^2 or 8% of the study) provided additional estimates of deer numbers across the study area.

Prior Research

Data are compared to those collected by Hemanta Raj Mishra (1982) in Nepal. He radio-collared 27 axis deer in Royal Chitwan National Park, Nepal. His study emphasized seasonal changes in home range relating to Nepal's three climatological seasons: February to May ('pre-monsoon' or 'hot-dry'), June to September ('monsoon') and October to January ('post-monsoon' or 'cool-dry') (Mishra 1982; Moe and Wegge 1994). In Nepal, these periods coincide with the following reproductive activities: a) pre-rut and fawning b) hard antler and rut c) velvet antler and pregnancy. Mishra (1982) analyzed seasonal home ranges for axis deer using a minimum of 15 locations per season. I analyzed my data similarly for direct comparisons.

Home Range & Movement

Results

Daytime locations are used in the following analyses (6am to 6pm) and error is presented as +/- S.D. Selective poaching of radio-collared animals, particularly bucks, made it difficult to gather long-term data sets. The total number of fixes obtained allowed approximated kernel estimates of semi-annual hunting periods. Subdivision into three seasonal periods was unworkable, owing to decreased accuracy.

Twenty-three adult axis deer (13 female, 10 male) were radio-collared on Maui from December 1997 through June 1999 and monitored for a maximum of 30 months (Figure 19). Female deer remained collared for an average of 508 +/- 172 days, while male deer remained collared for an average of 309 +/- 129 days. Female detections totaled 831, resulting in an average of 69 locations per doe (range: 50-121). In contrast, 283 male detections were recorded, averaging only 40 locations per buck (range: 21-58).

Annual home range data are summarized in Table VI. No significant difference between the sexes was found for MCP home ranges (F= 1.38, p=0.49), annual 95% kernel (F=2.11, p=0.36) or 50% kernel (F=3.9, p=0.22) estimates, but few males were monitored for a full year (n=3). The majority of both males (2 of 3) and females (7 of 9) had annual MCP ranges exceeding 10 km^2.

Annual MCP home range size varied widely among adult female deer (Figure 20). Extensive overlap of seasonal occupancy centers, and of individual home ranges, was seen for both sexes. One female annual home range (MCP) completely enclosed the annual core areas (50% kernel) of nine other females (Figure 21). The primary axis length (meters) of MCP home ranges varied widely (female range: 2,000-10,000; male range: 4,942-11,745), and, on average, both dimensions were larger for males (primary avg. = 7,457 +/- 2,369; secondary avg. = 3,435 +/- 1,210) than for females (primary avg. = 6,259 +/- 2,367; secondary avg. = 3,115 +/- 954).

Maui seasonal home range data appear in Table VII. Both sexes maintained their smallest home ranges from June to September. Females maintained their largest home ranges from February to May. Males maintained their largest home ranges from October to January, during the post-rut period. Pooling all animals, home range sizes are noticeably smaller on Maui from June to September (n=10; Paired-T, 2-tail; p=0.01).

While no obvious differences in home range size were evident between the sexes in any season, the largest difference occurred during the October to January period (post-monsoon). During this season the average female deer covered 57% of the area covered by male deer. Males and females moved over similar portions of their annual MCP home range area from February to May (males 43%, females 44%) and from June to September (Males 25%, females 21%), but from October to January, males covered a much larger fraction of their annual MCP home range (49%) than did females (28%).

Table VI Annual Home Ranges of *A. axis* on Maui

Annual Home Range:

ID	Sex	Fixes	MCP	95% Kernel	50% Kernel
407	F	121	1674	904	147
431	F	89	1559	1358	279
412	F	85	124	109	10
408	F	84	1236	906	87
410	F	81	1693	656	69
418	F	60	1752	1514	173
419	F	60	835	159	25
438	F	52	1854	2708	664
417	F	49	1374	1140	105
403	M	55	1773	1637	265
404	M	58	859	637	61
405	M	57	1524	1498	168

Summary:

Mean	MCP	95% Kernel	50% Kernel
Male	1385 +/- 473 (range: 859-1773)	1257 +/- 542 (range: 637-1637)	165 +/- 102 (range: 61-265)
Female	1344 +/- 555 (range: 124-1854)	1050 +/- 786 (range: 109-2708)	173 +/- 201 (range: 10-664)

Table VI presents data for animals monitored a minimum of 365 days during the study (n=12; 3 male, 9 female).

Table VII: Seasonal Home Ranges of *A. axis* on Maui

Anim. ID	Sex	# Locs	Season Feb-May	# Locs	Season Jun-Sept	# Locs	Season Oct-Jan
403	m	15	464	15	475	15	1036
404	m	15	382	15	148	15	363
405	m	16	969	16	402	16	631
4082	f	17	306	17	497	17	450
410	f	19	1167	19	556	19	211
412	f	25	85	27	67	25	56
419	f	15	334	16	107	15	31
431	f	23	928	23	238	23	724
408	f	19	585	19	255	19	749
407	f	24	734	24	215	24	459

Summary:

Mean	Feb-May	Jun-Sep	Oct-Jan
Male	605 +/- 318	342 +/- 172	677 +/- 339
Female	591 +/- 381	276 +/- 185	383 +/- 295

Table VII summarizes seasonal home range findings for A. axis on Maui. MCP home ranges are presented in hectares (Ha) +/- S.D. Included are deer monitored for a minimum of twelve months, with at least 15 locations per season (n= 7 female, 3 male).

Comparison with Prior Work

Axis deer home ranges recorded in this study on Maui are much larger than those recorded in Nepal (Table VI). Mishra (1982) documented average annual MCP home ranges of 301 ha for males and 202 ha for females in Nepal. Moe and Wegge (1997) documented annual MCP home ranges of 183 ha for males and 135 ha for females in Nepal. On Maui, comparable analyses show annual MCPs of 1385 ha for males and 1344 ha for females. These findings are 4.5-6.5 times as large as those of Mishra (1982) and 7.5-10 times those of Moe and Wegge (1994). Estimates of 95% kernel and core areas (50%) for male deer in lowland Nepal (Moe and Wegge 1994) were 16 % and 30% of those on Maui; female estimates were also substantially smaller, at 14% and 17% (core).

In Nepal, axis deer home ranges are consistently larger than female home ranges, both seasonally and annually (Mishra 1982; Moe and Wegge 1994). A similar seasonal pattern is found on Maui, although no difference in annual home range is evident. On Maui, as in Nepal (Moe and Wegge 1994), there is no evidence of increased male home range size during the peak rut (June to September). Instead, a decrease was found, possibly relating to seasonal hunting pressure.

Seasonally, deer of both sexes in Nepal maintain their largest home ranges from February to May, during the hot-dry season leading up to the monsoon (Mishra 1982; Moe and Wegge 1994). Findings for the smallest home range are mixed, but both sexes share the same season. In one study (Mishra 1982) the smallest seasonal home ranges were found during the monsoon, from June to September; another study found October to January (Moe and Wegge 1994). Maui data follow the former pattern, with a substantial reduction in home range size during mid-summer.

Group Size

Results

Five hundred sixty hours of observation resulted in the detection of 349 groups of deer, comprising 5480 individuals. The overall average group size was 15.7, with roughly 2 groups of deer encountered for every 3 hours of observation. Deer were usually seen in the afternoon, and in the largest groups. Drought conditions aided deer detection throughout the study. For equalized samples, nearly half (43%) of all observed deer were encountered between 1400 and 1800 hrs, with an average group size of 31.7. Morning (0600 to 1000 hrs) accounted for one third of all sightings, and a quarter (24%) were seen from 1000 to 1400 hrs. The smallest average group size (12.2) was seen in the middle of the day and the largest in the late afternoon (31.7). The minimum number alive on the study area was 678 (night census of nearly all preferred pastureland habitat on study area, 3.9 km^2). Group size data are presented in Figure 22 and Figure 23.

Overall, axis deer group sizes peaked in the spring and dipped in the summer, with the largest groups occurring from February to May. This coincides with a peak in the number of young deer observed (est. < 1 year). Thirty percent of all groups encountered (105 of 349) contained fewer than five individuals, and 14% of all groups contained more than 50 animals (49 of 349). Deer encounter rates decreased seasonally between June and September (0.31 groups/hour) from rates of 0.51 (October to January) and 0.55 (February to May) otherwise. During the summer months, roughly half as many deer were seen per hour of observation (8.8) as were seen in either spring (18.8) or fall (15.6).

Comparison with Prior Work

Several studies identify high spatio-temporal variation of group size in this species (Barrette 1991; Khan and Vohra 1992; Raman 1997). Group size is dynamic and influenced by a variety of factors, including predator protection, food availability, and hunting pressure (Mishra 1982; Tak and Lamba 1984; Anderson 2003). In native lands, group size naturally increases during the summer monsoon and rut (Mishra 1982), when mixed sex and age herds are most frequently encountered (Schaller 1967). Larger groups begin forming as forage improves throughout April and May (pre-monsoon), and groups become still larger (12-13 avg.), but harder to observe, during the monsoon months of July and August (Dinerstein 1980). On Maui, there is a tendency towards smaller groups during the summer.

There are conflicting reports of group size trends in native lands, even in identical areas of India. In the Gir forest of western India, one study (Berwick 1974) concluded that group sizes were greater in the spring (March through June) versus monsoon (July through September) season, while a second study found a doubling of average group size during the monsoon (Khan and Vohra 1992). It is likely these differences relate to the specific timing of rainfall during the two studies, as axis deer frequently descend in large numbers on new growth following rains (Schaller 1967; Anderson 2003) or fire (Moe and Wegge 1997).

In native areas, nearly all studies document median group sizes of less than ten deer (Miura 1981; Karanth and Sunquist 1992; Khan 1995; Khan, Chellam et al. 1996; Raman 1997; Biswas and Sankar 2002). Large groups are infrequent, and some studies rarely or never encounter groups of 30 or more (Karanth and Sunquist 1992). Mishra (1982) found that 63% of all groups consisted of five or fewer individuals and less than

5% of all groups totaled 30 individuals or more. This contrasts sharply with data from Maui.

Axis deer on Maui show a much larger average group size than is typically encountered in Nepal. Mishra (1982) documented an average group size of 7.5 in Nepal, in comparison to an average size of 15.7 on Maui. It is possible that different methods of group size estimation influenced these results, since Mishra's observations were from trails on elephant back instead of from a vehicle. Previous work on axis deer indicates that vehiciular roadside counts can result in estimates nearly twice those obtained by walking transects (Varman and Sukumar 1995).

A structuralist interpretation could also be advanced, since the distribution of plant communities across the landscape provides a context within which essential deer behaviors must occur (e.g. foraging, mating, resting). In Nepal, the distribution of such elements has previously been identified as an important factor influencing group size in this species (Moe and Wegge 1994). Group sizes might also increase on Maui simply from the presence of more open habitat (pastureland), as this is thought to increase group sizes in this species (Barrette 1991).

Overall, seasonal changes in grouping for Maui's axis deer closely resemble those for axis deer in Nepal (Figure 24). Mishra observed his largest axis deer group sizes between February and May (pre-monsoon), coinciding with a peak in young animals. Numbers then decreased during the summer (monsoon). At this time of year in Nepal, however, thick seasonal vegetation generally yields counts that overestimate the number of small groups (<5 individuals) (Dinerstein 1980).

As with most other cervids, season and habitat have been identified as primary factors influencing group size of axis deer in southern India (Raman 1997). Rut-related activity has also been correlated with increasing group sizes during late spring (Raman 1997). Most commonly, density and group size increase during the wetter months throughout native axis deer range (Barrette 1991). On Maui, this corresponds to the winter months.

Role of Hunting

As an aid to managers, two specific questions were examined regarding the influence of hunting on axis deer: is there a measurable change in axis deer home range size as a result, and do axis deer cluster or disperse in response to heavy hunting pressure? An increase in home range size during hunting season might suggest that axis deer are continually disturbed and kept moving by hunting. A decrease in home range could indicate that axis deer hide out, stay put, and minimize their chance of encountering hunters. Clustering might be suggested if fewer, larger, axis deer groups are encountered during the hunting season, while an opposing finding might suggest deer are dispersing.

Results

Home Range & Movement

During hunting season, 358 fixes were obtained for does and 208 for bucks. In the non-hunting season, 64 male and 443 female fixes were obtained. Table VIII summarizes the potential role of hunting on male and female movement patterns. For males, both the number of fixes (n=64) and the number of animals monitored (n=3) limit the utility of seasonal kernel comparisons.

Table VIII: Influence of Hunting on Axis Deer Movement

	Hunting (May-Oct)	*Non-Hunting (Nov-Apr)*	
Distance between fixes*			
Male avg.	1251 +/- 1121 (median 871)	1681 +/- 1594 (median 1242)	F-test; p=0.002
Female avg.	1001 +/- 886 (median 732)	1168 +/- 1064 (median 852)	F-test; p=0.001
MCP Home Range*			
Male avg.	577 +/- 237 (median 699)	486 +/- 108 (median 509)	Paired-T 2-tail; p=0.37
Female avg.	669 +/- 369 (median 732)	807 +/- 440 (median 872)	Paired-T 2-tail; p=0.39
95% Kernel**			
Male avg.	na	na	
Female avg.	547 +/- 283 (median 494)	960 +/- 517 (median 1213)	Paired-T; 2-tail; p=0.03
50% Kernel**			
Male avg.	na	na	
Female avg.	80 +/- 63 (median 87)	145 +/- 93 (median 161)	Paired-T; 2-tail; p=0.10

*n= 3 male, 11 females with at least 15 fixes per season

** n=9 females with > 20 locations/season

Table VIII summarizes the potential role of hunting on axis deer movement. Minimum Convex Polygons (MCPs) and fixed kernel estimates are presented in hectares (Ha) +/- S.D.

Female MCP home ranges appeared smaller, and male MCP ranges larger, during the hunting period. If minimum sample sizes of 20 fixes per observation period are used (instead of 15), females tend even more strongly towards a reduced MCP range during hunting months. For this same sample, 95% kernel estimates and core areas (50% kernel) also suggest decreased size during hunting season (Table VIII). The average female core area size during the hunting season was less than half of their annual average core area (Table VI), and nearly half the size of female core areas during non-hunting periods.

Hunting also appears to affect the distance between consecutive fixes of individuals (each 3-6 days), with both males and females showing reduced distances in the hunting period (Table VIII). These differences were most pronounced in three of seven females and two of three males. Overall, the median distance between consecutive fixes for males was 30% smaller, and for females 15% smaller, during the hunting season. The cumulative distance between consecutive fixes (equal samples, yielding the minimum total distance moved) also decreased during hunting, with females covering 82% of the distance moved during the non-hunting season and mals just 75%.

Group Size

Data show that average axis deer group size decreased noticeably during the hunting (May to October) versus non-hunting period (F test; p=0.02). The total number of deer encountered per hour also suggests a decrease between the hunting (0.51 +/- .32 groups; 8.98 deer) and non-hunting (0.81 +/- .52 groups; 13.95 deer) seasons (F-test; groups, p=0.42; deer, p=0.14). When adjusted for hours of observation, fewer groups of deer and fewer individual deer were encountered during firearms season (Figure 25 and Figure 26).

Discussion

Maui data indicate that axis deer on Maui may alter their ranging and grouping patterns as a result of hunting. Deer appear to decrease their home range size, cover smaller distances from week to week, and cover a reduced total distance during the firearms season than in the non-hunting period. Female deer show a 50% reduction in core area size during hunting. Both sexes show a 15-30% reduction in the distance between consecutive fixes and a 15-25% reduction in total measured distance traveled. During firearms season, mean group size of deer appears to decrease as well, quickly returning to former levels shortly after hunting season (January). Deer are also seen less frequently, with fewer total deer encountered during hunting periods.

Overall, the data suggest axis deer may be hiding out and dispersing in response to hunting pressure. This remains a cautious interpretation. Other factors might account for the observed results, such as a habitat shift during the summer months (hunting, foraging, or temperature related). In the dry forests of western India, under drought conditions, axis deer shifted diets from grass to browse (Khan 1994). If these sorts of foraging preferences drive habitat shifts on Maui during the summer, then the distribution of plant communities on the landscape alone will influence home range measurements, and structural or spatial aspects of habitat patches may instead drive group sizes. Home range size is also reduced during the summer in Nepal (Mishra 1982), so a more detailed analysis of seasonal habitat use might help to clarify these factors.

It appears that intensive hunting may directly affect axis deer behavior, but potential confounding factors include the deer's annual breeding cycle. 'Hunting season', as defined here (May-October), coincides with the male rut period and this may help explain the differences observed in home range size and movement patterns between the sexes. Unlike females, males show a larger average home range size during hunting season. If frequent rut-related forays occur in this species as in many polygynous cervids (de Vos, Brokx et al. 1967; Geist 1998), these would act to inflate MCP area. Similarly, female axis deer (and many cervids) are a 'hider' species (Cowan 1974), known to seek out secluded patches of thick vegetation for birthing (Eisenberg and Lockhart 1972). Worldwide, this occurs from November through April, coinciding with the 'non-hunting' season (Graf and Nichols 1967; Schaller 1967; Russ 1977). This behavior might also cause an inflation of MCP area during this season, as females search for fawning grounds.

Behaviorally, axis deer become extremely wary under continued harassment (Graf and Nichols 1967; Ables 1977; Waring 1996; Anderson 2003) and this can act to disrupt their natural social patterns (Graf and Nichols 1967; Anderson 2003). Axis deer are also capable of quick adaptive behavioral responses, such as becoming nocturnal (Anderson 2003; Nowak 1999), identifying spotlights with poachers (Anderson 2003) and habituating quickly to a wide array of scaring stimuli (Graf and Nichols 1967; Dinerstein 1979). Conditioning to such disturbances has been previously reported in Hawaii (Graf and Nichols 1967; Waring 1996) and Texas (Ables 1977). Given that overall group sizes on Maui are so much larger than groups in Asia, an alternative hypothesis exists. Although data show decreased axis deer group sizes during hunting season, it is possible that more generally axis deer in this area have 'learned' to form larger groups in the face of hunting pressure.

With only very limited hunting prior to 1997, the percentage of groups encountered containing more than 50 individuals steadily increased during the study.

From 1998 to 2000, the percentage of these groups steadily increased from 2% to 13% to 24% by the end of the study. This formation of large groups in exposed pastureland is consistent with most other ungulates. Herds, flocks, and schools all provide additional protection from predation (hunting) in open areas (Vine 1971; Barrette 1991). This is likely to extend to the similar pressures imposed by hunting as by natural predation.

Only two ‘rain events’ (> 5 cm) occurred during the study: in October 1999 and March 1999. As seen in native regions, axis deer formed large herds and concentrated around the richest new growth. Within a month, deer once again faced drought conditions with little new growth. Larger groups are evident during the October event in Figures 22, 24, and 25. Normally axis deer home range depends largely on the availability of high quality forage, moving as necessary to meet demands. Under drought conditions, there was little change in these variables. Influences of hunting, reproductive activities, and landscape structure may have instead come to dominate observed movement and grouping patterns.

Influences of hunting and habitat on home range can either decrease or increase home range area for a species (Root 1988). A ‘fine-grained’ (many small patches, evenly distributed) distribution of plant communities has previously been shown to reduce home range size (Clutton-Brock and Harvey 1977) in axis deer (Moe and Wegge 1994). On the ranch lands of Maui, the opposite occurs, with plant communities distributed in large, uneven, patches of pastureland, scrub, and dry forest. Such a landscape structure likely contributes to the large size of axis deer ranges on Maui. The distribution of thick patches of cover vegetation might result in smaller home ranges for deer during summer, simply based on its distribution.

Conclusions

Introduced axis deer on Maui exhibit a mix of potentially novel traits (home range size, group size) and patterns similar to those in native areas (breeding cycle, seasonal grouping patterns). Axis deer home range size is known to vary depending on many factors, including the availability of forage and cover (Mishra 1982), and also may be influenced by seasonal reproductive activities (Moe and Wegge 1994; Raman 1997). On Maui, home range and grouping data suggest axis deer are responding to the different environmental conditions of Maui. Further work is needed to determine whether hunting activity, or simply the distribution of landscape elements providing forage and cover on Maui, are driving the observed differences.

CHAPTER 3: Mammalian Species Account for *Axis axis*

Genus Axis

Hamilton-Smith, 1827: 312

Type species: *Cervus axis* Erxleben 1777 (Grubb 1992)
Syn. *Hyelaphus* (Sundevall 1846)

Congeners (4 recognized species):

Axis porcinus Zimmerman, 1780: The hog deer

Type locality: India, Bengal. (Grubb 1993)
CITES: Appendix I as Cervus (=Axis) porcinus annamiticus

Axis porcinus Zimmerman 1777
Axis porcinus Zimmerman 1780
Axis porcinus Jardine 1835
Axis porcinus porcinus Zimmerman 1780
Axis porcinus oryzus Kelaart 1852
Axis oryzus Kelaart 1852 (Ceylon = Axis porcinus)
Axis porcinus annamiticus Heude 1888
Hyelaphus annamiticus Heude 1888
Cervus porcinus Zimmerman
Cervus (Axis) porcinus Smith 1827
Cervus pumilio Fischer 1827
Cervus minor Sclater 1883
Axis annamiticus
Axis hecki
Axis pumilio
Axis porcinus oryzus Pocock 1943
Axis porcinus Ellerman Morrison-Scott 1951
Hyelaphus porcinus pumilio Fitzinger 1874
Hyelaphus porcinus porcinus Phillips 1935

Axis kuhlii Muller, 1840: The Baewan deer

Type Locality: "Java en Borneo", but is found only on Baewan Isl., Indonesia (Grubb 1993)
Type Specimen: Museum at Leyden (Lydekker 1898)
CITES: Appendix I
IUCN: Rare

Axis kuhlii Muller & Schlegel 1844 (Baewan Island)

Cervus kuhlii Muller and Schlegel 1844
Cervus kuhlii Sundevall 1844
Cervus (Hippelaphus) kuhlii Sundevall 1846
Rusa kuhlii Gray 1847
Cervus kuhli Brooke 1878

Axis calamianensis Heude, 1888: The Calamian Island deer of the Philippines

Axis calamianensis
Type locality: Philippines, Calamian Isls., Culion Isl.
CITES: Appendix I
IUCN: Vulnerable

Hyelaphus calamianensis Heude 1888 (Calamian Islands)
Axis culionensis
Cervus culionensis Elliott 1896

Context & Content

Order Artiodactyla (Owen 1841), suborder Ruminantia, family Cervidae (Goldfuss 1820), subfamily Cervinae (Goldfuss 1820: 374), tribe Cervini (Groves and Grubb 1987), genus Axis (Hamilton-Smith 1827). Although a number of authors have considered *Axis* a sub-genus of *Cervus* (Lydekker 1898; Lydekker 1916; Koopman 1967; Lekagul and McNeely 1977; Corbet and Hill 1991), *Axis* is currently recognized as a distinct genus following Simpson (1945). Recent authors believe that the genus *Axis* is comprised of two sub-genera: *Axis* and *Hyelaphus*. *Axis* is thereby monospecific, containing only *A. axis*. *Hyelaphus* contains *A. porcinus*, *A. kuhlii*, and *A. calamianensis* (Ellerman and Morrison-Scott 1966; Groves and Grubb 1987; Corbet and Hill 1992; Nowak 1999). Some also consider the mainland (*A. a. axis*) and Sri Lankan (*A. a. ceylonensis*) forms of *A. axis* to be subspecies (Ellerman and Morrison-Scott 1966).

A. porcinus is currently sub-divided into an eastern (*A. p. annamiticus*) and western (*A. p. porcinus*) subspecies (Groves and Grubb 1987). *A. kuhlii* and *A. calamianensis* have also been considered subspecies of *A. porcinus* (Corbet and Hill 1991; Nowak 1999) since these species might have originated from an early human introduction of *A. porcinus* (Mishra 1982), but this is not the widely held current view. Presently, the genus *Axis* contains four species [and as many as four subspecies]: *A. axis, A. porcinus, A. kuhlii*, and *A. calamianensis* [*A. p. annamiticus, A. p. porcinus, A. a. axis, A. a. ceylonensis*].

Diagnosis

A. axis is easily distinguished from its 3 congeners. Of the four species, only *A. porcinus* and *A. axis* co-occur on mainland Asia. The average body weight (bw), shoulder height (sh) and total length (tl) of adult *A. axis* are markedly greater than for *A. porcinus.* Average measurements are as follows: *A. Axis* buck (bw: 70-90 kg; sh: 90 cm; tl: 13-38 cm), *A. porcinus* (bw: 35-50 kg; sh: 60-75 cm; tl: 20 cm) (Whitehead 1993). Antler structure also differs between these species. *A. porcinus* has a longer pedicel (ca. 2 cm in *A. axis*, >5 cm in *A. porcinus*) and its brow tine forms a much more acute angle with the main beam (Pocock 1943). In *A. axis*, the brow tine forms a nearly right angle to the main beam (Mishra 1982). Antler length and spread for *A. axis* (al- 76 cm; as- 38-69 cm) is much larger than for *A. porcinus* (al- 42-62 cm; as- 16-40 cm). Anatomically, enlarged upper canine teeth in *A. porcinus* also distinguish it from its congeners. All other members of *Axis* have greatly reduced or absent upper canine teeth (Mishra 1982; Groves and Grubb 1987). *A. porcinus* pelage undergoes an annual molt, from a dark brown winter coat to a lighter chestnut colored coat through summer (Schaller 1967). Adults can have faint or marked spotting, and fawns are heavily spotted as in all cervinae (Groves and Grubb 1987).

A. porcinus is found in wetter habitats than *A. axis* (Dinerstein 1979), primarily alluvial grasslands (Sunquist and Sunquist 1988). *A. axis* is a grassland and forest edge species (Schaller 1967; Dinerstein 1979) that is most abundant in shorter grasslands, especially where fire or grazing maintains early seral stages (Elliott 1983). *A. porcinus* are mainly dwellers of tall grassland (Schaller 1967; Seidensticker 1976). Despite these general preferences the two species do co-occur in some grassland habitats (Schaller 1967).

A. porcinus is more solitary than *A. axis* (Lydekker 1898), with 55% of sightings of *A. porcinus* in Nepal being of solitary individuals versus 18% of encounters with *A. axis* (Seidensticker 1976). Similarly, Dinerstein (1980) observed solitary *A. porcinus* on 48 of 98 occasions. *A. porcinus* also has a different breeding cycle from its congener in Nepal. Hog deer (*A. porcinus*) are in velvet antler during the hot dry season, while *A. axis* are in hard antler and full rut at this time. Hog deer reach their rut several months later during the monsoon (Dinerstein 1980).

The remaining two species of the genus are confined to Pacific Islands. *A. calamianensis* is only found on several of the Calamian Islands (Caluit, Culion, Busuanga) (Nowak 1999) and *A. kuhlii* is found only on Baewan Island in Indonesia. There is much greater overlap in antler length between *A. porcinus* and *A. kuhlii* (range: 306-480cm), than there is between either species and *A. calamianensis* (range: 205-313cm) (Groves and Grubb 1987). *A. calamianensis* is distinguished from *A. porcinus* by having a more slender appearance, with longer legs (Groves & Grubb 1987). Antlers of *A. calamianensis* are ca. 100 mm shorter (205-313 mm) than in *A. porcinus* (306-444 mm) (Groves and Grubb 1987). It also has wider, more curved antlers. The ears of *A. calamianensis* are whiter and the legs are much darker than in *A. porcinus* (Groves and Grubb 1987). There is no dark mat of hair on the forehead and the inner haunches are buffy instead of white as in *A. porcinus* (Groves and Grubb 1987). *A. kuhlii* is less distinct from *A. porcinus*, but it has noticeably straighter antlers, a bushier tail, and less contrast between its dorsal and flank coloration (Groves and Grubb 1987).

A. axis is the only member of this genus that is not currently listed in the IUCN red data book. Of the two currently recognized subspecies (Groves and Grubb 1987) of *A. porcinus*, *A. p. annamiticus* is native to Thailand and Indo-China (Nowak 1999), and *A. p. porcinus* is found in Laos and Pakistan (Nowak 1999). The IUCN's deer specialist group first listed both subspecies in the 1996 red book. Today, each retains their original listing classification. *A. p. annamiticus* remains 'data deficient' (IUCN database; http://www.redlist.org) and *A. p. porcinus* remains 'lower risk- near threatened' on the 2000 IUCN red list (IUCN database; http://www.redlist.org). *A. calamianensis* is currently listed as endangered by the IUCN and is on Appendix I of CITES (Nowak 1999), where its status is B1+3d. Roughly 500 deer persist in a reserve on Caluit Island where they compete with numerous introduced African ungulates (Nowak 1999). Small populations also persist on Busuanga and Culion Islands (Nowak 1999).

A. kuhlii has been listed as globally endangered since first appearing on IUCN's list of rare species in 1972 (Blouch and Atmosoedirdjo 1987). This species has the most limited geographic range of any deer species in the world, being confined to the 200 km^2

island of Baewan (Blouch and Atmosoedirdjo 1987). It is currently a status D species, a change from its D1 listing in 1996 (IUCN database; http://www.redlist.org). In the late 1970s less than 400 deer were thought to remain in the wild (Blouch and Atmosoedirdjo 1987). All of these remain confined to small portions of the heavily populated island of Baewan, roughly 125 miles north of Java (Blouch and Atmosoedirdjo 1987). Numerous individuals of *A. kuhlii* and *A. calamianensis* exist in zoos worldwide.

Axis axis

Erxleben 1777

Axis Deer

(Chital or Spotted Deer)

Axis axis Erxleben. 1777: 312. Type locality: India, Bihar, "banks of the Ganges."

(Grubb 1993)

Axis axis axis Erxleben 1777
Cervus axis Erxleben 1777 "Banks of the Ganges, India"
Axis axis ceylonensis Fischer 1829 Type locality: "Ceylon"
Cervus axis var. *indicus* Fischer 1829
Cervus axis var. ceylonensis Fisher 1829 "Ceylon"
Cervus axis Lydekker 1898, 1913-16
Cervus axis Brooke 1878
Cervus (Axis) axis Smith 1827
*Cervus axis ceylonensis*Smith 1827
Cervus nudipalpebra Ogilby 1831 "Banks of the Ganges"
Cervus axis maculatus Kerr 1792 "Banks of the Ganges"
Cervus (Rusa) axis zeylonicus Lydekker 1905
Axis axis ceylonensis Phillips 1935
Axis axis axis Simpson 1945
Axis axis ceylonensis Simpson 1945
Axis ceylonensis
Axis indicus
Axis maculata Kelaart 1852
Axis maculata Gray 1843
Cervus (Hippelaphus) axis Sundevall 1846
Axis maculatus Jerdon 1867
Axis maculatus Sterndale 1884
Axis maculata ceylonensis Fitzinger 1874
Axis major Hodgson 1841
Axis minor Hodgson 1841
Axis nudipalpebra Fitzinger 1874
Hyelaphus maculatus Fitzinger 1874

Context & Content

Content same as for genus.

General Characters

The axis deer is a mid-sized deer species with an average shoulder height of 90 cm (Mishra 1982). It is one of few deer species to retain a juvenile spotted pelage year-round throughout adulthood (Groves & Grubb 1987). Adults have a rich russet brown coat, flecked with white spots running from head to rump in nearly linear rows along each flank (Figure 6). There is no mane. A black dorsal stripe is evident along the spine, where the white spots fuse into lines. The throat, abdomen, underside of the tail, and insides of the legs are white (Schaller 1967). In season, males have a large pair of lyre-shaped (Lydekker 1898) 3-tine antlers (longest 111 cm, avg. 75 cm) (Whitehead 1993) (Figure 5). Immediately upon shedding a set of antlers, growth begins on the next set (Schaller 1967). Antlers are shed annually.

As in most gregarious, open country cervids, axis deer exhibit sexual dimorphism (Clutton-Brock 1987). *A. axis* actually shows the greatest degree of sexual dimorphism among all cervidae (Barrette 1987). Axis deer are polygynous and, as is typical of polygynous mammals, bucks are substantially larger than does (Clutton-Brock 1987). Axis deer body size is relatively consistent worldwide, though a cline of decreasing body size occurs from the Himalayan foothills southwards through peninsular India (Lydekker 1898). The smallest axis deer occur on the island of Sri Lanka. Body weight and measurements are summarized in Table IX. *A. axis* can live up to 22 years in captivity (Crandall 1964), but more commonly live 13-17 years(Mungall and Sheffield 1994) .

Average body weights of male and female *A. axis* in Nepal are 71 and 50 kg (Mishra 1982). In Hawaii, averages and ranges of body dimensions (cm) for 92 male and

30 female (in parentheses) were: total length, 178, 164-207 (164, 144-168); shoulder height, 93.5 (75); body weight, 72, 44-98 (44, 33-55) (Graf & Nichols 1967). Averages and ranges of body dimensions (cm) for 13 male and 16 female (in parentheses) in Texas were: total length, 176, 169-189 (155, 149-163); shoulder height 91, 81-99 (78, 67-84); weight 85, 75-101 (49, 47-64) (Ables 1977). Tails range from 13-38 cm (Nowak).

Table IXWeights and Measurements of *A. axis*

Location	*Male*				*Female*				
	Ht. Shldr.	**Total Lgth.**	**Wt.**	**N**	**Ht. Shldr.**	**Total Lgth.**	**Wt.**	***N***	**Ref.**
Nepal	90 avg.	-	71 avg.	-	75 avg.	-	50 avg.	-	(Mishra 1982)
India	86-92	-	81 avg.	-	-	-	-	-	(Whitehead 1993)
Ceylon	80-88	-	70-75	-	-	-	-	-	(Whitehead 1993)
Ceylon	83 avg.	142 avg.	-	9	70	128	-	3	(Philips 1935)
Texas	91 avg. (81-99)	176 avg. (169-189)	85 avg. (75-100)	13 -	78 avg. (67-84)	155 avg. (149-163)	49 avg. (47-64)	16 -	(Ables 1977)
Texas	64-101	-	66-114	-	68-85	-	48-66	-	(Mungall and Sheffield 1994)
Hawaii	94 avg. -	178 avg. (164-207)	72 avg. (44-98)	92 -	75 avg. -	164 avg. (144-168)	- -	30 -	(Graf and Nichols 1967)

Table IX summarizes published weights and measures for axis deer worldwide. Weights (Wt.) are shown in kilograms (kg) and measurements in centimeters (cm). Averages and ranges are presented where available.

A. axis pelage maintains a full ontogenetic spotted pattern throughout adulthood. Albino axis deer have occurred in captivity (Nowak 1999). There is no evident seasonal change in axis coats in Nepal (Mishra), but the darker colors on the face and back of axis males become more pronounced during the rut (Brander 1927; Anderson 2003).

Axis deer antlers are among the simpler forms within the Cervinae, having only the minimum number of tines (three) that characterize the tribe Cervini (Groves and Grubb 1987). The main beam splits to a fork at the top. The brow tine is generally longer than the tine of the top fork at all ages that bear antlers (age > 16-20 months). Hard spike antlers appear by ca. 16 months (Schaller 1967), and trophy antler condition is obtained by 4-5 years of age when antlers approach their maximum length and thickness (Ables and Fuchs 1977). Buck size and condition are thought to decline after 8 or 9 years (Fuchs 1977).

In *A. axis*, the upper jaw lacks incisors and canines (Mishra 1982). The dental formula is i 0/3, c 0-1/1, p 3/3, m 3/3 (Nowak 1999). Captive fawns indicate that milk teeth are replaced with permanent teeth after ca. 12 months (Graf and Nichols 1967). In one captive male, upper incisors were lost between the 49^{th} and 65^{th} week, middle incisors at 63 weeks, and the second set of incisors at 65-68 weeks (Graf and Nichols 1967).

The skull lacks a sagital crest in Cervidae (Groves and Grubb 1987). Measured brain volume of axis deer was similar for both sexes (m=143.9 ml; f= 145.2 ml) (Wemmer and Wilson 1987). Auditory bullae of *A. axis* are hollow as in most cervids, but large and inflated in this genus (Pocock 1943). The greatest length of skull dimension overlaps entirely across the four species in the genus Axis (*A. kuhlii, A. porcinus, A. axis, and A. calamianensis*), with a range of 204-241 cm (Groves and Grubb 1987).

Axis deer have long, deep, pouch-shaped glandular pockets on their hind feet only that are distinct from the interdigital space in this genus (Groves and Grubb 1987). Distinct gland tufts are evident on the metatarsal glands. Preorbital glands are also present, as in all cervinae (Groves and Grubb 1987).

Distribution

A. axis is native to mainland Asia and Sri Lanka (Ceylon). A range map appears as Figure 28. Axis deer are found throughout the Indian subcontinent and into Nepal, at elevations below ca. 1000m (Schaller 1967). *A. axis* was formerly common and widespread from the southwestern corner of Bhutan, along both the northern and southern foothills of the Himalayas to nearly Punjab. The Great Indian Desert forms their western range limit (Schaller 1967). Their range extends southwest, around the desert, to the coast in Gujarat. Prior to land conversion for agriculture, deer were found throughout the drier forests of the plateau region, extending to the southern tip of India in Tamil Nadu (Prater 1965; Schaller 1967). They persist today only in fragmented pockets throughout the region. Larger expanses of their preferred Indian habitats, moist and dry deciduous forests, continue to hold deer today. Deer penetrate wetter regions in the state of West Bengal. There, in the Sunderbans, they are found in mangrove swamps (Schaller 1967) and extend into wet forests receiving more than 500 cm of rain per year (Ables 1977). *A. axis* is historically absent from Assam and east of the Bay of Bengal (Lydekker 1898).

Axis deer have been introduced to many parts of the world (Lever 1985). Introductions in Europe include Croatia, Moldova, the Caucuses (Nowak 1999), parts of the former western Soviet republics including Ukraine and Yugoslavia (Evtushevskii 1977; Fadeev 1986). Axis deer have also been introduced to New Guinea (Groves and Grubb 1987), Australia, Brazil, Java, Nicobar (Bentley 1967), Argentina, Uruguay (Grubb 1992), the United States (Texas, Georgia, California, Florida), and the Andaman Islands. In Hawaii they are currently found on Maui, Molokai and Lanai (Kramer 1971). They inhabited Oahu for nearly 100 years, from 1868-1965 before they were extirpated by the 1950s owing to their confinement in a single valley (Moanalua) (Tomich 1986). Axis deer were introduced to New Zealand in 1867, but were apparently eradicated thereafter owing to the damage they had caused (Clark 1949). Introductions to New Guinea have also died out (Nowak 1999).

Axis deer have had success across an extremely wide range of latitude, from the Ukraine at 51° N. to nearly the southern tip of Argentina at 41° S. (Veblen, Mermoz et al. 1989). Wherever they occur axis deer are frequently hunted, snared, and poached for trophies and subsistence (Graf and Nichols 1967; Schaller 1967; Fuchs 1977; Dinerstein 1979; Mungall and Sheffield 1994; Anderson 2003). The axis deer's success as an exotic species is frequently attributed to the deer's behavioral and foraging flexibility (Mungall and Sheffield 1994).

Fossil Record

Cervids are a mainly Eurasian and northern group, first evident in the early Miocene (Groves and Grubb 1987). *A. porcinus* has been considered the most primitive of all the cervini (Flerov 1952). It retains a primitive antler structure and is built like the muntjak (*Muntiacus muntjak*), which has often been considered the oldest living member of the artiodactyla (Colbert 1969; Mishra 1982). Axis deer existed in Asia during the Pliocene and Pleistocene, and *A. oppenoorthi* is thought to be a mainland ancestor (Groves and Grubb 1987). It and *A. lydekkeri* may also be the ancestors of *A. kuhlii*. Both species are known as upper Pleistocene fossils on Java (Blouch and Atmosoedirdjo 1987). At this time Java and Baewan were joined by a land bridge. *Axis shansius* is also known from the lower Pleistocene in China (Groves and Grubb 1987). Following the extinction of Cervavitus in the early Pliocene (Flerov 1952), two ancestral lineages emerged in Asia that gave rise to modern cervid forms (*Eucladocerus*, *Cervus*). Present-day members of *Muntiacus*, *Rusa* and *Axis* are considered most similar to ancestral *Cervus*, remaining small and little changed since the end of the Pliocene (Flerov 1952).

Maintenance of some spotting is one of the few evident derived characters for the tribe Cervini (Groves and Grubb 1987). Another possible synapomorphy of Cervini is the dark dorsal stripe that persists along the spinal column, adjacent to white spots arranged in tight rows along the flanks (Groves and Grubb 1987). Both of these traits are evident in *A. axis* (Figure 6).

In the jaw, *A. axis* has a metaconid that is developed more like a distinct conid instead of fused to the paraconid or parastylid (Groves and Grubb 1987). Less distinct molarization is therefore evident in this Genus than in other forms (e.g. *Elaphodus, Elaphurus, Cervus* and *Dama*). Canines are also greatly reduced such that they are almost always absent in this species (Groves and Grubb 1987). Axis deer are further characterized by a primitive type of incisor dentition, whereby the first incisor is especially broad relative to both crown height and the remaining, narrower, teeth (Groves and Grubb 1987).

Ontogeny and Reproduction

Axis deer populations have been shown to increase rapidly with good forage conditions, both in native (Schaller 1967) and introduced areas such as California (Wehausen and Elliott III 1982) and Texas (Mungall and Sheffield 1994), with annual increases of 20-23.5% (Wehausen and Elliott III 1982). Even though axis deer can produce no more than 1 fawn every 8 months, they can become pregnant while nursing a recent fawn (Sadleir 1987). If a doe loses her fawn early, she is able to give birth a second time within a year (Crandall 1964).

Where introduced, *A. axis* begin breeding early. *A. axis* does were impregnated by 10 months of age in Point Reyes, California (Wehausen and Elliott III 1982), and several females in Hawaii reached sexual maturity by 6 months (Graf and Nichols 1967). *A. axis* breed year-round in captivity throughout the world (Crandall 1964) and, regardless of antler condition, wild axis bucks are capable of breeding year-round in both native (Schaller 1967; Mishra 1982) and introduced areas, including Hawaii (Graf and Nichols 1967), Texas (Fuchs 1977; Howery, Pfister et al. 1989), California (Elliott 1973) and Australia (Bentley 1967). This may help explain the variation in reported rut and fawning peaks throughout the world (Figure 28).

High annual pregnancy rates and low pre-natal mortality characterize the cervidae (Sadleir 1987). Annual pregnancy rates in *A. axis* have been reported as follows: Hawaii (95%), Texas (100%), and India (95%) (Graf and Nichols 1967; Schaller 1967; Ables 1977). Rapid growth of wild axis deer populations has been documented in India where estimated populations rose quickly from 1,500 to 13,000 in eight years (Martin 1987) and from 10,500 to 51,000 4 years (Khan 1995).

A. axis females ovulate in their first 12 months (Graf and Nichols 1967; Sadleir 1987) and are polyestrous (Asdell 1964) with a mean estrous cycle of 19.3 +/- 1.3 days (range: 17-21) (Chapple, English et al. 1993). Axis deer are capable of ovulating while pregnant (Graf & Nichols 1967), and most female axis deer breed within their first 14-17 months (Schaller 1967). In Hawaii, female deer as young as 10 months have been found pregnant (Nichols 1960).

Axis deer females are in estrus cyclically throughout the year, and inter-estrous intervals varied widely in Texas (range: 17-56 days) (Fuchs 1977). One study indicated that females come into heat for 12 to 30 hours (Fuchs 1977). Bucks reach sexual maturity at ca. 18 months (Schaller 1967). In Hawaii, a captive axis buck first exhibited erections at 60 weeks of age (Graf and Nichols 1967) and viable, active, sperm was found in 1-2 year old bucks (Graf and Nichols 1967). Little is known about axis deer dispersal, but a juvenile male deer in Nepal dispersed 36 km from its point of capture over 3 years (Mishra 1982).

Gestation for *A. axis* is reported as 234.5 +/- 3.0 days (median=235; range: 228-239) (Chapple, English et al. 1993). Earlier published reports varied significantly. Gestation has been listed as 6 months, 7 ¼ months (Schaller 1967), 7-7 ½ months (Asdell 1964) or 8-8½ months (Schaller 1967). In Hawaii, gestation was given as 229 days (Graf and Nichols 1967).

A. axis fetuses begin to show limb buds and eye sockets within the first month (Fuchs 1977). By 80 days, genitalia are evident and pale white hooves are developing

The fetus remains hairless and without coloration throughout its first 90 days. Near 100 days the ears and snout are well developed, but metatarsal glands have yet to appear. By 125 days, hair appears on the face and eyelashes are evident. Metatarsal glands are apparent and teeth are beginning to form. The coat also begins to show signs of coloration and spotting. By 200 days, the fetus appears like a small fully developed fawn. Teeth are completely formed at this time (Fuchs 1977).

As in all deer, the most marked increase in fetal body size of *A. axis* occurs in the final 3 months of pregnancy (Dinerstein 1980). A Texas study shows that axis fetuses remain small through their first 100 days, both sexes weighing less than 500 grams and measuring less than 200 mm in overall length (Fuchs 1977). A late–term female fetus weighed 3632 grams (est. 225 days) and a late-term male fetus weighed 3292 grams (est. 200 days). They measured 517 mm and 482 mm total length respectively (Fuchs 1977).

A study of 17 captive births revealed birth weights ranging from 2.7 to 4.2 kg (Chapple, English et al. 1993). Captive axis deer fawns in Hawaii reached 10 kg by 6-7 weeks, and 20 kg at ca. 15 weeks. Growth of a captive buck slowed markedly after the 50^{th} week, at a weight of 52 kg (Graf and Nichols 1967).

Fawning worldwide consistently peaks from December to April (Figure 28). As is common among deer that adopt a ‘hiding’ rather than ‘following’ strategy (Bunnell 1987), *A. axis* females seek solitude to fawn. Fawns stay hidden for at least two (Anderson 2003) and up to four weeks (Dinerstein 1980), with their mother nearby. Shortly thereafter, the mother and fawn rejoin a group. During fawning season in Hawaii, the majority of herds consist solely of females and fawns since velvet antlered males simultaneously form buck-only groups (Anderson 2003).

Axis deer fawns are capable of running shortly after birth but appear unsteady (Graf and Nichols 1967). In introduced and native locations, axis deer fawns are present throughout the year (Graf and Nichols 1967; Fuchs 1977; Mishra and Wemmer 1987). In Texas and India, 76% to 80% of births occurred during the peak season from January-April (Schaller 1967; Fuchs 1977). Fawn mortality can be high in native regions (Sharatchandra and Gadgil 1975). In India, an estimated 95 fawns were born to 100 does, but nearly half of these were lost in their first year (Schaller 1967). As early as fawns, *A. axis* males habitually urinate on their bed sites (Ables 1977); females do not.

Axis deer are monotocous (Bunnell 1987). Thus, although capable of twinning they cannot produce a true litter of young. In order for this species to increase its lifetime reproductive output, only three options are available: reproduce earlier, reduce fawn mortality or decrease the inter-breeding interval (Bunnell 1987). It is possible that shifts have occurred in Texas, California and Hawaii. Twinning is widely agreed to be rare in *A. axis*. Only one of 347 zoo births was twins (Schaller 1967), and Crandall (1964) reported only one twin in 225 births at the NY Zoological Park. Twinning has been documented in Hawaii (Graf and Nichols 1967) and Texas (Fuchs 1977), but remains a rarity.

The most permanent 'herd' association of axis deer is the close relationship between a doe and her fawn (Schaller 1967; Mishra 1982). When together, frequent licking of the fawn by the mother is observed which may aid individual recognition (Schaller 1967). Fawns stay in close association with their mothers for up to 2 years (Schaller 1967), with yearling does staying close for a second year (along with a newborn fawn). Males generally leave prior to their first rut period, ca. 15-18 months (Schaller

1967). Fawns are well tolerated by unrelated does (Seidensticker 1976). Fawns that get separated from their mothers during foraging frequently find another available doe whom they shadow until reuniting with their mothers (Schaller 1967). This was considered a potentially adaptive strategy for a heavily predated animal with high fawn mortality (Schaller 1967).

Axis deer have 2 pairs of mammae (Nowak 1999). There is little published information on the milk of most tropical Asian deer species (Robbins, Oftedal et al. 1987), but suckling is frequent, occurring as often as 10 times a day. There is documented communal nursing in captive populations of this species, and a number of wild does have been observed suckling fawns that were not their own (Schaller 1967). Fawns as young as 2 weeks in India (Schaller 1967) and 1 month on Maui (Anderson 2003) nibble grass. Captive fawns in Hawaii are seen nibbling grass by the age of 1 week and eating it regularly by 5 weeks (Graf and Nichols 1967). In Texas, green forage intake is reported by 5.5 weeks, with full weaning occurring from 4 to 6 months (Mungall and Sheffield 1994).

Antlers are present only on bucks and are shed annually, generally within a day of each other (Schaller 1967; Fuchs 1977), after which growth immediately begins on the next set (Schaller 1967). Visual evidence of new growth appears within 2 weeks (Fuchs 1977). During the annual re-growth of antlers, larger antlers take longer to develop from 'velvet' through 'hard' antler. Antlers over 75 cm can take as long as 26 weeks to fully develop from velvet 'knobs' to shed velvet (Schaller 1967) (Fuchs 1977). During the velvet stage, antlers are actively growing and supplied with blood from a fine capillary network (Bubenik and Bubenik 1987). As antler growth subsides, the capillary network is cut off and antlers harden into bone. This generally occurs in the weeks just prior to the rut and coincides with a rise in testosterone levels (Bubenik and Bubenik 1987). The entire cycle in *A. axis* can last as long as fifty weeks from one antler shedding to the next (Schaller 1967).

Antler length provides an estimate of buck age in *A. axis*, with a steady increase in antler length throughout a buck's first 5 years (Schaller 1967). Antlers greater than 75 cm are considered trophies and are rarely encountered on bucks less than 4 or 5 years old (Schaller 1967). Axis deer males get their first set of 'spike' antlers between 12-16 months (Schaller 1967) and they harden by 17-20 months (Fuchs 1977), though a captive buck in Hawaii hardened by 14 months (Graf & Nichols 1967). Yearlings generally develop their first spike antlers in time to participate in the rut at ca. 18 months of age (Schaller 1967). Bucks lose their first set of spike antlers at 20-22 months (Schaller 1967) and obtain their first set of branched antlers by 25-28 months (Fuchs 1977). A buck of ca. 22-28 months is shown in velvet, developing his first set of branched antlers (Figure 4).

Ecology

A. axis is the most widespread and common of nine deer species in India (Bhat and Rawat 1995), and is the most successful and abundant of 65 attempted species introductions to Texas (Mungall and Sheffield 1994). In parts of Nepal axis deer comprise 68% of the entire wild ungulate population (5 total species), in terms of animal numbers (Dinerstein 1980). Axis deer are found throughout grasslands and edges of dry and mixed deciduous forests (Eisenberg and Seidensticker 1976; Seidensticker 1976; Dinerstein 1980; Mishra 1982; Moe and Wegge 1994). Axis deer gather together in large groups and forage in more open grasslands late in the day (Schaller 1967; Seidensticker 1976) and nighttime foraging can continue well past midnight (unpublished data).

Diurnal behavior patterns are influenced by temperature (Dinerstein 1979; Tak and Lamba 1984), predation (Karanth and Sunquist 1995), hunting (Anderson 2003) and food availability (Dinerstein 1980; Dinerstein 1987). Axis deer are mostly crepuscular in their natural habits, preferring to bed down during the heat of the day (Dinerstein 1979). While bedded, deer will chew their cud for several hours, using the same daytime rest areas frequently (Fuchs 1977) and clearing these sites of edible vegetation (Graf and Nichols 1967; Ables 1977).

Axis deer move in a clustered manner to track available forage(Dinerstein 1980; Moe and Wegge 1994). Axis deer have a strong preference for newly sprouting grasses, whether created by fire (Dinerstein 1979; Mishra 1982; Moe and Wegge 1997), cattle grazing (Elliott 1983) or mowing (Smith 1977; Moe and Wegge 1997). Group size and distribution of axis deer are clearly influenced by rainfall and resulting forage availability (Dinerstein 1979; Dinerstein 1987). Where vital needs of shade, food and water are met locally, axis remain faithful to a relatively small area (Seidensticker 1976).

Group size and herding behavior is among the more studied elements of axis deer ecology. Herds are not stable associations, but rather are very dynamic (Schaller 1967; Dinerstein 1980; Mishra 1982; Barrette 1991; Khan and Vohra 1992). This is characteristic of all of the south-Asian ungulates, except the elephant (*Elephas maximus*) (Dinerstein 1980). The social structure of axis deer herds has been termed a 'fusion-fission' association (Barrette 1991). The continual aggregation and fragmentation of sub-groups creates 'subherds' and 'superherds' (Tak and Lamba 1981: 12). In native areas, *A.*

axis naturally associate in clusters of 100-200 animals (Schaller 1967). The largest groups are seen when individual groups come together. Group size increases in response to forage availability (Dinerstein 1977, 1980), but in a non-linear manner (Raman 1997). In native habitats this generally occurs when emerging new growth follows rainfall, burning or mowing (Dinerstein 1980; Moe and Wegge 1997). Up to 2000 deer might gather under these conditions (Martin 1987). Large concentrations of deer appeared following fires on meadows in Kanha, India (Schaller 1967).

In Texas, resting groups (avg. 49; range: 4-134) were generally smaller than feeding groups (avg. 101; range: 41-156) (Fuchs 1977). Several studies identify high spatio-temporal variation of group size in this species (Khan and Vohra 1992). Group size is dynamic and influenced by a variety of factors including predator protection, food availability and hunting pressure (Tak and Lamba 1984; Anderson 2003). Female axis deer frequently lead herds when they move as a group; 80-85% of mobile herds observed in India were led by females (De Rames and Spillett 1966; Schaller 1967).

In native lands, group size naturally increases during the summer monsoon (rut) (Mishra 1982). This is when mixed sex and age herds are most frequently encountered in India (Schaller 1967). Buck only groups are most frequent prior to the onset of the rut (Schaller 1967; Mishra 1982), from January to April in India (Schaller 1967), Hawaii (Graf & Nichols 1967) and Texas (Fuchs 1977), the same period when doe-young herd associations are most common (Graf and Nichols 1967; Schaller 1967). 'Nursery' herds are also common at this time in Hawaii (Graf and Nichols 1967; Anderson 2003) and Texas (Ables and Fuchs 1977). These herds consist of one or many adult females with fawns up to an estimated six weeks of age (Anderson 2003). Under cover of nightfall, a single yearling may attend more than 50 young fawns at once (Anderson, pers. observation) while the adults forage separately.

Density estimates for *A. axis* are listed in Table X. Abrupt shifts in deer density between differing plant communities has been documented, both in Nepal and in Hawaii (Dinerstein 1979; Anderson 2003). In Nepal, axis deer vacate the Sal forest habitat as their favored food plants lose their leaves or go dormant (Dinerstein 1979). Dinerstein (1980) observed a drop in deer density from 24/km^2 to 12.2/km^2 in the middle of the hot dry season (April-May). In Hawaii, more than 500 deer relocated to lands adjacent to crop and golf course margins during the peak of drought in 1999. This shift persisted for roughly 2 months, after which the animals returned to formerly occupied areas (unpublished data). Where confined to a peninsula on Molokai, hundreds of axis deer rapidly lost condition and perished during the 1999 drought, yet there were no signs of starvation on Maui. Sex ratio data is summarized in Table XI. Despite the female bias in naturally occurring populations, data from the West Berlin Zoo (n=52) show a 9% male bias in *A. axis* births (Fradrich 1987).

Table X: Comparison of Density Estimates for *A. axis*

Author	Location	Number/km^2	Study Area Size (Sample Area)
(Schaller 1967)	India	23	No data
(Varman and Sukumar 1995)	India	25	127 km^2 (967 km)
(Johnsingh 1993)	India	43-45	No data
(Karanth and Sunquist 1995)	India	48-52	104 km^2 (468 km)
(Khan, Chellam et al. 1996)	India	39-57	1412 km^2 (1008 km)
(Biswas and Sankar 2002)	India	81	61.1 km^2 (458 km)
(Tamang 1982)	India	17	No data
(Seidensticker 1976)	Nepal	17	No data; (66.2 km^2)
(Dinerstein 1980)	Nepal	30-34	11.8km^2 (7 km^2)
(Eisenberg and Lockhart 1972)	Sri Lanka	6	580 km^2 (25 km^2)
(de Silva and de Silva 1993)	Sri Lanka	10	140 km^2 (no data)
(Anderson 2003)	Maui, HI	20	51km^2 (48 km)

Table X summarizes density estimates for *A. axis* worldwide. Sample area is indicated in parentheses as km^2. Where line transect methods were used, linear kilometers are shown.

Table XI Comparis on of Sex-ratio Data for *A. axis*

Author	Location	Males:	Females:	Fawns
(Schaller 1967)	India	42-72	100	16-68
(Biswas and Sankar 2002)	India	51	100	45
(Karanth and Sunquist 1992; Karanth and Sunquist 1995)	India	76	100	47
(Tak and Lamba 1984)	Nepal	69-80	100	17-54
(De Rames and Spillett 1966)	Nepal	52-60	100	31-37
(Dinerstein 1980)	Nepal	58	100	53
(Seidensticker 1976)	Nepal	115	100	28
(Fuchs 1977)	Texas	73	100	41
Unpublished data	Maui, HI	30-55	100	13-66

Table XI summarizes worldwide findings for axis deer sex-ratios, Males:Females:Fawns.

Worldwide, axis deer consume a minimum of 513 plant species from 86 plant families and 344 genera (Anderson 2003). Along with grass, they also consume a full spectrum of plant parts including leaves, stems, fruits, seeds, flowers and bark (Schaller 1967). Although capable of standing on their hind legs and foraging, axis rarely browse above 1.5 meters (Dinerstein 1979). In Texas, Mungall and Sheffield (1994) credit the deer's flexibility with its tremendous success. Substantial seasonal variation in diet, based on availability, is well documented (Dinerstein 1987; Martin 1987; Johnsingh and Sankar 1991).

Axis deer clearly have a strong preference for newly sprouted and immature grasses (Elliott 1973; Smith 1977; Dinerstein 1987). This can constitute more than 90% of an axis deer's rumen volume in India (Schaller 1967), Nepal (Dinerstein 1979) and Texas (Henke, Demarais et al. 1988). *Paspalum* species were most frequently consumed in Texas (Smith 1977), *Botriochloa odorata* and *Themeda triandra* in central India (Martin 1987), and a number of fire-adapted grass species in Nepal, including *Imperata cylindrica, Saccharum spontaneum, Cynodon dactylon, Vetiveria zyzanoides, Erianthus ravennae, Desmostachia bipinnata* (Dinerstein 1979; Dinerstein 1987). In Nepal, a significant increase in browse consumption was seen in the Fall (Dinerstein 1987).

Axis deer have also been shown to consume a wide range of other forage items throughout native [Schaller, 1972 #33] and introduced areas (Elliott 1973; Elliott 1983). When pressed, axis deer can turn to extremely unpalatable plants and plant parts. In India and Nepal, *A. axis* consume young leaves of several toxic species including *Solanum nigirium, Lantana camera* and the poisonous *Callotropis gigentia* (Sharatchandra and

Gadgil 1975; Seidensticker 1976; Dinerstein 1979; Tak and Lamba 1984). Axis deer also eat a wide variety of fruits (India: *Cordia myxa, Syzygum cumini, Zizyphus jujuba, Bridelia squamosa, Emblica officialis, Embelia tseriamcottam, Moghania stricta* Schaller 1967; Nepal: *Acacia catechu, Adina cordifolia, Bauhinia racemosa, Dalbergia sissoo, Eugenia jambolana, Schleichera trijuga, Semecarpus anacardium, Zizyphus spp. Leea robusta, Thespesia lampas*) (Dinerstein 1979), trees (India: *Acacia torta, Bauhinea racemosa, Bombax malabaricum, Cassia fistula, Miliusa tomentosa, Shorea robusta*) (Seidensticker 1976), shrubs (India: *Diospyros tomentosa, Ougeinia oojenensis, Phoenix humilis, Wrightia tinctoria*), vines (India: *Cryptolepis buchanani, Dioscorea bulbifera*), flowers (Nepal: *Bassia lattifolia, Bombax ceiba, Mallotus philippinensis*) (Dinerstein 1979), and bark. In Kanha, axis deer ate 4 species of *Terminalia* (Schaller 1967). In Nepal, *A. axis* ate seedlings of a wide variety of trees and vines (*Acacia catechu, Aegle marmelos, Alstonia scholaris, Antidesma diandrum, Ehretia laevis, Emblica officianalis, Gardenia turgida, Holoptelia integrifolia, Randia dumetorum, Streblus asper, Terminalia tomentosa, Milletia auriculata, Spathalobis roxburghii*) (Dinerstein 1979). Fruits dropped by foraging monkey troops, primarily the arboreal feeding Langur (*Presbytis entellus*), are known to make at least two dozen additional species of fruit available to axis deer (Schaller 1967; Seidensticker 1976; Newton 1989).

Axis deer are blamed for heavy crop damage, both throughout their native range of India (Schaller 1967; Sushil, Thakur et al. 1993), Sri Lanka (Santiapillai, Chambers et al. 1981), and Nepal (Dinerstein 1979) as well as in introduced areas such as Hawaii (Graf 1966; Brewbaker 1988) and the Andaman Islands. In the Andamans, they are considered an agricultural pest (Schaller 1967). Crop damage typically peaks in times of limited forage availability (Dinerstein 1987; Anderson 2003).

With unfettered access to crops, axis deer diets can constitute a larger percentage intake of crops than naturally occurring forage species (Dinerstein 1979). Crop damage is most severe where thick vegetation occurs nearby (Nepal, Seidensticker 1976; Hawaii, Graf & Nichols 1967, Anderson 2003; India, Sekhar 1998). Herds of deer will rest nearby and emerge a few hours after sunset into fields (Seidensticker 1976) and golf courses (Anderson 2003). In native regions, crops eaten include lentils, mustard, radishes, beans, tomatoes, maize, rice and wheat (Dinerstein 1979; Dinerstein 1987). On Maui, they frequently consume strawberries, lettuce, corn, sweet potatoes, eggplant, pineapples, avocados, onions and tomatoes (Anderson 2003).

Generally, more than half of tiger (*Panthera tigris*) feces collected contain axis deer hair (Schaller 1967; Dinerstein 1980; Martin 1987; Biswas and Sankar 2002). Predation was the single largest source of mortality for *A. axis* during Schaller's (1967) Kanha study. Tigers in Central India and Nepal take fewer male than female or young axis deer (Schaller 1967, Seidensticker 1976), as do free-ranging dog packs (*Canis familiaris*) on Maui, where 57 of 71 kills were of does and young (Anderson 2003).

In native regions, additional documented predators include leopards (*Panthera pardus*) (Seidensticker 1976; Ramakrishnan, Coss et al. 1999), hyaenas (*Hyaena hyaena*), and jackals (*Canis aureus*) (Schaller 1967; Tak and Lamba 1984). Where tigers and leopards overlap, leopards take proportionately more axis deer as prey than where leopards occur alone (Seidensticker 1976). Historically, lions (*Panthera leo persica*) (Khan 1995), cheetahs (*Acionyx jubatus*) and hunters have also acted as predators

(Schaller 1967). *A. axis* is a highly prized game species wherever it is found and even where hunting is illegal they are frequently poached and snared (Choudhury 1966; Sekhar 1998; Madhusudan and Sunquist 2002).

Axis deer are attuned to the alarm calls of other species, including langur monkeys (*Presbytis entellus*) in native habitats (Schaller 1967; Dinerstein 1979) and mynah birds (*Acridotheres tristis)* in Hawaii (unpublished data). This provides an additional element of protection to vigilant herds (Newton 1989). When alarmed, axis deer stand stiffly with their eyes and ears fixed in the direction of the disturbance. A series of barks follows, orienting others to the potential disturbance. Alarmed animals may also stomp on the foreground in the direction of the disturbance (Schaller 1967). These alerted animals often remain fixated for several minutes before determining whether to flee (Schaller 1967).

When an axis deer flees, it usually begins with a sharp bark and a series of high bounding jumps. Then, the animal generally remains low to the ground as it heads for thick cover (Schaller 1967). As in white-tailed deer, the underside of the tail is evident during flight (Schaller 1967). When running in open country, disturbed herds will frequently stop and look back at the source of flight from several hundred feet away (Schaller 1967; Anderson 2003).

Axis deer rely primarily on their keen hearing and sense of smell for predator detection (Schaller 1967). *A. axis* can be quite indifferent to down-wind, motionless, human forms (Waring 1996; Anderson 2003). Under these conditions deer have approached to within 15 m, even in heavily hunted areas (Schaller 1967; Waring 1996; Anderson 2003).

Disease screening in Texas suggests an apparent natural resistance (Mungall and Sheffield 1994) to ticks, nematodes, and other parasites (Robinson, Galvin et al. 1977). An overview of diseases and parasites is found in Appendix II. In Texas, the following nematodes were reported (Robinson, Galvin et al. 1977): *Gonglyonema spp., Trichostrongylus axei, Setaria yehi, Capillaria spp.* In India, one adult doe examined had pentastomids (*Liguatula serrata*), an *Oesophagostomum* nematode, and the *Paramphistomum cauliorchus* trematode (Schaller 1967). Until recently, *Echinococcus granulosus* was the only cestode parasite reported from India (Nama 1990).

Among Ectoparasites, Schaller (1967) documented *Boophilus microplus* and *Hyalomma marginatum isaaci* in India and noted that *Hyalomma brevipunctata* was recorded on axis deer from Bengal. In Texas, axis deer were found with only *Amblyoma americanum* ticks despite the presence of large numbers of *A. maculatum* in the area (Robinson, Galvin et al. 1977). The only ectoparasite documented in Hawaii is a biting louse (*Bovicola* spp.) (Kramer 1971). Internally, deer in Hawaii are documented with a trichostrongylid worm (*Cooperia punctata*) and liver flukes have been reported from the wetter forests of Molokai (Kramer 1971).

In India, *A. axis* is susceptible to rinderpest (Schaller 1967) and its role in significant reductions of axis deer populations in Uttar Pradesh has been documented (Schaller 1967). The only other disease that has led to significant reductions in deer populations (in both India and Texas) is malignant catarrhal fever (Clark, Robinson et al. 1970; Clark, Robinson et al. 1972). On Point Reyes, California introduced axis deer have been documented with Johne's disease and paratuberculosis (Rieman, Ruppanner et al.

1979). In Texas, all four axis given a serologic test for *Anaplasma marginale* tested positive, though none showed symptoms of the disease (Mungall and Sheffield 1994).

Behavior

Axis deer do not defend specific territories (Nowak 1999). Instead, males wander widely in search of females during the rut (Ables 1977, Nowak 1999) and only occasionally defend specific females (Nowak 1999). Axis deer inhabit a small home range (Dinerstein 1979; Moe and Wegge 1994), but Tak and Lamba (1981) documented composite home ranges (minimum convex polygon, hereafter MCP) in Dhikala, India of 18 to 19 km^2. In several locations (India, Maui, Nepal), axis deer were sighted within a location for a period of weeks or months before shifting entirely to a new area up to several kilometers distant (Schaller 1967; Bhat and Rawat 1995). The limited home range data available for *A. axis* appears in Table XII.

Table XII: Home range comparison for *A. axis*

Author	Location	Sex	Home Range
(Moe and Wegge 1994)	Nepal	Male	183
(Moe and Wegge 1994)	Nepal	Female	135
(Mishra 1982)	Nepal	Male	280
(Mishra 1982)	Nepal	Female	236
(Schaller 1967)	India	Male	600
(Ables 1977)	Texas	All	648
(Anderson 2003)	Maui. HI	Male	1385
(Anderson 2003)	Maui. HI	Female	1345

Table XII summarizes home range findings for axis deer worldwide. Minimum Convex Polygon (MCP) data are shown, in hectares (Ha).

In native habitats, a peak in rutting activity occurs from spring into summer, followed by a peak in pregnant females in October and November (Tak and Lamba 1984). The same seasonality is found in Hawaii (Graf and Nichols 1967) and Texas (Ables 1977), with births occurring from December into April. Despite significant variation in antler casting by bucks worldwide, the peak birthing season remains quite consistent (Figure 28), from December to February (Mishra 1982; Moe and Wegge 1994). Worldwide, the shedding of antlers is most common from September to December (Schaller 1967, Anderson 2003).

A. axis exhibits variation in rut timing and duration based on geographic location, even over small geographic areas. An asynchrony in timing of the rut between central India and southern Nepal is evident (Schaller 1967). In the month of February, one-third more bucks were in hard antler at Kanha National Park (40%) than at Corbett National Park (10%) in the Himalayan foothills. The same was also true just 90 km north of Kanha, in Keoladeo Ghana sanctuary. There, 17% were in hard antler versus 47% in Kanha. In the Himalayan foothills (Corbett National Park) bucks retained their antlers into late November, while in central India, *A. axis* cast their antlers by late September (Schaller 1967). On Maui, the majority of antlers are retained into December (Anderson 2003), while in Queensland, Australia *A. axis* shed their antlers in July and August roughly 6 months out of phase with the Northern hemisphere (Bentley 1967).

Axis deer are polygynous, and males do not defend a harem or territory (Miura 1981). The rut in *A. axis* is most readily identified by the peak occurrence of hard antlers (Schaller 1967). Immediately upon shedding of velvet axis deer begin to demonstrate agonistic behavior, coinciding with a testosterone peak (Schaller 1967). At this time, bucks also begin to 'signpost' areas in their range by rubbing the ground bare of vegetation under trees (Graf and Nichols 1967; Schaller 1967; Fuchs 1977). There is no evidence of specific rank order among free-ranging does (Schaller 1967).

During the rut, large groups of mixed sex and age classes form (Mishra 1982), and there is an increase in agonistic male-male interactions(Schaller 1967; Fuchs 1977) . As with most cervidae, bucks face off against other bucks for dominance during the rut. When direct challenges occur, bouts rarely last more than one minute (Schaller 1967). Evidently the 'display' value of antlers in *A. axis* is particularly significant, since the loss of antlers at the end of the rut instantaneously causes a male to lose all rank (Schaller 1967). There is also evidence that larger antlered deer might purposely 'pick fights' with smaller counterparts to demonstrate rank, since 77 percent of fight initiators went on to 'win' (Schaller 1967). In Texas, more than half of all challenges resulting in sparring (n=256) occurred between young animals with 39-48 cm antlers (Ables and Fuchs 1977).

When bucks face off, one approaches the other in a stiff-legged walk, with his head erect and ears laid back. He then adopts a position parallel to, but facing the other buck. Up to eight animals may interact at one time, and there is rarely physical use of antlers in a direct attempt to wound (Schaller 1967), though injuries resulting in death do occur (Ables and Fuchs 1977). More commonly, the process amounts to a visual sizing up process (Schaller 1967). Prior to or during the encounter, bucks frequently engage in redirected aggression by thrashing at vegetation (Schaller 1967). Fuchs (1977) presents a more detailed description of axis deer sparring & mating behavior in Texas.

In *A. axis*, as in many cervinae, the largest bucks are responsible for the majority of copulations. In Nepal, 54.5% of copulations went to bucks with antlers >60 cm

(Mishra and Wemmer 1987). In Texas, the largest axis bucks were responsible for 82% of all copulations (Fuchs 1977). Dinerstein (1980) hypothesized that actual mating in axis occurs at night or in thick brush, based on the rarity with which he observed actual copulations. Females may rebuff several male advances (Barrette 1987) by slowly walking away on approach. When ready, a receptive doe will indicate this by urinating and bobbing her tail as the buck sniffs and exhibits a flehmen response (Graf & Nichols 1967).

In many introduced locations, owing primarily to benign environments, *A. axis* face little consequence to breeding out of 'season'. In the absence of strong selective pressure against this, a cycle of aseasonality can develop. Male fawns born in July will be found in hard 'spike' antler condition and ready to mate roughly 18 months later in February, during the peak fawning season. With axis deer in breeding condition year-round, February copulations yield fawns in September or October when the majority of does are pregnant (Graf and Nichols 1967; Anderson 2003). On Maui, hard antlered bucks were frequently encountered out of season. A summary of breeding and fawning patterns worldwide is presented as Figure 28.

Axis deer are considered amongst the most vocal of all the cervidae. A ubiquitous alarm call, sounding like the sharp yelp of a small dog is a very effective predator defense mechanism in this species. The most frequent vocalizations, aside from the alarm call, are the yips and squeals made back and forth between does and fawns. These frequent vocalizations may help to maintain contact in thick brush (Schaller 1967). The deer also emit a nasal toned 'bleat' (Schaller 1967). Young fawns will also emit a jarring shriek if captured or handled. It is said that this call will bring does in the vicinity running to investigate the alarm (Graf & Nichols 1967).

Buck bellows are most common during the rut period (Schaller 1967), and are emitted in bouts of 1 to 11 elements with 3 to 5 being most common (Mishra and Wemmer 1987). The largest bucks call most frequently, with 76% of all bellows belonging to bucks with antlers >75 cm (Fuchs 1977). In India, large bucks (antler length >80 cm) are responsible for more than 95% of male vocalizations (Schaller 1967). In India, buck bellowing is most frequent from March to June, corresponding with the peak of the rut (Schaller 1967). In Nepal, bellows were rarely heard from August to January (Dinerstein 1980) and they are rare in Texas from September to April (Fuchs 1977). Two distinct tones distinguish males in the largest antler size class from those with smaller antlers (Dinerstein 1980). The largest bucks emit the deepest tones and call more frequently than others (Schaller 1967; Dinerstein 1980).

Axis deer are good swimmers (Schaller 1967), and they frequently swim among islands and spits of land in the Sunderbans of India (Lydekker 1898). Numerous anecdotal reports document axis deer swimming in the ocean off Maui, Molokai and Lanai.

Behaviorally, axis deer become extremely wary under continued harassment (Graf and Nichols 1967; Ables 1977; Waring 1996; Anderson 2003) and this can act to disrupt their natural social patterns (Graf and Nichols 1967; Anderson 2003). Axis deer are also capable of quick adaptive behavioral responses, such as becoming nocturnal (Anderson 2003; Nowak 1999), identifying spotlights with poachers (Anderson 2003) and habituating quickly to a wide array of scaring stimuli (Graf and Nichols 1967; Dinerstein 1979).

Genetics and Hybridization

Axis deer have 66 diploid chromosomes and an acrocentric X chromosome. They have 4 metacentric and submetacentric autosomes, with 60 acrocentric autosomes and 68 autosome arms (Groves & Grubb 1987). Since the primitive karyotype of cervids is 2N=70 chromosomes (as in *Mazama gouazoubira*) (Neitzel 1982), it is thought that there has been one Robertsonian fusion and a subsequent chromosomal fusion in *A. axis* (Groves & Grubb 1987). Morphological evidence indicates that this may be a derived fusion (Groves and Grubb 1987).

A. axis hybridizes in the wild with its congener *A. porcinus* (Mishra 1982). These two species also interbreed in captivity (Pocock 1943; Crandall 1964), and fertle offspring have been backcrossed to *A. axis* (Mungall and Sheffield 1994). Natural hybridization between *A. axis* and *C. nippon* has also been reported (Asher, Gallagher et al. 1999). *A. axis* has been successfully cross-bred on Texas game ranches as follows: *A. axis* x *C. duvaceli*, *A. axis* x *C. elaphus*, *A. axis* x *O. virginianus*. *A. axis* also hybridizes with *C.c. xanthopygus* (Whitehead 1972).

Remarks

A. axis has the potential to serve as a vital umbrella species in south Asian habitats, since preferred habitat for axis deer is also favored by a number of critically endangered Asian mammals. In India, these include the tiger (*Panthera tigris*), swamp deer (*Cervus duvaceli*), and one-horned rhinoceros (*Rhinoceros unicornis*) (Dinerstein 1980). The taxonomic classification of *A. axis* has also been based largely on phenotypic traits that are notoriously changeable among the cervidae (Groves and Grubb 1987). Clinal variation, artificial selection, and translocation have led to numerous forms of the same species (Groves & Grubb 1987). Caution is urged in interpretation, where phenotypic or antler characteristics have been heavily relied on (Janis and Scott 1987).

Figure 1: Geographic Isolation of the Hawaiian Islands

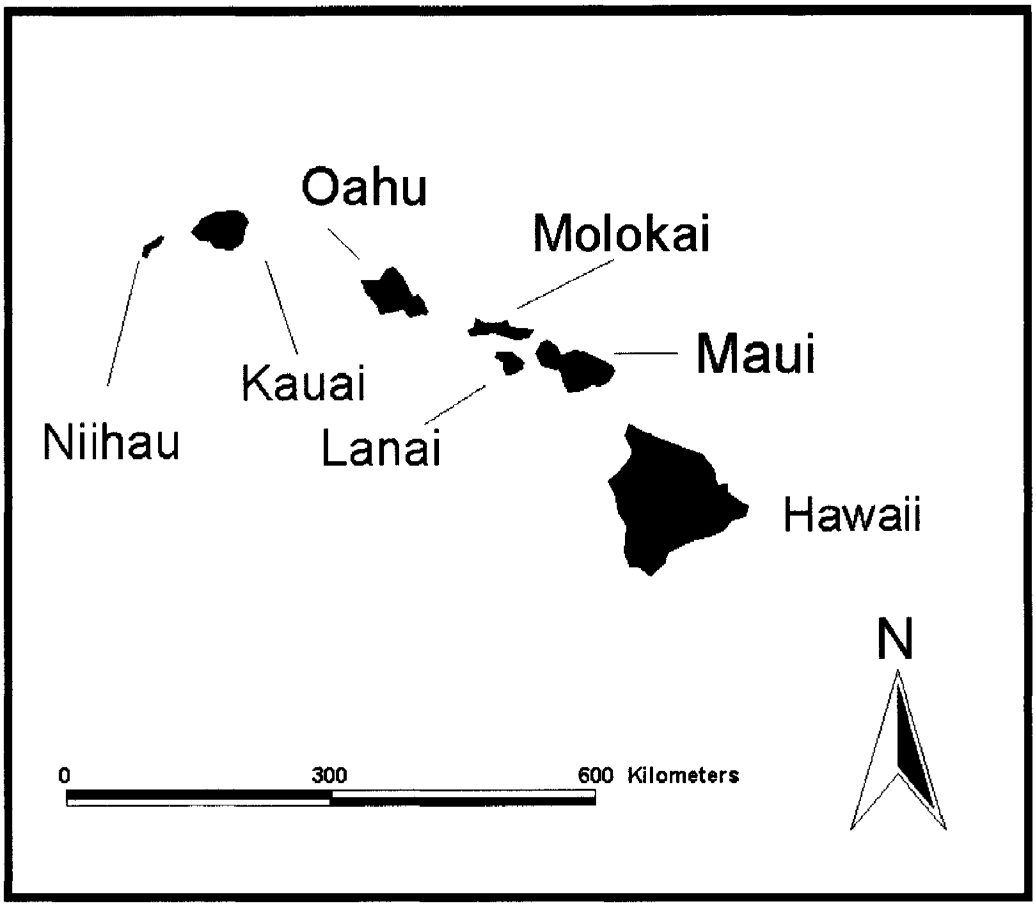


Figure 2: The Main Hawaiian Islands

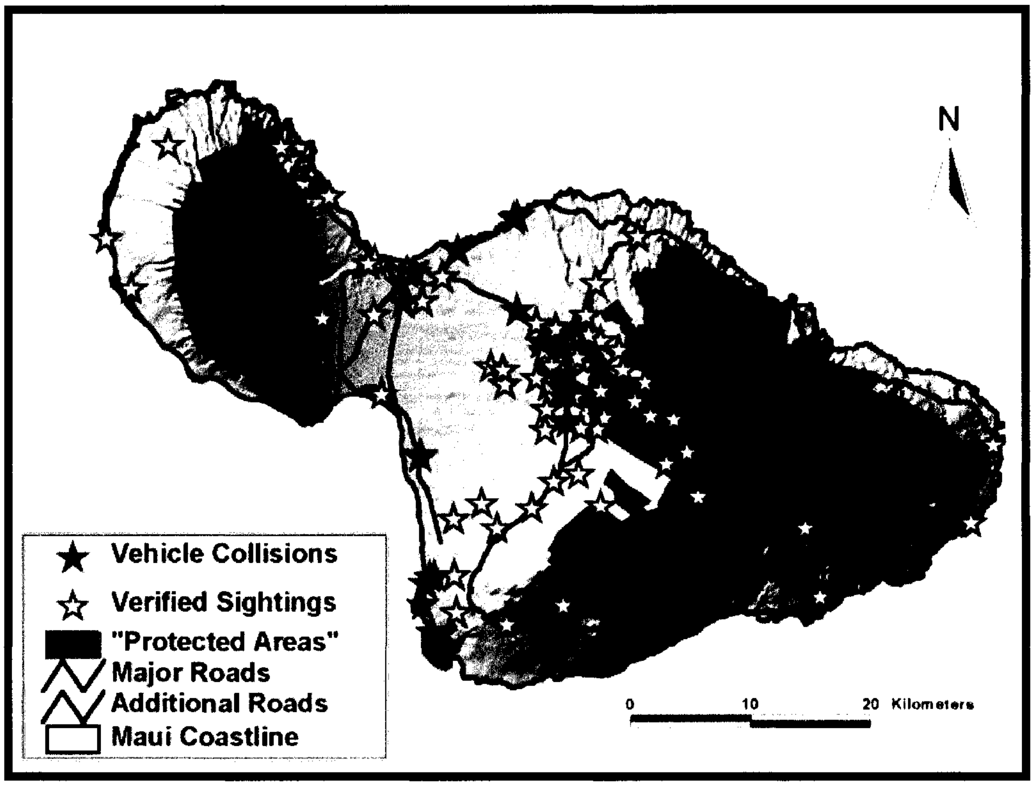


Figure 3: Documented Deer Distribution on Maui

(June, 2000)

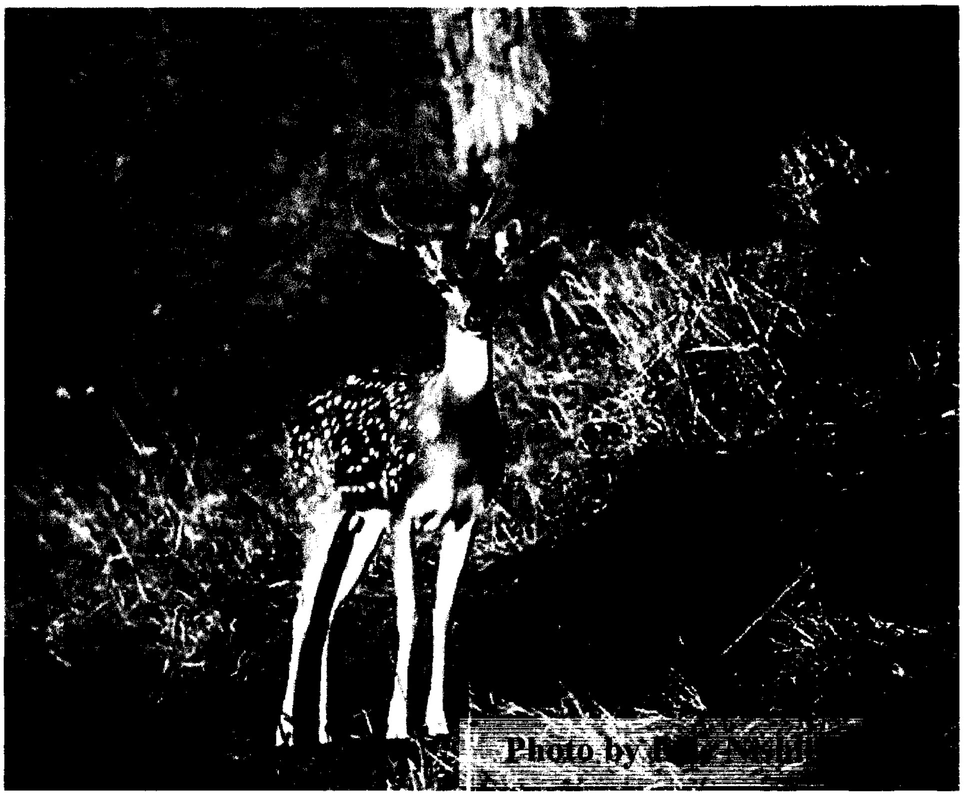


Figure 4: Young Male Axis Deer in Velvet Antler

Figure 5: Adult Male Axis Deer in Hard Antler

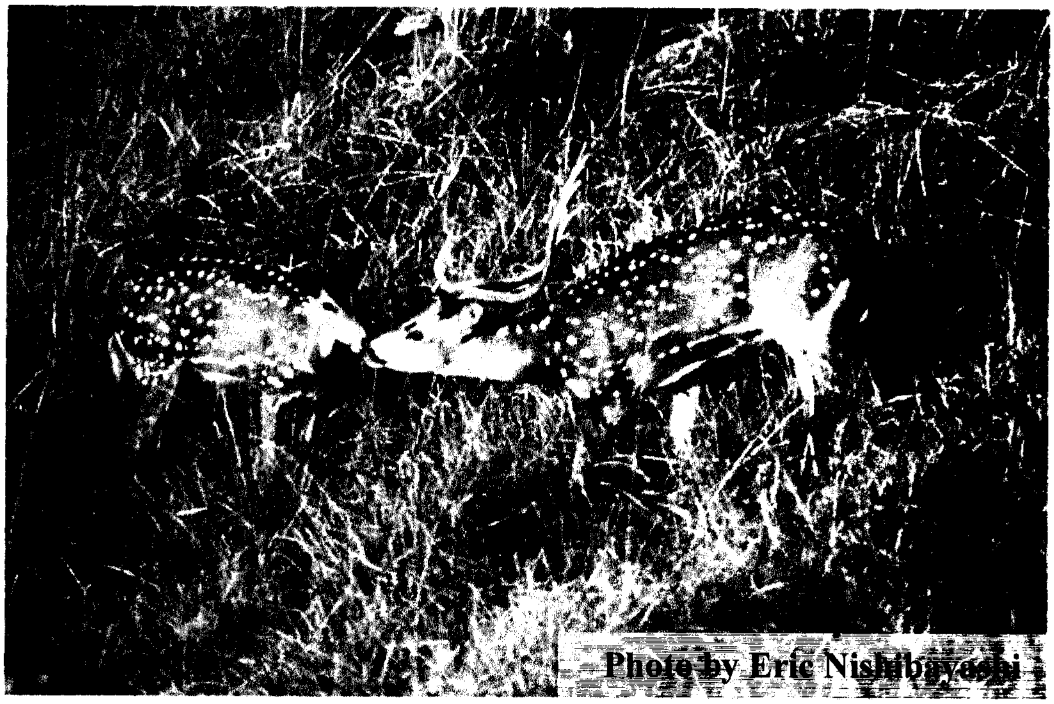


Figure 6: Axis Deer Male vs. Female

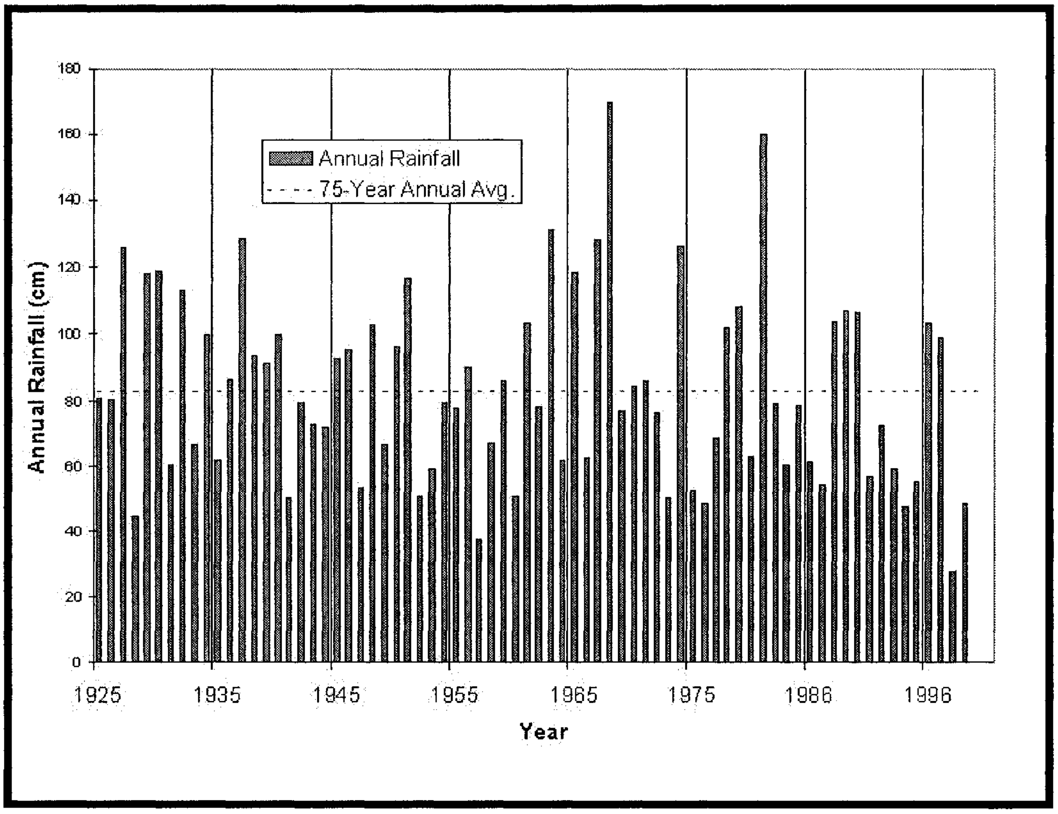


Figure 7: 75-year Rainfall for Region of Deer Introduction

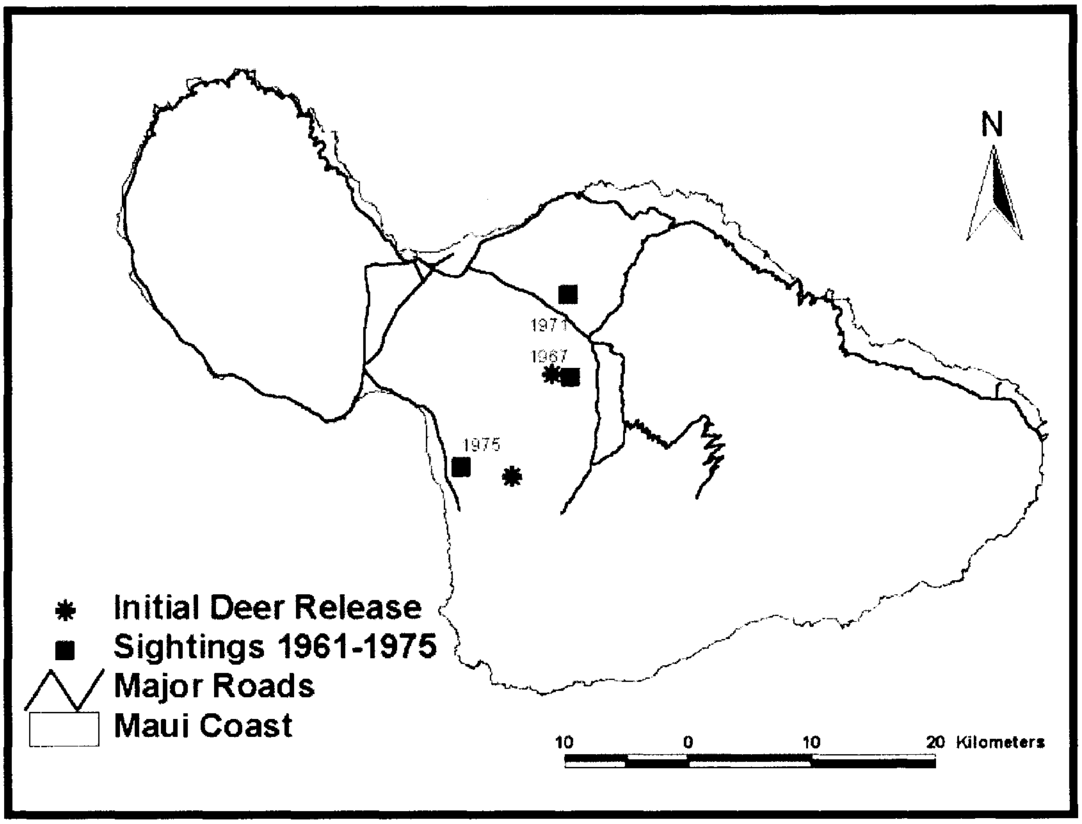


Figure 8: Verified Axis Deer Sightings, 1961-75

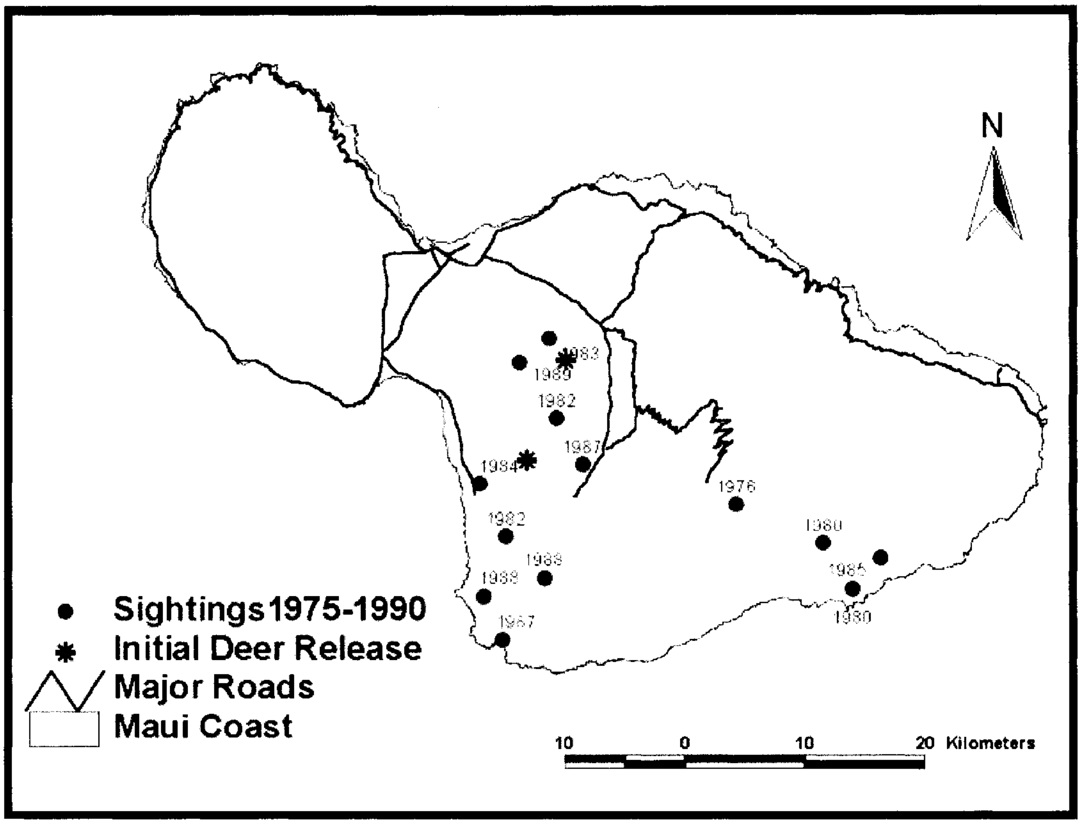


Figure 9: Verified Axis Deer Sightings, 1975-90

Figure 10: Overview of Regional Deer Management

Regional estimates of deer populations on the Eastern half of Maui through May, 2000. Hatched areas represent regional population estimates for deer on Maui. **Green** shading indicates where deer are rare or sparsely distributed, with no documented sightings of herds numbering more than 25 animals. **Yellow** shading indicates where deer number in the hundreds, with several verified sightings of herds numbering more than 25 animals. **Red** shading indicates areas where deer number in the thousands, with frequent sightings of groups numbering 50 or more. **Solid green** represents natural areas, under protective management. Data are based on a combination of local census work, hotline sightings and regional habitat characteristics.

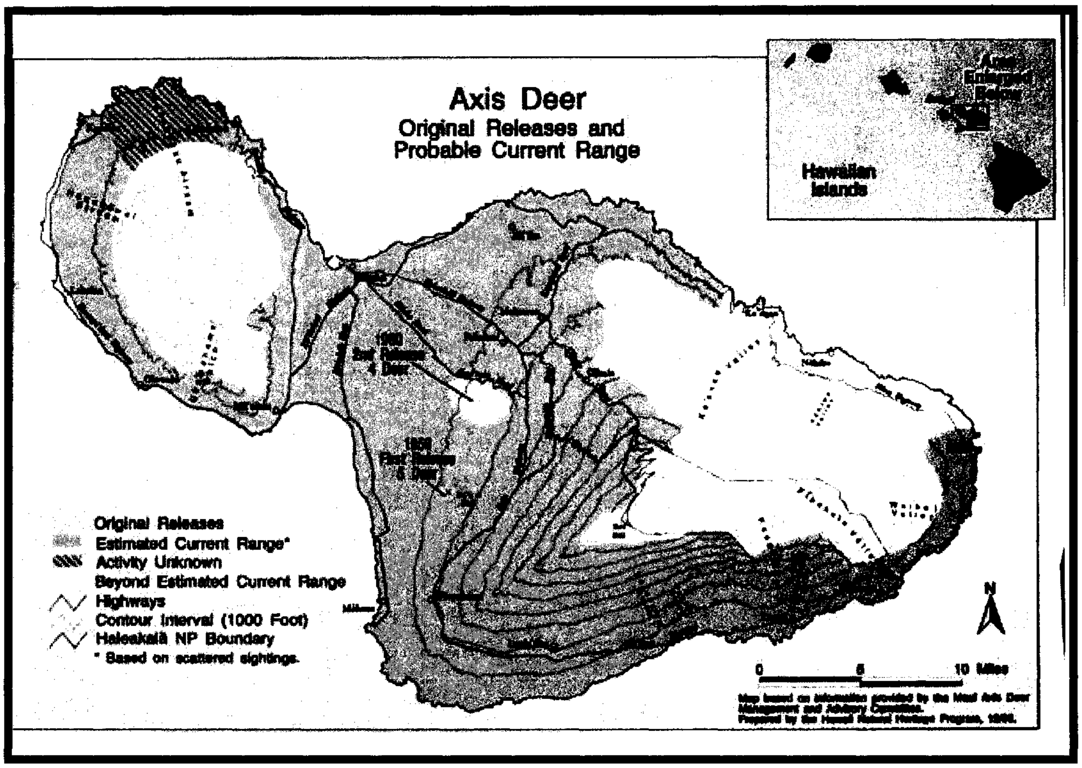
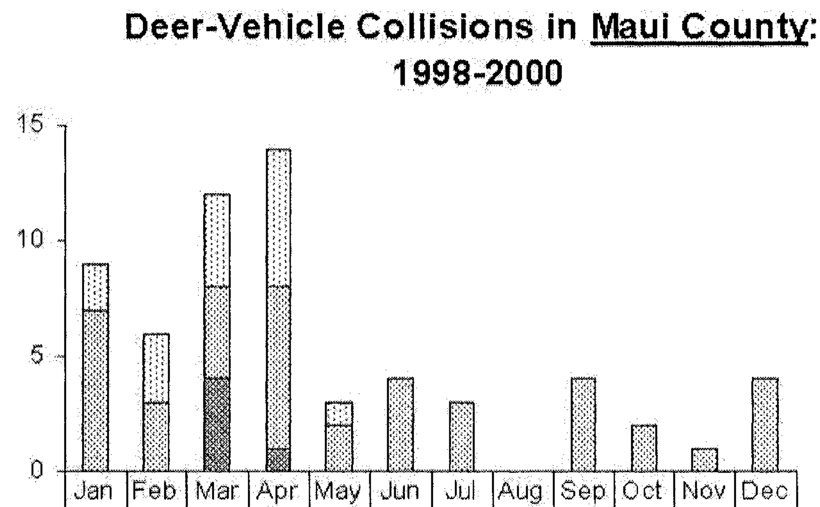


Figure 11: Map of Predicted Axis Deer Habitat on Maui

This map, based solely on habitat characteristics and knowledge of where axis deer currently occur, indicates where deer are thought to be most capable of establishing breeding populations on Maui. Map provided by the Maui office of The Nature Conservancy.



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2000	2	3	4	6	1							
1999	7	3	4	7	2	4	3	0	4	2	1	4
[1998]	0	0	4	1	0							

Month

Figure 12: Deer-Vehicle Collision Data for Maui County

Maui County (Maui, Molokai, and Lanai) deer vehicle collision data through May 2000, compiled from police records, State Department of Land and Natural Resources (DLNR) salvage data, and hotline information. Data represent the minimum number of collisions recorded for Maui County, as there are few records of deer collisions prior to 1999, and DLNR files are incomplete for 1998.

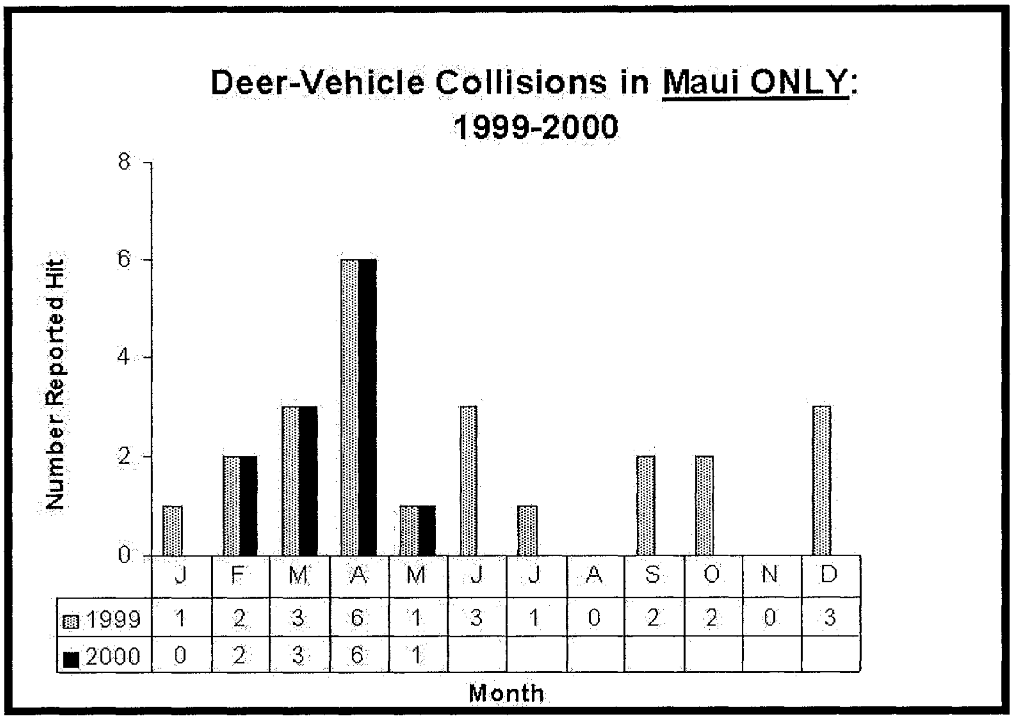


Figure 13: Deer-Vehicle Collision Data for Maui

Maui deer vehicle collision data through May 2000, compiled from police records, State Department of Land and Natural Resources (DLNR) salvage data, and hotline information. There are no official records of deer vehicle collisions on Maui prior to 1999.

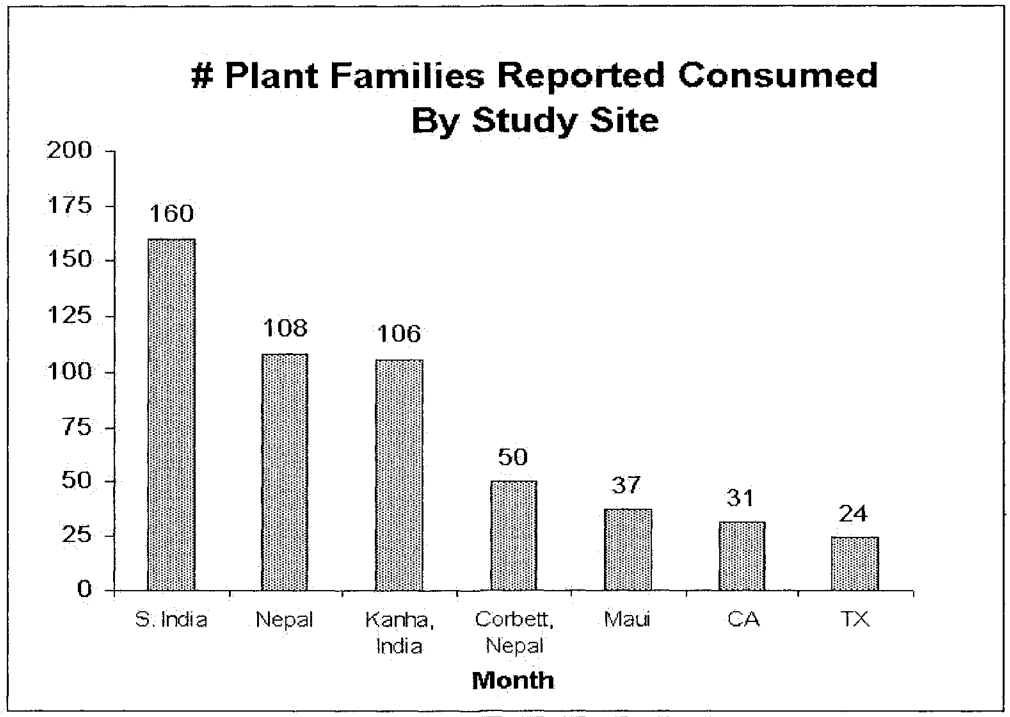


Figure 14: Plant Families Consumed by Study Site

Data on axis deer foraging preferences are compiled from a number of published studies (Graf and Nichols 1967; Schaller 1967; Smith 1977; Dinerstein 1979; Johnsingh 1981; Mishra 1982; Elliott 1983; Elliott and Barrett 1986)

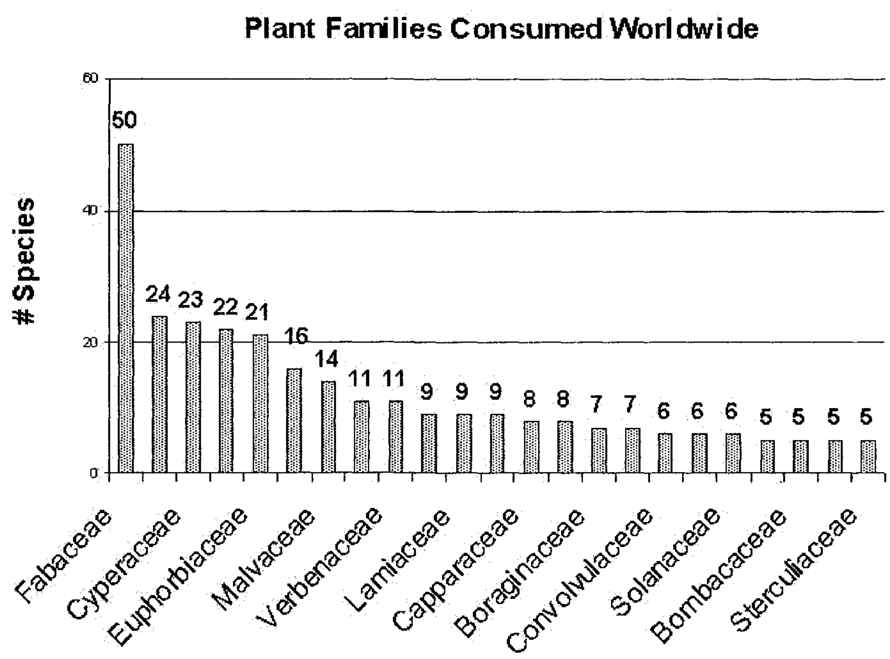


Figure 15: Major Plant Families Consumed (by # Species)

Data on axis deer foraging preferences are compiled from a number of published studies (Graf and Nichols 1967; Schaller 1967; Smith 1977; Dinerstein 1979; Johnsingh 1981; Mishra 1982; Elliott 1983; Elliott and Barrett 1986). *Poaceae* led the list with 104 species, and has been excluded from this chart.

Figure 16: Damage from Deer 'Trailing' Behavior

Figure 17: Seasonal Damage from Axis Deer Antler Rubs

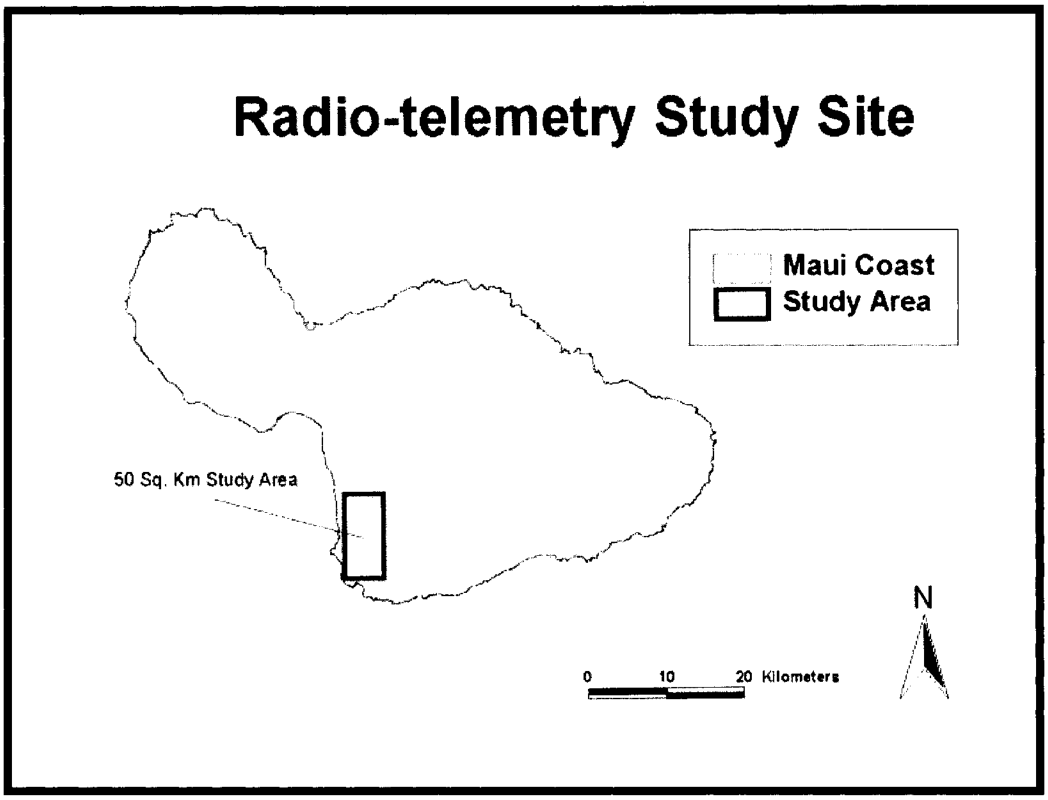


Figure 18: Study Site Location

Radio-telemetry work was conducted on actively grazed ranchlands throughout the western slope of Haleakala, at elevations ranging from sea level to ca. 800m.

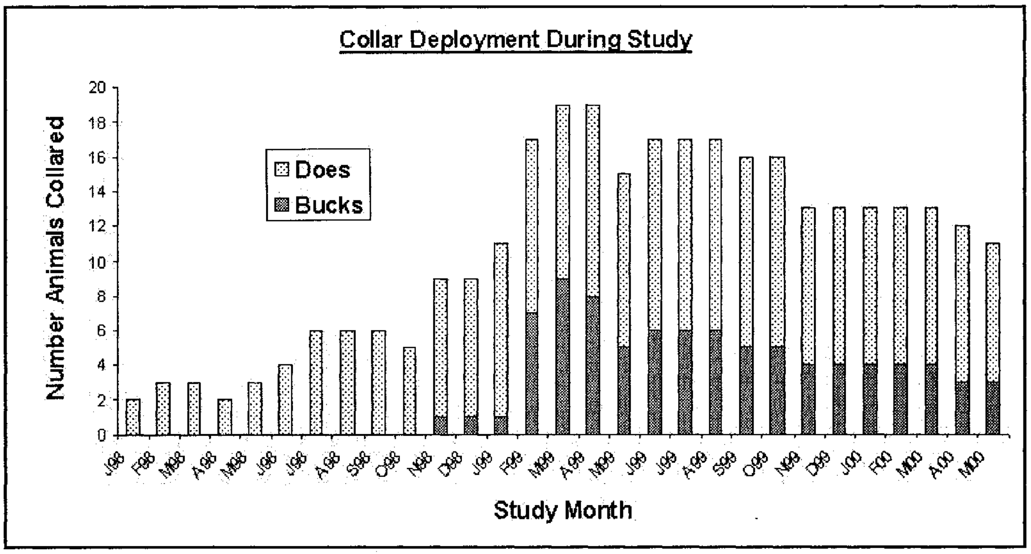


Figure 19: Radio-collar Deployment

Continual efforts were made to radio-collar adult animals throughout the first 13 months of the study. In February 1999, owing to decreasing effectiveness of collaring procedures (see text) and increasing poaching of radio-collared animals, a helicopter was used to boost sample sizes. A minimum of ten animals wore collars simultaneously during the latter 16 months of the study.

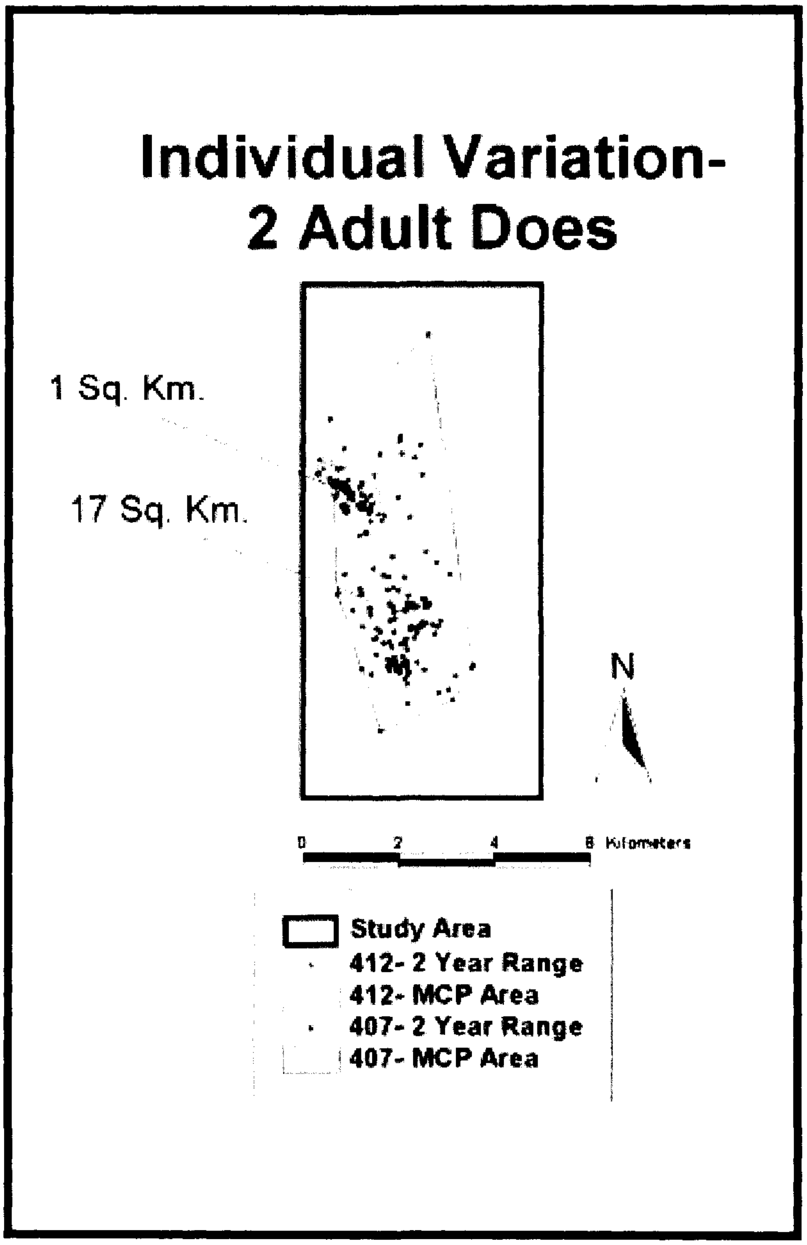


Figure 20: Variation Among Individual Females

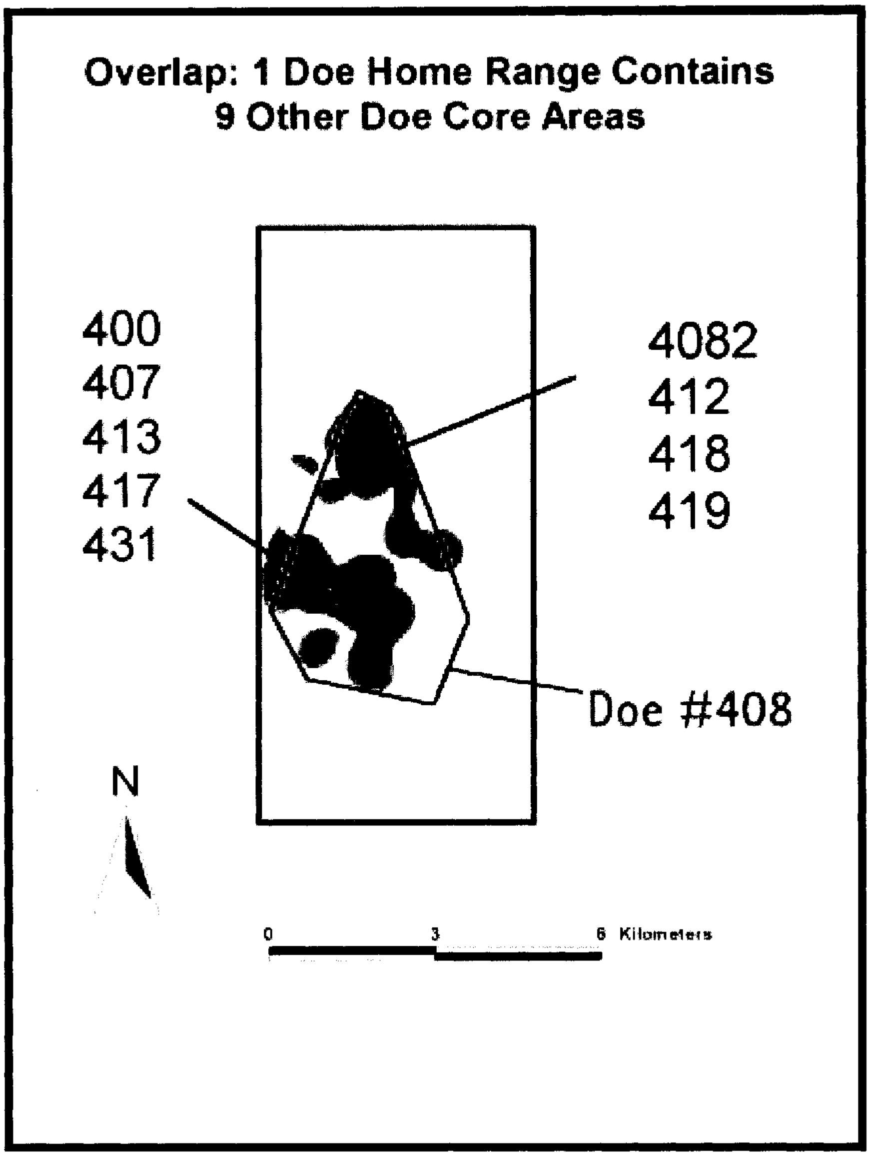
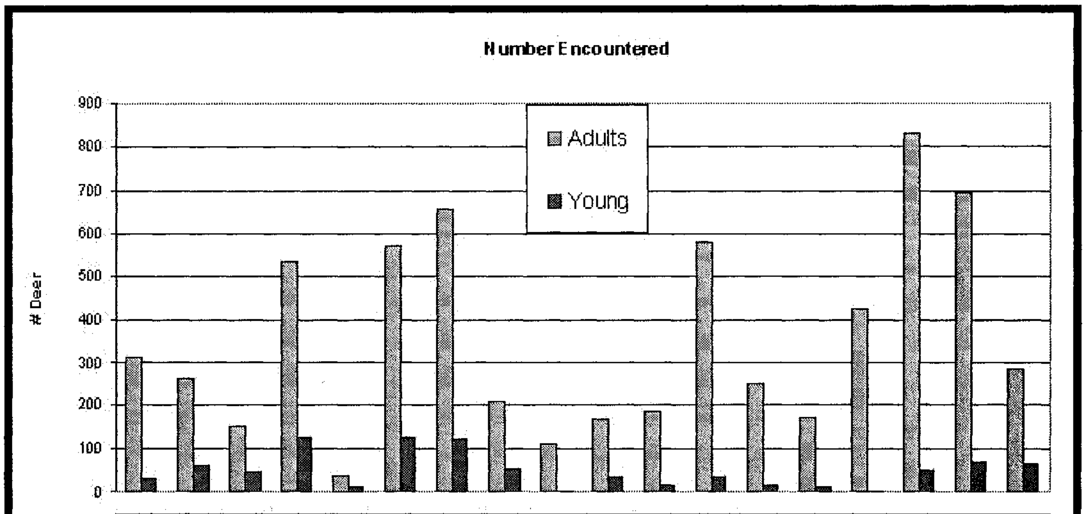


Figure 21: Overlap Among Adult Females



	Nov98	Dec-98	Jan-99	Feb-99	Mar-99	Apr-99	May99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	Nov99	Dec-99	Jan-00	Feb-00	Mar-00	Apr-00
Adults	310	261	153	536	40	572	656	209	112	168	184	581	252	171	423	832	694	285
Young	31	63	45	124	12	126	121	54	4	34	15	36	17	14	4	51	70	65

Figure 22: Total Number of Deer Encountered

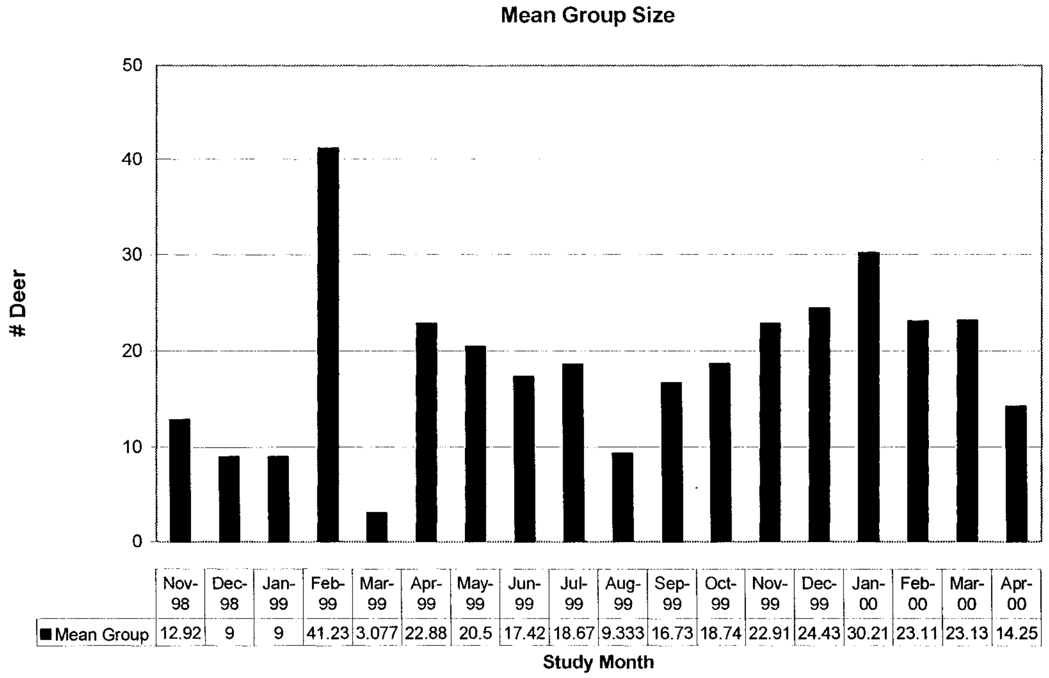


Figure 23: Mean Group Size Encountered

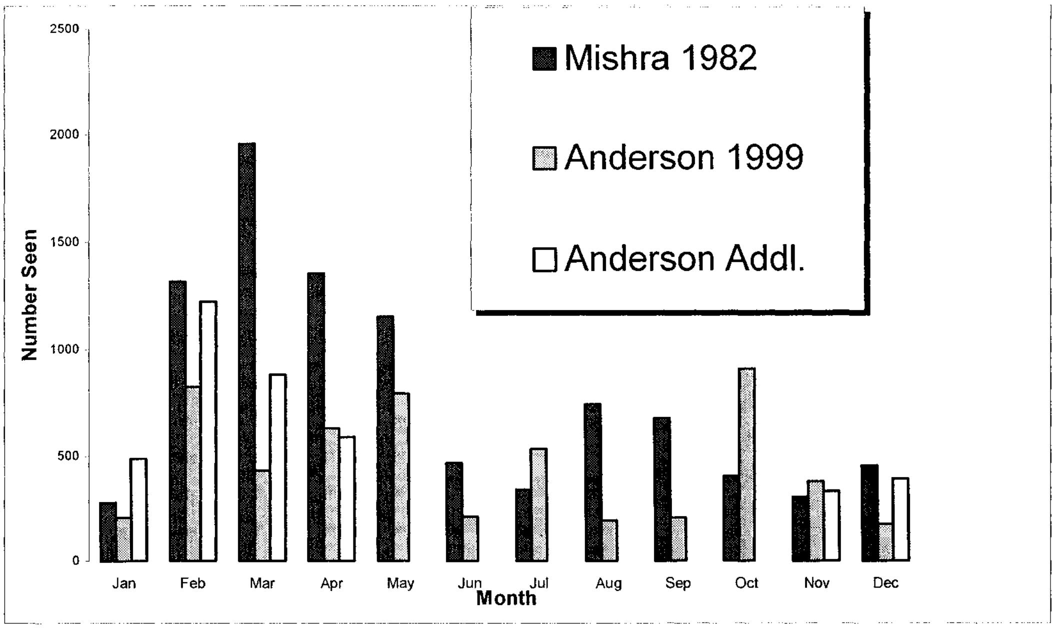


Figure 24: Total Number Seen by Month, Maui vs. Nepal

Additional data from Anderson includes the following months' observations: November and December 1998, January through April 2000.

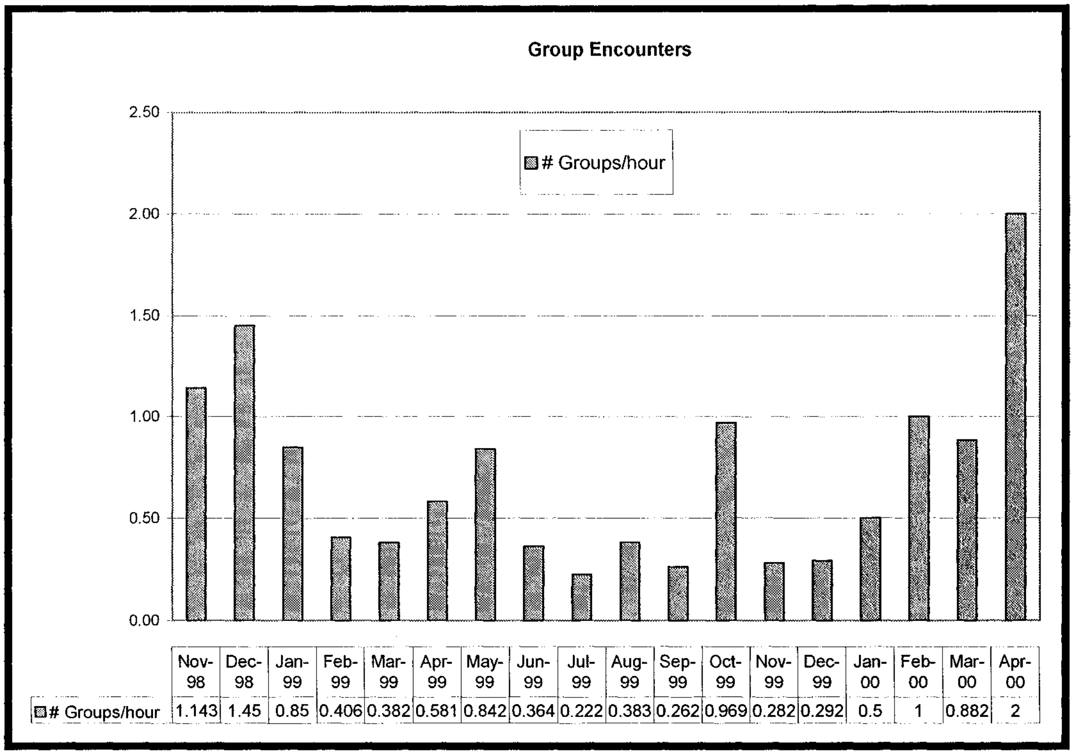


Figure 25: Number of Groups Encountered per hour

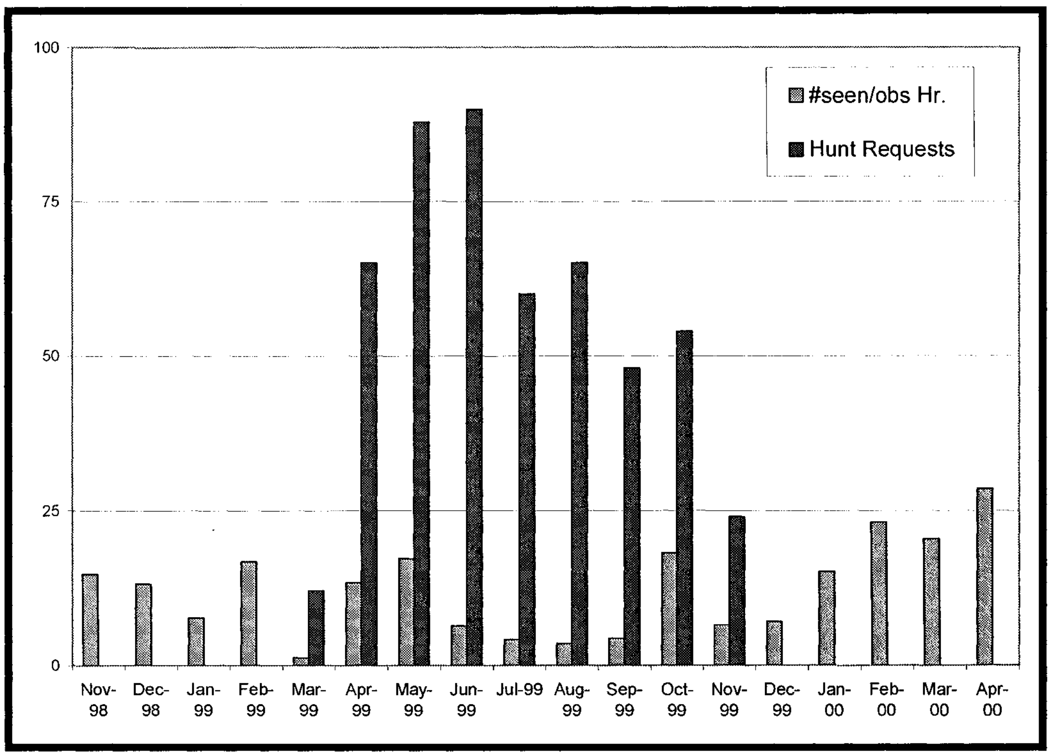
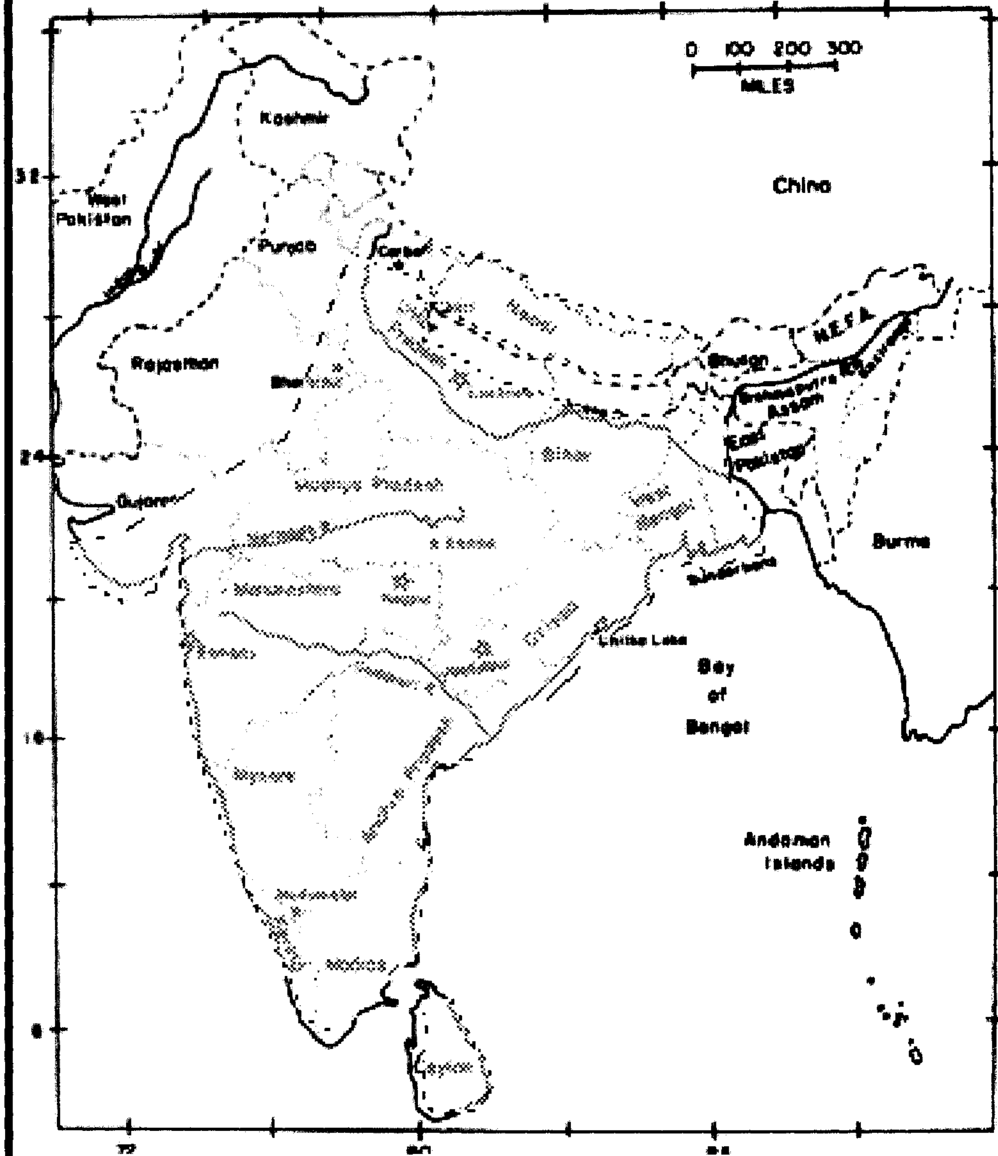


Figure 26: Relationship Between Hunting Requests and Deer Encounters



Background map of India from Schaller 1967

Figure 27: Native Range of *Axis axis*

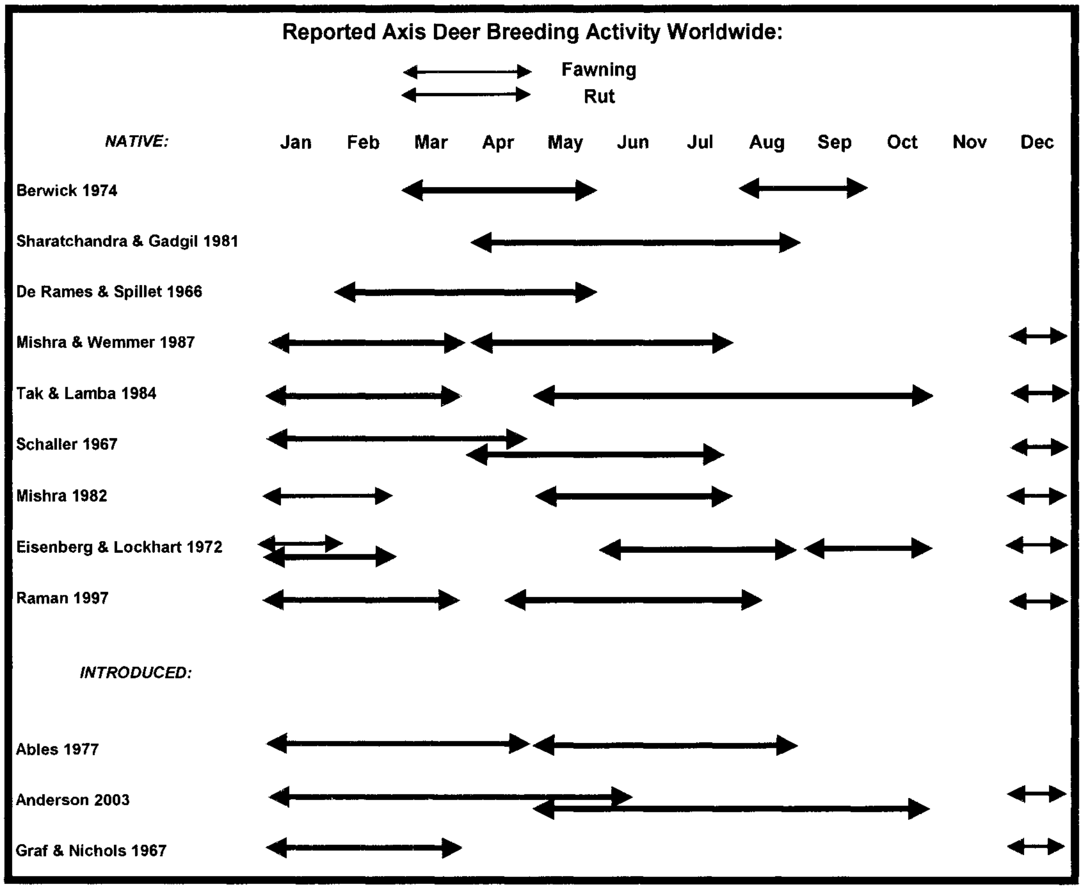


Figure 28: Worldwide Breeding and Fawning Data

Appendix I: Axis Deer in Hawaii

History

The most complete source of information regarding the history of axis deer in Hawaii is the discussion Quentin Tomich presents in Mammals in Hawaii (1986). Tomich spent years researching historical newspaper articles and the literature in an effort to accurately recount the deer's history in the Hawaiian Islands. He sought documented historical evidence of claims made. He also served as the Animal Ecologist for Hawaii's Department of Health for more than 25 years, and was therefore involved in many issues relating to exotic species introductions. The result is the most accurate account available.

According to Tomich (1986) the axis deer first arrived in Hawaii in December, 1867 on a ship from Hong Kong as a gift to King Kamehameha V. After a brief holdover in Honolulu, 8 deer (3 bucks, 4 does, 1 male fawn) were released on the King's grounds on Molokai in January 1868. Tomich also cites a newspaper article stating that within 20 years, the Molokai herd had reached 1000 animals. Slightly more than 30 years after their initial introduction to Molokai, he quotes (Sabin 1934) with saying, "At the end of the century they had become so numerous that experienced hunters were engaged to dispose of a considerable proportion. These hunters were from California, remained in the islands for about a year, killing nearly 3000 deer." Tomich states that (Cooke 1949) listed the number killed as 3500-4000. Graf & Nichols (1967) noted the years of these culling operations as 1900-01. A research report compiled by the USFWS (Swedberg and Walker 1978) cites (Lennox 1950) with a population estimate on Molokai for 1898 of 6-7000 animals. A former manager of Molokai Ranch (George Cooke) lists 4500 as his minimum estimate of the number removed by this action, as does Lyon (1950). The table below summarizes what is known about the axis deer's history throughout Hawaii.

Axis Deer History in Hawaii

(Data from Tomich 1986; Waring 1996; Kramer 1977)

Molokai

1868	8 deer released: 3 bucks, 4 does, and 1 male fawn.
1888	1000 deer estimated on the island.
1900	7000 deer estimated on the island.
1901-02	Hired hunters kill a minimum of 3500 deer.
1958	1500 deer estimated on the island. A "few" on the Kalaupapa Peninsula.
1961	3000 deer estimated on the island.
1999	Nearly 2000 deer on Kalaupapa Peninsula alone.
2000	Roughly 4-5000 deer estimated on the island.

Oahu

1870	Several Molokai deer transferred to Oahu.
1898	Herd "well-established" at Diamond Head.
1910	Escaped deer establish in Moanalua Valley.
1938	Peak of herd at Moanalua Valley (no estimate given)
1950	Deer "scarce" on Oahu at this time.
1962	Very few deer left on Oahu. Estimated 25 or fewer.
1971	One report of deer, none since.

Lanai

1920	12 deer transferred from Molokai to Lanai
1958	700-800 deer estimated on the island.
1961 1962	1500-2000 deer estimated on the island (1675 reported).
2000	More than 2000 deer estimated on the island.

Maui

1959	5 deer released at Pu'u o' Kali: 2 bucks, 3 does.
1960	4 additional deer released at Ka'onoulu Ranch.
1968	90 deer estimated on the island.
1995	3000-4500 deer estimated on the island.
1997-2000	At least 1500 deer removed by hunting, poaching and management.
2000	2000-4000 deer estimated on the island.

Hawaii

1950s-1970s	Extensive debates over Axis deer introduction: no deer officially released.
2000	Rumors of deer persist, but remain unconfirmed.

Debates Over Translocation to Other Islands

The axis deer originally arrived for hunting on the King's grounds. However, once established on Molokai, other islands in the chain began to consider their introduction. This fueled a long history of debates in Hawaii over the introduction of axis deer to additional islands (AAUW 1970). Deer were moved to Lanai in 1920 (Kramer 1971). However, from 1950-1975 there were numerous debates over introduction of axis deer to the Big Island and Maui. They never made it to the Big Island, owing principally to the very well-founded objections of ranchers, botanists, and agricultural interests (Tomich 1986). Unfortunately, it is clear today that the negative impacts mentioned by these opponents were understated.

A report prepared by the Kohala Branch of the American Association of University Women (AAUW 1970) distills many of the statements put forward during the later introduction debates (1963-70). They cite R.L. Cushing's letter to Governor Burns (April 23, 1964). He wrote, " it seems apparent that the possibility of serious damage to crops and to natural vegetation is so great that the risk should not be taken...I visited Lanai and saw the damage the deer had caused to growing pineapple plants. It is severe and it is extensive". Specifically regarding crop damage, the AAUW quote Lynn Pendry, the acting manager of the Lanai Plantation, writing to the Head of Hawaii's Division of Fish & Game saying "the deer are again beginning to damage the pineapple on Lanai. Prior to the one inch of rain March 23-26, the deer had damaged approximately $45,000 worth of Pineapple" (Lynn Pendry in a letter to M. Takata May 1, 1964) (AAUW 1970). Concerning damage to native plants, they quote Dr. C.E. Pemberton (in a letter to Dr. Cushing January 20, 1964) (AAUW 1970), saying that "this deer is an omnivorous feeder on vegetation of many sorts and botanists claim that much endemic flora on Molokai has been destroyed". They also cite Dr Walter Howard of UC Davis (in a letter to Dr. Cushing March 16, 1964) (AAUW 1970). He wrote that "wherever deer have become established, there has been an irreversible change in the species composition of vegetation". Dr. Quentin Tomich also noted (in an open letter of 4/8/70) "our environmental concern demands that the deer not be introduced. Once here, they would only be another factor in destroying the ecological balance of our environment (AAUW 1970)."

Additional insightful concerns were voiced regarding axis deer translocation. Many foreshadow precisely the kinds of problems that the axis deer currently present on Maui. Robert Nelson, the director of the Institute of Pacific Islands Forestry, wrote (in a letter to Mrs. Banks April 16, 1970) that "entire vegetation types might be destroyed. Since hunting is not allowed in National Parks, excluding or controlling deer could be a problem. Control of deer on private lands may offer many difficult kinds of problems" (AAUW 1970). Dr. C.E. Pemberton notes two additional issues (in a letter to Dr. Cushing January 20, 1964), "the axis deer is a high jumper and it will not be economically feasible to fence it out…and poachers will invade private lands in their enthusiasm to get a deer. Molokai Ranch has much trouble with hunters breaking fences or gates to get at the deer at night (AAUW 1970)." Finally, P.D. Hooten a member of the Highway Safety Committee noted that "pigs are a problem on highways…why add another animal?" (AAUW 1970).

The translocation debates were serious and somewhat high-profile. Very early on, the American Society of Mammalogists drafted a statement on the issue at their meeting (July 25-28, 1950- Yellowstone, WY) and it passed unanimously:

> *"Be it resolved: that the American Society of Mammalogists expresses its strong disapproval of the plan of the local Territorial Board of Agriculture and Forestry to introduce axis deer to the island of Hawaii. If deer are introduced, their reproduction and increase will not stop until checked by starvation. That, unfortunately, would come only after much of the island's unique vegetation has been badly depleted or destroyed by deer. Disaster to the island would include the Hawaii Section of Hawaii National Park. The local Board is urged to consider the danger and folly of such an introduction and rescind the vote it has taken favoring the plan."*

Unfortunately, all of the concerns expressed over these two decades of debate have now come to fruition. Each warning foreshadowed problems with axis deer that are commonplace on Maui today. Recognizing the truth of this 50-year old statement, and witnessing deer damage for themselves, a number of landowners, agencies and farmers and concerned citizens formed the Maui Axis Deer Group (MADG) in 1996. This group has since helped to raise money for axis deer research, apprised both Mayor Apana and Mayor Lingle of deer concerns and acted to raise public awareness of axis deer issues on Maui by hosting several public forums.

Appendix II: Summary of Parasites and Diseases in Axis Deer

Affliction	Location	Reference
Tick		
Boophilus microplus	India	Schaller 1967
Hyalomma marginatum isaaci	India	Schaller 1967
Hyalomma brevipunctata	Bengal	Kaiser & Hoogstraal 1964
Amblyoma americanum	Texas, USA	Mungall & Sheffield 1997; Robinson et al. 1977
Nematode		
Gonglyonema spp.	Texas, USA	Mungall & Sheffield 1997; Robinson et al. 1977
Trichostrongylus axei	Texas, USA	Mungall & Sheffield 1997; Robinson et al. 1977
Setaria yehi	Texas, USA	Robinson et al. 1977
Capillaria spp.	Texas, USA	Mungall & Sheffield 1997; Robinson et al. 1977
Oesophagostomum spp.	India	Schaller 1967
Pentastomid		
Liguatula serrata	India	Schaller 1967
Trematode		
Paramphistomum cauliorchus	India	Schaller 1967
Cestode		
Thysanosoma actinoides	Texas, USA	Mungall & Sheffield 1997
Echinococcus granulosis	India	Nama 1990
Worms		
Lungworm	California, USA	unpub. Report Brunetti 1976
Cooperia punctata (trichostrongylid)	Hawaii	Kramer 1977
Hippoboscid Flies		
Lipoptina indica	India	Schaller 1967
Other		
Liver fluke	California, USA; Hawaii, US	unpub. Report Brunetti 1976; Kramer 1977
Biting louse (Bovicola spp.)	Hawaii	Kramer 1977
Ostertagia spp.	Texas, USA	Mungall & Sheffield 1997
Documented Diseases		
Rinderpest	India	Schaller 1967
Bovine tuberculosis	India	Fahimudden 1963
Myxovirus parainfluenza	India	Shah 1965
Malignant catarrhal fever	India; Texas, USA	Clark et al. 1970, 1972
Anthrax	India, Texas, USA	Schaller 1967; Robinson et al. 1977
Salmonella	Texas, USA	Mungall & Sheffield 1994
Clostridia	Texas, USA	Mungall & Sheffield 1994
Cornebacterium	Texas, USA	Mungall & Sheffield 1994
Serologic Profiles (antibodies present)		
Anaplasma marginale	California, USA	Rieman et al. 1979
Bluetongue virus	California, USA	Rieman et al. 1979
Bovine viral diarrhea virus	California, USA	Rieman et al. 1979
Infectious bovine rhinotracheitis virus	California, USA	Rieman et al. 1979
Leptospira interrogans	California, USA	Rieman et al. 1979

Appendix III: Rumen Contents from Lanai

Species	Family	% Rumen Contents	Exotic/Native
Acacia farnesiana	Fabaceae	6	E
Ageratum conyzoides	Asteraceae	<1	E
Atriplex semibaccata	Chenopodiaceae	11	E
Cassia leschenaultiana	Fabaceae	<1	E
Cassia occidentalis	Fabaceae	<1	E
Chloris virgata	Poaceae	<1	E
Desmanthus virgatus	Fabaceae	<1	E
Diospyros sandwicensis	Ebenaceae	2	N
Erythrina monosperma	Fabaceae	<1	N
Eupatorium adenophorum	Asteraceae	<2	E
Euphorbia loriflora [now Chamaecyse]	Euphorbiaceae	<1	N
Heteropogon contortus	Poaceae	<1	N
Hypochaeris glabra	Asteraceae	4	E
Hypochaeris radicata	Asteraceae	<1	E
Lantana camera	Verbenaceae	4	E
Leucaena glauca	Fabaceae	9	E
Melinis minutiflora	Poaceae	9	E
Osmantus sandwicensis	Oleaceae	2	N
Osteomeles anthyllidifolia	Rosaceae	22	N
Panicum maximum	Poaceae	30	E
Panicum torridum	Poaceae	<2	N
Portulaca oleracea	Portulacaceae	<1	E
Prosopis chilensis	Fabaceae	33	E
Rhyncelytrum repens	Poaceae	<1	E
Santalum ellipticum	Santalaceae	<2	N
Sida fallax	Malvaceae	<2	N
Solanum sodomeum	Solanaceae	5	E
Sonchus oleraceus	Asteraceae	<1	E
Styphelia tameiameiae	Epacridaceae	10	N
Verbesina encelioides	Asteraceae	<1	E
Zinnia pauciflora	Asteraceae	<1	E

[Data from Swedberg, 1978]

Appendix IV: Rumen Contents from Molokai

Species	Family	% Rumen Content	Exotic (E) or Native (N)
Acacia farnesiana	Fabaceae	3	E
Ageratum conyzoides	Asteraceae	<2	E
Amaranthus gracilis	Amaranthaceae	<2	E
Atriplex semibaccata	Chenopodiaceae	3	E
Bidens pilosa	Asteraceae	<2	E
Cassia leschenaultiana	Fabaceae	<2	E
Cenchrus echinatus	Poaceae	<2	E
Centella asiatica	Apiaceae	<2	E
Chloris virgata	Poaceae	<2	E
Cyperus polystachyus	Cyperaceae	<2	E
Digiteria sanguinalis	Poaceae	<2	E
Drymaria cordata	Caryophyllaceae	45	E
Eupatorium adenophorum	Asteraceae	<2	E
Fimbristylis diphylla	Cyperaceae	<2	N
Galinsoga parviflora	Asteraceae	<2	E
Gnaphalium luteo-album	Asteraceae	<2	E
Gouldia spp. *[now Hedyotis]*	Rubiaceae	6	N
Heteropogon contortus	Poaceae	8	N
Hypochaeris radicata	Asteraceae	5	E
Indigofera suffruticosa	Fabaceae	<2	E
Jussiaea suffruticosa *[now Oenethera or Ludwigia]*	Onagraceae	2	E
Lantana camera	Verbenaceae	18	E
Leucaena glauca	Fabaceae	4	E
Panicum maximum	Poaceae	5	E
Paspalum conjugatum	Poaceae	39	E
Pennisetum ciliare	Poaceae	<2	E
Phaseolus lathyroides	Fabaceae	<2	E
Portulaca oleracea	Portulacaceae	<2	E
Prosopis chilensis	Fabaceae	33	E
Rhynchelytrum repens	Poaceae	<2	E
Sida fallax	Malvaceae	4	N
Solanum nodiflorum	Solanaceae	<2	E
Solanum sodomeum	Solanaceae	~2	E
Sonchus oleraceus	Asteraceae	<2	E
Stachytarpheta jamaicensis	Verbenaceae	<2	E
Waltheria indica var. americana	Sterculiaceae	<2	N
Xanthium strumarium	Asteraceae	<2	E

[Data from Swedberg 1978]

Appendix V: Axis Deer Management Calendar

January	February	March	April	May	June	July	August	September	October	November	December
	[---------DOE/FAWN HERDS--------]										
	[-----Buck-only groups-----]										
[--------Lethargic, pregnant does---------]											
					PEAK of "bellowing"						
				[---------Buck rutting "bellows" -----------]							
									[-------Majority of does pregnant------]		

October-December: Hunting efforts geared towards does should begin in earnest, before does give birth.

January-February: Does will be heavy pregnant at this time and very sedentary. Sightings in an area are likely to recur there.

March-April: A critical time for management hunting. Does, some pregnant does, and many fawns will form tight herds at this time.

June-July: Buck vocalizations are very common. AM & PM listening likely to reveal buck locations and mixed sex/age herds.

References

AAUW (1970). Should axis deer be released on the island of Hawaii? A compilation of comments on the issue. Honolulu, American Society for University Women, Kohala Branch: 14 pp.

Ables, E. D. (1977). The axis deer in Texas. College Station, The Experiment Station.

Ables, E. D. (1977). Introduction. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 7-23.

Ables, E. D. and E. R. Fuchs (1977). Conclusions. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 79-83.

Amarasekare, P. (1993). "Potential Impact of Mammalian Nest Predators on Endemic Forest Birds of Western Mauna-Kea, Hawaii." Conservation Biology 7(2): 316-324.

Anderson, S. B. (2003). An examination of introduced axis deer (*Axis axis*) in Hawaii. Graduate Group od Ecology. Davis, CA, University of California- Davis.

Anonymous (2000). Report of the Pierce's Disease Research and Emergency Response Task Force: Glassy-Winged Sharpshooter (*Homalodisca coagulata*), University of California Agriculture and Natural Resource News & Information Outreach.

Asdell, S. A. (1964). Patterns of mammalian reproduction. Ithaca, N.Y.,, Cornell Univ. Press.

Asher, G. W., D. S. Gallagher, et al. (1999). "Hybridization between sika deer (Cervus nippon) and axis deer (Axis axis)." Journal of Heredity **90**(1): 236-240.

Atkinson, I. A. E. (1977). "A reassessment of factors, particulalrly Rattus L., that influenced the decline of endemic forest birds in the Hawaiian Islands." Pacific Science **31**: 109-133.

Baker, J. K. and D. W. Reeser (1972). Goat management problems in Hawaii Volcanoes National Park : a history, analysis, and management plan. Washington, D.C., National Park Service.

Barrette, C. (1987). The comparative behavior and ecology of the chevrotains, musk deer, and morphologically conservative deer. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 21-59.

Barrette, C. (1991). "The Size of Axis Deer Fluid Groups in Wilpattu-National-Park, Sri-Lanka." Mammalia **55**(2): 207-220.

Bentley, A. (1967). An introduction to the deer of Australia, with special reference to Victoria. Melbourne,, Hawthorn.

Berwick, S. H. (1974). The community of wild ruminants in the Gir forest ecosystem, Yale University.

Bhat, S. D. and G. S. Rawat (1995). "Habitat use by chital (*Axis axis*) in Dhaulkhand, Rajaji National Park, India." Tropical Ecology **36**(2): 177-89.

Biswas, S. and K. Sankar (2002). "Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India." J. Zool. Soc. London **256**: 411-420.

Blouch, R. A. and S. Atmosoedirdjo (1987). Biology of the Baewan deer and prospects for its management. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 320-27.

Brander, A. D. (1927). Wild Animals in Central India. London, Edward Arnold & Co.

Brockie, R. E., L. L. Loope, et al. (1988). "Biological Invasions of Island Nature Reserves." Biological Conservation **44**(1-2): 9-36.

Bruegmann, M. M. (1996). "Hawaii's dry forests." Endangered Species Bull. **11**: 26-27.

Bruinderink, G. and E. Hazebroek (1996). "Ungulate Traffic Collisions in Europe." Conservation Biology **10**(4): 1059-1067.

Bryant, J. P., F. D. Provenza, et al. (1991). "Interactions between Woody Plants and Browsing Mammals Mediated by Secondary Metabolites." Annual Review of Ecology and Systematics **22**: 431-446.

Bubenik, G. A. and A. B. Bubenik (1987). Recent advances in studies of antler development and neuroendocrine regulation of the antler cycle. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 99-109.

Bunnell, F. L. (1987). Reproductive tactics of the cervidae and their relationships to habitat. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 21-59.

Cabin, R. J., S. G. Weller, et al. (2000). "Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest." Conservation Biology **14**(2): 439-453.

Carlquist, S. (1980). Hawaii: a natural history. Lawai.

Caughley, G. (1981). Overpopulation. New York, Academic Press.

Caughley, G. (1983). The deer wars : the story of deer in New Zealand. Auckland, N.Z. ; Exeter, N.H., Heinemann.

Chapple, R. S., A. W. English, et al. (1993). "Characteristics of the Oestrous Cycle and Duration of Gestation in Chital Hinds (Axis-Axis)." Journal of Reproduction and Fertility **98**(1): 23-26.

Choudhury, K. C. R. (1966). "Behaviour of chital (Axis axis Erxleben)." Journal of the Bombay Natural History Society **63**: 747.

Clark, A. H. (1949). The Invasion of New Zealand by People, Plants and Animals. Trenton, NJ, Rutgers Univ. Press.

Clark, K. A., R. M. Robinson, et al. (1970). "Malignant cattarhal fever in Texas cervids." J. Wildlife Diseases **6**: 376-83.

Clark, K. A., R. M. Robinson, et al. (1972). "Further observations on malignant catarrhal fever in Texas cervids." J. Wildlife Diseases **8**: 72-74.

Clutton-Brock, T. H. (1987). Sexual selection in the cervidae. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 110-22.

Clutton-Brock, T. H. and P. H. Harvey (1977). "Mammals, resources and reproductive strategies." Nature **273**: 191-95.

Coblentz, B. E. (1990). "Exotic Organisms A Dilemma for Conservation Biology." Conservation Biology **4**(3): 261-265.

Coblentz, B. E. (1997). "Goat eradication on Isabella Island." Conservation Biology **11**(5): 1047-1048.

Colbert, E. H. (1969). Evolution of Vertebrates. New York, NY, John Wiley & Sons.

Cole, F. R., L. L. Loope, et al. (2000). "Food habits of introduced rodents in high-elevation shrubland of Haleakala National Park, Maui, Hawai'i." Pacific Science **54**(4): 313-329.

Cole, F. R., A. C. Medeiros, et al. (1992). "Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland." Ecology (Tempe) **73**(4): 1313-1322.

Cooke, G. P. (1949). Moolelo O Molokai. Honolulu Star Bulletin. Honolulu, HI.

Corbet and Hill (1991). "World list of mammalian species."

Corbet and Hill (1992). "Mammals of the Indomalayan region."

Cowan, I. M. (1974). Management implications of behavior in the large herbivorous mammals. The behaviour of ungulates and its relation to management : The papers of an international symposium held at the University of Calgary, Alberta, Canada, 2-5 November 1971. V. Geist and F. R. Walther. Morges, Switzerland, International Union for Conservation of Nature and Natural Resources: 921-34.

Cox, G. W. (1999). Alien species in North America and Hawaii : impacts on natural ecosystems. Washington, D.C., Island Press.

Crandall, L. (1964). The management of wild animals in captivity. Chicago, IL, Univ. Chicago Press.

Cuddihy, L. W. and C. P. Stone (1990). Alteration of Native Hawaiian Vegetation Effects of Humans Their Activities and Introductions: XII+138P.

Cutler, T. L. and D. E. Swann (1999). "Using remote photography in wildlife ecology: a review." Wildlife Society Bulletin **27**(3): 571-581.

De Rames, C. and J. J. Spillett (1966). "A study of the chital or spotted deer in Corbett National Park, Uttar Pradesh." Jnl. Bombay Nat. Hist. Soc. **63**: 576-98.

de Silva, P. K. and M. de Silva (1993). Population structure and activity rhythm of the spotted deer in Ruhuna National park, Sri Lanka. Deer of China. N. Ohtaishi and H. I. Sheng, Elsevier Science Publishers B.V.: pp. 285-94.

de Vos, A., P. Brokx, et al. (1967). "A review of the social behavior of the North American cervids during the reproductive period." American Midland Naturalist 77(2): 390-417.

Dinerstein, E. (1979). "An ecological survey of the Royal Karnali-Bardia wildlife reserve, Nepal. Part I. Vegetation, modifying factors and successional relationships." Biol. Conserv. **15**: 127-50.

Dinerstein, E. (1979). "An ecological survey of the Royal Karnali-Bardia wildlife reserve, Nepal. Part II: habitat/animal interactions." Biol. Cons. **18**: 5-37.

Dinerstein, E. (1980). "An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part III: Ungulate Populations." Biol. Conserv. **18**: 5-38.

Dinerstein, E. (1987). Deer, plant phenology, and succession in the lowland forests of Nepal. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: xiii, 577.

Diong, C. H. (1982). Population biology and management of the feral pig (Sus scrofa L.) in Kipahulu Valley, Maui. Honolulu, Univ. of Hawaii: 408.

Dobson, A. P., J. P. Rodriguez, et al. (1996). "The geographical distribution of endangered species in the United States." Bulletin of the Ecological Society of America 77(3 SUPPL PART 2): 115.

Dzialak, M. R., T. L. Serfass, et al. (2001). "Reversible chemical restraint of fishers with medetomidine-ketamine and atipamezole." Journal of Wildlife Management **65**(1): 157-163.

Ehrlich, P. R. (1989). Attributes of invaders and the invading process: Vertebrates. Biological invasions : a global perspective. J. A. e. a. Drake. Chichester ; New York, Published on behalf of the Scientific Committee on Problems of the Environment (SCOPE) of the International Council of Scientific Unions (ICSU) by Wiley: pp. 85-109.

Eisenberg, J. F. and M. C. Lockhart (1972). "An ecological reconnaisance of Wilpattu National Park, Ceylon." Smithsonian Contrib. Zool. **101**: 1-118.

Eisenberg, J. F. and J. Seidensticker (1976). "Ungulates in southern Asia. A consideration of biomass estimates for selected habitat." Biol. Conserv. **10**: 293-308.

Ellerman, J. and T. Morrison-Scott (1966). Checklist of Palaeartic and Indian Mammals 1758-1946. London, England.

Elliott, H. W. (1973). A field survey of the exotic axis deer at Point Reyes National Seashore. Range Management: vii, 40 leaves.

Elliott, H. W. (1983). Ecological relationships of cattle, axis deer, fallow deer, and black-tailed deer on Point Reyes Peninsula. Davis, Calif.: 197 leaves,.

Elliott, H. W., III and R. H. Barrett (1986). "Dietary overlap among axis [Axis axis axis] fallow [Dama dama dama] and black-tailed deer [Odocoileus hemionus columbianus] and cattle [Bos taurus]." Journal of Range Management **38**(6): 546-550.

Evtushevskii, N. N. (1977). "Some results of the acclimatization of the axis deer in the Chekassy Oblast. [In Russian]." Vestnik Zoologii **1**: 7-11.

Fadeev, E. V. (1986). "Distribution of the Ussuri axis deer in the USSR." Biologicheskie Nauki (Moscow)(6): 39-46.

Fahimudden (1963). Animal production in Bihar. Bombay.

Flerov, C. (1952). Musk deer and deer. Fauna of the USSR: Mammals., Academy of Science of the USSR. **1**.

Foote, D., C. P. Stone, et al. (1992). "The Impact of Alien Pigs on Native Arthropods in Hawaii Volcanoes National Park." Bulletin of the Ecological Society of America **73**(2 SUPPL): 177.

Fradrich, H. (1987). The husbandry of tropical and temperate cervids in the West Berlin Zoo. Biology and management of the Cervidae : a conference held at the

Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 422-28.

Fuchs, E. R. (1977). Behavior. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 24-52.

Fuchs, E. R. (1977). Behavior patterns of axis deer in Texas. College Station, Texas A&M University: 177.

Geist, V. (1998). Deer of the world : their evolution, behaviour, and ecology. Mechanicsburg, Pa., Stackpole Books.

Gogan, P. J. P., R. H. Barrett, et al. (2001). "Control of ungulate numbers in a protected area." Wildlife Society Bulletin **29**(4): 1075-1088.

Goldfuss, G. A. (1820). Handbuch der Zoologie. Nèurnberg, J.L. Schrag.

Goodrich, J. M. and S. W. Buskirk (1995). "Control of Abundant Native Vertebrates for Conservation of Endangered Species." Conservation Biology **9**(6): 1357-1364.

Graf, W. and L. Nichols, Jr. (1967). "The axis deer in Hawaii." Journal of the Bombay Natural History Society **63**(3): 629-734.

Groves, C. P. and P. Grubb (1987). Relationships of living deer. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 21-59.

Grubb, P. (1992). Order Artiodactyla. Mammal Species of the World. D. E. D. M. W. Wilson, eds. Washington D.C., Reeder Smithsonian Institution Press: 1206pp.

Grubb, P. (1993). Mammal species of the world.

Hamann, O. (1979). "Regeneration of vegetation on Santa Fe and Pinta Islands, Galapagos, after the eradication of goats." Biol. Cons. **15**: 215-36.

Hamilton-Smith (1827). Anim. Kingdom **5**: 312.

Healy, W. M., D. S. deCalesta, et al. (1997). "A research perspective on white-tailed deer overabundance in the northeastern United States." Wildlife Society Bulletin **25**(2): 259-263.

Henke, S. E., S. Demarais, et al. (1988). "Digestive capacity and diets of white-tailed deer and exotic ruminants." Journal of Wildlife Management **52**: 595-98.

Hooge, P. N. and B. Eichenlaub (2000). Animal movement extension to ArcView. Anchorage, AK, Alaska Science Center- Biological Science Office, U.S. Geological Survey.

Howarth, F. G. (1985). Impacts of alien land anrthropods and mollusks on native plants and animals in Hawaii. Hawai°i's terrestrial ecosystems : preservation and management : proceedings of a symposium held June 5-6, 1984, at Hawai°i Volcanoes National Park. C. P. Stone and J. M. Scott. Honolulu, Cooperative Park Studies Unit: 149-179.

Howery, L. D., J. A. Pfister, et al. (1989). "Seasonal reproductive activity of 4 exotic ungulates in Texas, U.S.A." Journal of Wildlife Management **53**(3): 613-17.

Hu, D. E. (1998). Causes of endangerment and extinction in Hawaiian birds: 130 leaves.

Jacobson, H. A., J. C. Kroll, et al. (1997). "Infrared-triggered cameras for censusing white-tailed deer." Wildlife Society Bulletin **25**(2): 547-556.

Janis, C. M. and K. M. Scott (1987). "The Interrelationships of Higher Ruminant Families with Special Emphasis on the Members of the Cervoidea." American Museum Novitates(2893): 1-86.

Jewel, J. J., D. J. O'Dowd, et al. (1999). "Deliberate introductions of species: Research needs: Benefits can be reaped, but risks are high (International Workshop; Waimea, Kauai, Hawaii; June 1997; USDA Foreign Agricultural Service)." Bioscience **49**(8): 619-630.

Johnsingh, A. J. T. (1981). "Importance of fruits in the diet of chital in dry season." Jnl. Bombay Nat. Hist. Soc. **78**: 594.

Johnsingh, A. J. T. (1993). "Large mammalian prey-predators in Bandipur." Journal of the Bombay Natural History Society **80**: 1-57.

Johnsingh, A. J. T. and K. Sankar (1991). "Food Plants of Chital, Sambar and Cattle on Mundanthurai Plateau, Tamil-Nadu, South India." Mammalia **55**(1): 57-66.

Joyce, T. L. and S. P. Mahoney (2001). "Spatial and temporal distributions of moose-vehicle collisions in Newfoundland." Wildlife Society Bulletin **29**(1): 281-291.

Juvik, S. P., J. O. Juvik, et al. (1998). Atlas of Hawaii. Honolulu, University of Hawaii Press.

Karanth, K. U. and J. D. Nichols (1998). "Estimation of tiger densities in India using photographic captures and recaptures." Ecology **79**: 2852-62.

Karanth, K. U. and M. E. Sunquist (1992). "Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India." Journal of Tropical Ecology **8**: 21-35.

Karanth, K. U. and M. E. Sunquist (1995). "Prey selection by tiger, leopard and dhole in tropical forests." Journal of Animal Ecology **64**: 439-50.

Katahira, L. K., P. Finnegan, et al. (1993). "Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes National Park." Wildlife Society Bulletin **21**(3): 269-274.

Keegan, D. R., B. E. Coblentz, et al. (1994). "Feral Goat Eradication on San-Clemente-Island, California." Wildlife Society Bulletin **22**(1): 56-61.

Khan, J. A. (1994). "Food Habits of Ungulates in Dry Tropical Forests of Gir-Lion-Sanctuary, Gujarat, India." Acta Theriologica **39**(2): 185-193.

Khan, J. A. (1995). "Conservation and management of Gir lion sanctuary and National Park, Gujarat, India." Biol. Cons. **73**: 183-88.

Khan, J. A., R. Chellam, et al. (1996). "Ungulate densities and biomass in tropical dry deciduous forests of Gir, Gujarat, India." J Trop. Ecol. **12**: 149-62.

Khan, J. A. and U. Vohra (1992). "Group Size and Group Composition of Chital (Axis-Axis) in Gir, Gujarat, India." Mammalia **56**(4): 662-665.

Kilpatrick, H. J., A. J. Denicola, et al. (1996). "Comparison of Standard and Transmitter-Equipped Darts for Capturing White-Tailed Deer." Wildlife Society Bulletin **24**(2): 306-310.

Koopman, K. (1967). Artiodactyls. Recent Mammals of the World. New York, NY, Ronald Press: 385-406.

Kramer, R. J. (1971). Hawaiian Land Mammals. Rutland, VT, Charles E. Tuttle.

Kreeger, T. J., A. Vargas, et al. (1998). "Ketamine-medetomidine or isoflurane immobilization of black-footed ferrets." Journal of Wildlife Management **62**(2): 654-662.

Kubota, G. (2001). Deer population boom threatens Maui forests and farms. Honolulu Star Bulletin. Honolulu: 1.

Lamoreaux, C. H. (1998). Native Plants. Atlas of Hawaii. S. a. J. J. Juvik, eds. Hilo, HI: 135-139.

Lekagul, B. and J. A. McNeely (1977). Mammals of Thailand. Bangkok, Thailand, Kurushpa.

Lennox, C. G. (1950). Factors considered by Board of Commissioners of Agriculture and Forestry in Aprroving Projects to Introduce Deer to Hawaii. Honolulu, HI, Territory of Hawaii, Board of Commissionersof Forestry and Agricultrue: 8pp.

Lever (1985). Naturalized mammals of the world. New York, NY, Longman Group, Ltd.

Loope, L. (1998). Hawaii and the Pacific Islands. Status and trends of the nation's biological resources. M. J. Mac, P. A. Opler, C. A. Puckett-Haecker and P. D. Doran. Reston, VA, U.S. Dept. of the Interior. **II:** 747-774.

Loope, L. and A. C. Medeiros (1995). Haleakala silversword (Argyroxiphium sandwicense DC. ssp. macrocephalum). Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals and ecosystems. E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran and M. J. Mac. Washington D.C., U.S. Dept. Interior: Natl. Biological Service: 363-64.

Loope, L. and J. Scowcroft (1985). Vegetation response within exclosures in Hawaii: a review. Hawai°i's terrestrial ecosystems : preservation and management : proceedings of a symposium held June 5-6, 1984, at Hawai°i Volcanoes National Park. C. N. P. R. S. U. U. o. Hawaii. Honolulu: xxviii, 584 , [1] leaf of plates.

Loope, L. L. and J. O. Juvik (1998). Protected Areas. Atlas of Hawai*i. S. P. Juvik and J. O. Juvik. Honolulu, University of Hawai*i Press: 154-157.

Loope, L. L., A. C. Medeiros, et al. (1991). "Invasion and Control of the European Rabbit on the Island of Maui Hawaiian Islands Usa." Bulletin of the Ecological Society of America **72**(2 SUPPL): 178.

Lydekker, R. (1916). Catalogue of ungulate mammals in the British Museum 5 vols. London, England.

Lydekker, R. L. (1898). The Deer of all Lands: A History of the Family Cervidae Living and Extinct. London, England, Rowland Ward.

Lyon, H. L. (1950). What habitat will the spotted deer choose if liberated on the island of Hawaii. Honolulu, Hawaiian Academy of Science: 9 pp.

Madhusudan, M. D. and M. E. Sunquist (2002). "Local hunting and the conservation of large mammals in India." Ambio **31**(1): 49-54.

Martin, C. (1987). Interspecific Relationships between Barasingha and Axis Deer in Kanha National Park, India, and Relevance to Management. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: pp. 300-306.

Mauchamp, A. (1997). "Threats from alien plant species in the Galapagos islands." Conservation Biology **11**(1): 260-263.

McKay, G. M. and J. F. Eisenberg (1974). Movement patterns and habitat utilization of ungulates in Ceylon. The behavior of Ungulates and its Relation to Management. V. a. F. W. Geist, eds., IUCN publs.: 708-21.

McShea, W. J. and J. H. Rappole (1997). "The science and politics of managing deer within a protected area." Wildlife Society Bulletin **25**(2): 443-446.

Mehrhoff, L. A. (1998). Endangered and Threatened Species. Atlas of Hawaii. S. a. J. J. Juvik, eds. Hilo, HI: 150-153.

Mills, E. L., J. A. Leach, et al. (1995). "Exotic species and the integrity of the Great Lakes: Lessons from the past." Bioscience **44**(10): 666-76.

Mishra, H. R. (1982). The ecology and behaviour of chital (Axis axis) in the Royal Chitwan National Park, Nepal : with comparative studies of hog deer (Axis porcinus), sambar (Cervus unicolor) and barking deer (Muntiacus muntjak): 203, [44] leaves.

Mishra, H. R. and C. Wemmer (1987). The comparative breeding ecology of four cervids in Royal Chitwan National Park. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: xiii, 577.

Miura, S. (1981). "Social behavior of the axis deer during the dry season in Guindry sanctuary, Madras." Journal of the Bombay Natural History Society **78**: 125-38.

Mlot, C. (1995). "Biological Surveys - in Hawaii, Taking Inventory of a Biological Hot Spot." Science **269**(5222): 322-323.

Moe, S. R. and P. Wegge (1994). "Spacing behaviour and habitat use of axis deer (Axis axis) in lowland Nepal." Can. J. Zool. **72**: 1735-44.

Moe, S. R. and P. Wegge (1997). "The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal." Journal of Tropical Ecology **13**(PT2): 279-292.

Mungall, E. C. and W. J. Sheffield (1994). Exotics on the range: the Texas example. College Station, Texas A&M University Press.

Nama, H. S. (1990). Cestode parasites of Indian mammals. Jodhpur, India, Scientific Publishers.

Newton, P. N. (1989). "Associations between Langur Monkeys (Presbytis-Entellus) and Chital Deer (Axis-Axis) - Chance Encounters or a Mutualism." Ethology **83**(2): 89-120.

Nichols, L. (1960). Ecology of the axis deer. Honolulu, HI, Hawaii Div. Fish & Game: 32pp.

Nowak (1999). Order Artiodactyla. Mammals of the World vol. II. Walker. **2**: pp. 1051-.

Owen (1841).

Philips (1935). Mammals: 329.

Pocock, R. I. (1943). "The larger deer of British India. Part IV. The chital (Axis) and the hog deer (Hyelaphus)." Journal of the Bombay Natural History Society **44**: 169-78.

Prater, S. H. (1965). The book of Indian mammals, Prince of Wales museum of Western India.

Pratt, L. W. a. S. M. G. (1998). Terrestrial Ecosystems. Atlas of Hawaii. S. a. J. J. Juvik, eds. Hilo, HI: 121-129.

Rainbolt, R. E. and B. E. Coblentz (1997). "A different perspective on eradication of vertebrate pests." Wildlife Society Bulletin **25**(1): 189-191.

Ramakrishnan, U., R. G. Coss, et al. (1999). "Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India." Biological Conservation **89**(2): 113-120.

Raman, T. R. S. (1997). "Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India." Journal of Bioscience **22**(2): 203-18.

Rieman, H., R. Ruppanner, et al. (1979). "Serologic profile of exotic deer at Point Reyes National Seashore." J. Amer. Vet. Med. Assoc. **175**(9): 911-913.

Robbins, C. T., O. T. Oftedal, et al. (1987). Lactation, early nutrition and hand-rearing of wild ungulates, with special reference to deer. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 429-42.

Robinson, R. M., T. J. Galvin, et al. (1977). Diseases. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 76-78.

Rollins, D. and B. J. Higginbotham (1997). "Extension education in Texas: deer dilemmas and opportunities on private lands." Wildlife Society Bulletin **25**(2): 371-377.

Root, B. G. (1988). "Effects of intensive deer hunting on white-tailed deer movement." Wildlife Society Bulletin **16**: 145-51.

Russ, W. B. (1977). Reproduction/Population. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 53-61.

Rutledge, D. T., C. A. Lepczyk, et al. (2001). "Spatiotemporal dynamics of endangered species hotspots in the United States." Conservation Biology **15**(2): 475-487.

Sabin, W. (1934). Hunting in Hawaii's Islands. Paradise Pacific. **46**: 34-41.

Sadleir, R. M. F. S. (1987). Reproduction of Female Cervids. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: xiii, 577.

Santiapillai, C., M. R. Chambers, et al. (1981). "A preliminary study of bark damage by cervids in the Ruhuna National Park, Sri Lanka (Mammalia, Cervidae) mostly spotted deer (Axis axis)." Spixiana **4**(3): 247-54.

Schaller, G. B. (1967). The deer and the tiger; a study of wildlife in India. Chicago,, University of Chicago Press.

Schofield, E. K. (1989). "Effects of Introduced Plants and Animals on Island Vegetation - Examples from the Galapagos Archipelago." Conservation Biology **3**(3): 227-238.

Seaman, D. E. and R. A. Powell (1996). "An evaluation of the accuracy of kernel density estimators for home range analysis." Ecology **77**(7): 2075-85.

Seidensticker, J. (1976). "On the cological separation between tigers and leopards." Biotropica **8**(4): 225-34.

Seidensticker, J. (1976). "Ungulate populations in Chitawan Valley, Nepal." Biol. Conserv. **10**: 183-210.

Sekhar, N. U. (1998). "Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India." Environmental Conservation **25**(2): 160-71.

Sharatchandra, H. C. and M. Gadgil (1975). "A year of Bandipur." Journal of the Bombay Natural History Society **72**(3): 623-47.

Simpson, G. G. (1945). "Principles of classification and the classification of mammals." Bull. Amer. Mus. Natural History **85**: 1-350.

Smallwood, K. S. (1994). "Site Invasibility by Exotic Birds and Mammals." Biological Conservation **69**(3): 251-259.

Smith, J. C. (1977). Food Habits. The Axis deer in Texas. E. D. Ables. College Station, Texas Agricultural Experiment Station College Station. Dept. of Wildlife and Fisheries Sciences,: pp. 62-75.

Smucker, T. D., G. D. Lindsey, et al. (2000). "Home range and diet of feral cats in Hawaii forests." Pacific Conservation Biology **6**(3): 229-237.

Soule, M. E. (1990). "The Onslaught of Alien Species and Other Challenges in the Coming Decades." Conservation Biology **4**(3): 233-239.

Stone, C. P. and J. O. Keith (1990). Control of Feral Ungulates and Small Mammals in Hawaii's National Parks USA Research and Management Strategies. Control of Mammal Pests; IV Congress. C. G. J. Richards and T. Y. Ku. London, England, UK, Taylor and Francis: 406pp.

Stone, C. P. and L. L. Loope (1987). "Reducing Negative Effects of Introduced Animals on Native Biotas in Hawaii Usa What Is Being Done What Needs Doing and the Role in National Parks." Environmental Conservation **14**(3): 245-258.

Stout, R. J., B. A. Knuth, et al. (1997). "Preferences of suburban landowners for deer management techniques: A step towards better communication." Wildlife Society Bulletin **25**(2): 348-359.

Sundevall, K. (1846). Svenska Vet. Ak. Handl. for 1844: p. 179.

Sunquist, F. and M. E. Sunquist (1988). Tiger moon. Chicago, University of Chicago Press.

Sushil, K., M. L. Thakur, et al. (1993). "A note on Cheetal, Axis axis, damage to nursery stock at Satyanarayan forest nursery, Dehra Dun (U..P.)." Indian Forester **119**: 157-58.

Swedberg, G. and R. Walker (1978). The axis deer (Axis axis): its history and management in Hawaii, U.S. Fish & Wildlife Service: 81pp.

Tak, P. C. and B. S. Lamba (1984). Ecology and ethology of the spotted-deer, Axis axis axis (Erxleben) (Artiodactyla:Cervidae). Calcutta, Zoological Survey of India.

Tamang, K. M. (1982). The status of the tiger (Panthera tigris) and its impact on principal prey populations in the Royal Chitawan National Park, Nepal. Lansing, MI, MI State Univ.

Taylor, D. and L. Katahira (1988). "Radio-telemetry as an aid in erdaicating remnant feral goats." wildl soc. bull **16**: 297-99.

Tomich, P. Q. (1986). Mammals in Hawaii : a synopsis and notational bibliography. Honolulu, Hawaii, Bishop Museum Press.

Varman, K. S. and R. Sukumar (1995). "The line transect method for estimating densities of large mammals in a tropical deciduous forest: an evaluation of models and field experiments." J. Biosci. **20**: 273-87.

Veblen, T. T., M. Mermoz, et al. (1989). "Effects of Exotic Deer on Forest Regeneration and Composition in Northern Patagonia." Journal of Applied Ecology **26**(2): 711-724.

Vine, I. (1971). "Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior." J. Theor. Biol. **30**: 405-22.

Vitousek, P. M., L. L. Loope, et al. (1987). "Introduced Species in Hawaii Usa Biological Effects and Opportunities for Ecological Research." Trends in Ecology & Evolution **2**(7): 224-227.

Waring, G. H. (1996). Preliminary study of the behavior and ecology of axis deer on Maui, HI, NBS Research Laboratory at Haleakala National Park: 11.

Wehausen, J. D. and H. W. Elliott III (1982). "Range relationships and demography of fallow and axis deer on Pt. Reyes National Seashore." Cal. Fish and Game **68**: 132-45.

Wemmer, C. M. and D. E. Wilson (1987). Cervid brain size and natural history. Biology and management of the Cervidae : a conference held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, August 1-5, 1982. C. M. Wemmer. Washington, Smithsonian Institution Press: 21-59.

Whitehead, G. K. (1972). Deer of the World. London, England, Constable.

Whitehead, G. K. (1993). The Whitehead encyclopedia of deer. Shrewsbury
Stillwater, MN, Swan Hill Press ;
Voyageur Press.

Williams, T. (2002). Wanted: more hunters. Audubon: 43-51.

Yocom, C. F. (1967). "Ecology of feral goats in Haleakala National Park." American Midl. Naturalist 77: 418-51.