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ECOLOGY OF INTRODUCED GAME BIRDS IN HIGH-ELEVATION SHRUBLAND OF HALEAKALA NATIONAL PARK

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ABSTRACT

The Ring-necked Pheasant (Phasianus colchicus) and the Chukar (Alectoris chukar) are the dominant component of the avifauna in high-elevation shrubland (2070 - 3000 m) of Haleakala National Park, Maui, Hawaii. This study focused on the natural history, ecological niche, and effects on native biota of these alien game birds in this Hawaiian ecosystem. Game-bird abundance varied within census periods, elevations, and seasons. Highest numbers of pheasants (17 - 94 birds/100 ha) occurred at 2430 - 2450 m elevation; highest number of Chukars (77 - 161 birds/100 ha) occurred at 2640 - 2660 m. Analyses of crop contents indicated that diets of the two species were similar. Ring-necked Pheasant and Chukar consumed predominantly fruits of native, woody dicots (39% and 47% respectively), and leaves (29% and 24% respectively) and flower parts (12% and 17% respectively) of alien, herbaceous dicots. Both species generally selected food items according to their relative availability, although other factors influenced choice of certain items. Invertebrates were found to be a minor component of the game bird diet, suggesting that their impact on native invertebrate populations is minimal. Pheasant and Chukar occupy, at least partially, an ecological niche once held by now-extinct or rare birds, and appear not to be significant competitors with the endangered Nene. The role of these alien birds in facilitating seed dispersal and germination of native plant species is beneficial in restoring degraded ecosystems; native species dispersed include Styphelia tameiameiae, Vaccinium reticulatum, Coprosma ernodeoides, C. montana, Carex wahuensis, and Geranium cuneatum. However, game birds may indirectly threaten native Hawaiian avifauna by providing a seasonal food source for alien predators and serving as reservoirs/vectors for various bird parasites.

INTRODUCTION

Human introduction of alien organisms, whether accidental or intentional, is a major cause of global loss of biological diversity (Mooney & Drake 1986; Diamond 1989; Macdonald et al. 1989). The biotas of oceanic islands in general and the Hawaiian Islands in particular are especially vulnerable to invasions because major elements of continental biotas are lacking (Moulton & Pimm 1986) and because of their evolution in isolation, which often results, for example, in a relative lack of defenses against grazing or predation (Howarth 1985; Vitousek 1988; Loope & Mueller-Dombois 1989).

The high-elevation shrubland ecosystem of Maui's Haleakala National Park is more intact than many Hawaiian ecosystems but has been significantly modified by alien species, especially introduced ungulates (Vitousek et al. 1987). Cattle, and feral goats, and pigs have had the most obvious effects. Cattle were removed from this area in the 1930s whereas goat populations were eliminated during the 1980s with the aid of fencing and hunting. In addition, during the last decade, fencing and control efforts minimized the impacts of pigs on this ecosystem (Stone & Loope 1987). Other alien species are also threatening the endemic biota of this ecosystem, including the Argentine ant (Iridomyrmex humilis) (Cole et al. 1992), the western yellowjacket (Vespula pensylvanica) (Gambino et al. 1987, 1990), the house mouse (Mus musculus) and black rat (Rattus rattus) (Cole et al., unpubl. data), and alien plants (Loope et al. 1992). The control or elimination of these alien species pose difficult challenges for conservation biologists and park resource managers, but are important for protection of the unique biota of this ecosystem.

Birds are sparse in the high-elevation shrubland of Haleakala volcano, a circumstance that reflects massive extinctions in the Hawaiian avifauna following arrival of Polynesian colonizers (Olson & James 1982). Two alien game bird species, the Ring-necked Pheasant (Phasianus colchicus) and the Chukar (Alectoris chukar), comprise the dominant element of the avifauna in this ecosystem. The pheasant and Chukar overlap in distribution, habitat, and ecological niche with the endemic and endangered Nene or Hawaiian goose (Branta sandvicensis), which has been reintroduced to Maui from captive-reared populations beginning in the 1960s (Kear & Berger 1980). They may also facilitate seed dispersal and germination of native species (see Temple 1977), a role formerly filled by species now rare (the Nene) or extinct (Olson & James 1991). In addition, the presence of these alien game birds may interfere with restoration of the Nene population (Kear & Berger 1980). Several passerine species can also be seen regularly in the study area including native species -- Amakihi (Loxops virens) and Apapane (Himatione sanguinea) and alien species -- House Finch (Carpodacus mexicanus) and Japanese White-eye (Zosterops japonicus).

A rich literature exists on the ecology, food habits, and management of game birds in North America and Europe (see Hill & Robertson 1988). We are not aware, however, of any study that has attempted to evaluate the ecological effects of pheasants or other introduced species of game birds on a native, insular ecosystem in the tropics. This investigation focused on the natural history and the ecology of the Ring-necked Pheasant and the Chukar in the high-elevation shrubland of Haleakala National Park and on the conservation implications for the native biota (including the endangered Nene) in this Hawaiian ecosystem.

HISTORY OF INTRODUCTION AND DISTRIBUTION

The native range of the Ring-necked Pheasant extends roughly from the Black Sea east to Japan, but these birds have been introduced successfully to North America, Europe, Australia, New Zealand, and various islands around the world (Sibley & Monroe 1990). Besides Hawaii, the only other successful establishment in the tropics has been on St. Helena, near the west coast of Africa (Hill & Robertson 1988). Pheasants were first introduced to the Hawaiian Islands in 1865 (Hill & Robertson 1988) and eventually brought to all the major Hawaiian islands (Schwartz & Schwartz 1949). Currently, the pheasant is abundant in Haleakala National Park in two disjunct areas: in pastures near sea level dominated by alien grasses (Stemmermann 1980) and in native-dominated shrublands and grasslands from 1200m to over 2500m elevation in the Crater and 2100m to 3000m on the western slope of Haleakala volcano (Conant & Stemmermann 1979). Pheasants are also abundant downslope from the park boundary in middle- to high-elevation pasturelands on the western and northwestern flanks of the mountain.

Chukar are native to southeastern Europe and southwestern Asia (Heinzel et al. 1972) but subsequently have become established in western North America. This species was originally introduced to the islands of Lanai and Molokai in 1923-36 (Schwartz & Schwartz 1949), but is now established on all the main Hawaiian Islands except Oahu (Pratt et al. 1987). About 34 Chukar from Lanai were released on East Maui near the summit of Haleakala in the early 1950s, probably comprising the original release of birds on this island (C. McCall, retired Maintenance Chief, Haleakala National Park and M. Ueoka, Hawaii Division of Forestry and Wildlife, personal communication).

Other game bird species introduced to Maui and occasionally observed in high-elevation shrublands of Haleakala National Park during the past 30 years include California quail (Callipepla californica), Japanese quail (Coturnix japonica), Erckel's francolin (Francolinus erckelii), and gray francolin (Francolinus pondicerianus) (Conant & Stemmermann 1979; unpublished data). Of these, only the California quail was encountered (once) in this study.

STUDY AREA

Haleakala National Park extends from sea level to 3056 m and comprises the core of one of the most viable conservation units in the Hawaiian Islands, protecting rainforest, montane bogs, dryland forest, high-elevation grassland, and high-elevation shrubland. Our study area was located in high-elevation shrubland at 2070 - 3000 m elevation on the western and northwestern slopes of Haleakala volcano within Haleakala National Park.

Mean annual rainfall is estimated to range from 1000-2000 mm (Giambelluca et al. 1986), with total rainfall decreasing with increasing elevation and with lessened exposure to tradewind clouds. Mean annual rainfall at Park Headquarters (elevation 2146 m), the only long-term weather station in the area, averages 1440 mm but varies widely, with totals for the last twenty years ranging from a high of 3077 mm in 1980 to a low of 517 mm in 1983. Typically, over 75% of the mean annual precipitation falls during the November-April rainy season. Mean monthly temperature at park headquarters ranges only 3.7°C, from 9.8°C in February to 13.5°C in July (National Oceanic and Atmospheric Administration 1939-1990); mean monthly temperature at the mountain's summit (3056 m) is about 3°C lower than at park headquarters.

Whiteaker (1983) subdivided Haleakala's upper shrubland zone into structural-floristic communities and elaborated species composition at representative sites. Shrubs and grasses dominate the vegetation of upper Haleakala volcano (above 1950 m) on the wetter, windward (northern and western) flanks and extend lower on drier, leeward slopes. Native shrubs occur at high density below 2500 m and become mixed with open grasslands at 2500-2700 m. Vegetation is sparse above 2700 m elevation. Soil is generally poorly developed on a substrate of cinder or volcanic rock.

Potential predators of pheasant and Chukar present in the study area include the small Indian mongoose (Herpestes auropunctatus), feral cat (Felis catus), feral dog (Canis domesticus), and native Hawaiian Short-eared Owl (Asio flammeus sandwichensis). The mammalian predators occur in low numbers throughout the study area. An extensive network of traps established as part of a resource management program to protect the endangered Nene or Hawaiian goose (Branta sandvicensis) and the Dark-rumped Petrel (Pterodroma phaeopygia sandwichensis) further reduces the abundance of these potential predators. The Hawaiian Short-eared Owl is uncommon within the study area. Little evidence of predation on game birds has been noted by resource managers or park scientists despite extensive time working in the study area.

METHODS

Vegetation: Species Composition and Phenology

Vegetation was characterized at the following elevations: 2860-2900 m (T1), 2640-2660 m (T2), 2430-2450 m (T3), and 2070-2130 m (T4) using a modified Braun-Blanquet relevé method (Mueller-Dombois & Ellenberg 1974). Mean cover values were determined using four quadrats, each 10 meters by 10 meters, established at equal intervals along transects located at each of the four elevations. Slight adjustments in transect positioning were made as necessary to avoid rough terrain. In choosing transect locations, an attempt was made to pass through habitat representative of a given elevation and relatively undisturbed by alien species.

A list of vascular plant species was compiled for each quadrat; nomenclature for vascular plant species follows Wagner et al. (1990). Cover was estimated to the nearest 5% for each 100 square meters, except for species occurring at less than 2.5% cover which were assigned a value of 1%. Mean cover values calculated using data from the four quadrats located along a transect represent composite cover estimates for that transect. Additional plant species found along the transect but not recorded in quadrats were noted.

Notes on phenology of plant species on each transect were made at three month intervals (February, May, August, and November) during 1985 and intermittently thereafter. Reference specimens of leaf, seed, and fruit material were collected from the sites, identified, and stored at the Haleakala National Park research laboratory.

Field Surveys of Pheasant and Chukar Populations

Strip transects (80 meters by 750 meters - 700 meters for Transect 2) were established at each of the four elevations within our study site and marked with flagging. Surveys were conducted along each strip transect using a team of four people walking parallel and approximately 10 m apart. The group followed marked paths, first along one side, then returning along the opposite side of the transect. The average flushing distance of game birds in the study area was about 10 m, and the effective area covered in a 750 m transect was approximately 6.0 ha (750 meters by 40 meters by 2 = 60,000 m^2) and 5.6 ha for the 700 m transect. Each new bird was recorded by species, sex (pheasants only), distance from observer when flushed, and position relative to the flagged transect. Precautions were taken to minimize the probability of duplicate counting of individual birds.

The game bird breeding season extends from roughly February to June (Schwartz & Schwartz 1949). Surveys were conducted on a total of three dates during April-May 1985 (breeding) and three dates during November 1985-January 1986 (nonbreeding) for each transect. Censuses were separated by at least seven days to minimize the impact of human activity on game bird distribution along a transect. The relative abundance values reported here equal the mean of the three censuses determined for each time period and expressed per 100 ha.

Analysis of Crop and Stomach Contents

Adult birds were collected opportunistically, using shotguns, from April 1985 through December 1988 as time, weather conditions, and availability of birds permitted. Collections were grouped into breeding and nonbreeding seasons: February to June and September to January respectively. Chicks were very difficult to obtain due to seasonal appearance, cryptic coloration, and their ability to escape by alternately running through the vegetation and remaining immobile, but were collected when possible. Most collections were made on Haleakala's west slope, but five pheasants (11.6% of the total) and five Chukars (26.3% of the total) were obtained from Haleakala Crater where similar habitat exists. Crops were removed and stored in 70% alcohol until analyzed. The following collections were made: Ring-necked Pheasant -- 23 adult males, 20 adult females, and 9 chicks (pre-flight); Chukars -- 19 adults. No sexing of Chukars was attempted due to difficulties in sexing this species in the field. No Chukar chicks were collected.

Contents of each crop were separated by species. Plant material was categorized as fruit, seed, flower part, or leaf (including stems and stolons). Crop contents were identified by comparing to a reference collection. The relative abundance of diet items was determined by wet mass and by volume of water displaced. Since no meaningful difference was detected between these two measures of determining relative abundance, data are presented by mass. The species and number of individuals per species of arthropod and gastropod taxa also were recorded.

Seed Germination from Game Bird Droppings

Pheasant and Chukar droppings were randonly collected throughout the study area in June 1988. Droppings were uniformly distributed over the surface of each greenhouse flat on a sterile soil medium (peat moss and perlite). Ten flats containing pheasant droppings and two with Chukar droppings (an average of approximately 40 g per flat) were placed in a greenhouse located near park headquarters (elevation 2146 m) with partial shading and were watered intermittently for two years. The trays were examined periodically and the emergence of all vascular plant species recorded. Germinants were removed from each flat after they were identified

RESULTS

Vegetation Structure and Species Composition

The highest elevation site (2860-2900 m; Transect 1) had relatively few native plant species consisting primarily of low shrubs of Styphelia tameiameiae (Epacridaceae) which rarely exceeded 0.5 m in height (Table 1). Vegetation cover averaged only 10.5% along this transect. Three endemic Hawaiian bunchgrasses, Deschampsia nubigena, Trisetum glomeratum, and Agrostis sandwicensis, were widely scattered components of the low vegetation. The endemic composite shrub Dubautia menziesii (Asteraceae) was locally common. Tetramolopium humile (Asteraceae), a small, mat-forming, endemic composite, occurred only in these barren, high-elevation conditions. Only two introduced herbaceous species, Hypochoeris radicata (Asteraceae) and Rumex acetosella (Polygonaceae), were present, but inconspicuous.

Transect 2 (2640-2660 m) passed through open shrubland with substantial (to 30% locally) cover of the native grass Deschampsia nubigena. Vaccinium reticulatum (Ericaceae), Coprosma montana (Rubiaceae), Styphelia, and Sophora chrysophylla (Fabaceae) were the dominant native shrubs, with total shrub cover ranging from 5% to 30% over the transect (Table 1). The tallest of these, Sophora, rarely exceeded 3 meters in height at this site. Introduced plant species were not conspicuous here, with Hypochoeris radicata, Rumex acetosella, Holcus lanatus, and Poa pratensis comprising less than 10% cover. The percent of bare ground was high (53.7%).

Transect 3 (2430-2450 m) had slightly higher native species diversity than Transects 1 and 2 (Table 1). Styphelia and Vaccinium were the dominant native shrubs, with cover estimates of 24.0% and 16.0% respectively. This was the only site sampled where the relatively rare endemic species Santalum haleakalae (Santalaceae) and Geranium cuneatum (Geraniaceae) exceeded one percent of the cover (two and six percent respectively). Santalum is a small tree (to 3-4 meters tall) forming small, scattered groves while Geranium is a shrub (to 0.5 meters tall). Cover of alien species, dominated by Holcus, rarely exceeded 15% locally. Bare ground covered 25% of this transect.

Transect 4 (2070-2130 m) was similar to Transect 3 in cover by native shrubs (approximately 57%) (Table 1). Styphelia was the dominant shrub, with Sophora and Vaccinium very common. This transect also had the highest mean cover of alien plant species (20.4%), with cover of introduced grasses (primarily Holcus lanatus and Anthoxanthum odoratum) ranging from 5% to 35%. The endemic grass Deschampsia nubigena was not recorded on this transect and other native monocots were uncommon. Total vegetation cover approached 100% in places. On average, bare ground covered only 14.2% of the transect.

Though largely representative, the transects did not cover the full range of vegetation available to game birds. The primary unrepresented habitat was the disturbed areas near roadsides and trailsides where weedy, primarily alien flora dominates (such as Oenothera biennis, Trifolium repens, Medicago lupulina).

Phenology of Vegetation

Phenology within the high-elevation shrubland of Haleakala volcano varies from year to year and among plant species, but some generalizations are possible. Maximum vegetative growth for most plant species occurs during the months of March-June, at the end of the rainy season when soil moisture is generally high, temperatures are warming, and day length is increasing. Most, if not all, native species appear to have a dormant period, usually winter, when little or no vegetative growth occurs. Some alien species (Hypochoeris radicata, Rumex acetosella, Trifolium repens) may produce leaves continually throughout the year if soil moisture is adequate.

Both native and alien species have definite peak periods of flowering and fruiting, although almost any species may flower occasionally at any time of the year. Native shrubs flower sequentially. Styphelia tameiameiae has a flowering peak in February-March, Sophora chrysophylla in March-April, Vaccinium reticulatum, Coprosma montana, and C. ernodeoides in May-June, Geranium cuneatum in August-September, and Dubautia menziesii in September-October. Peak production of ripe fruits by native shrubs occurs near the beginning of the November-April rainy season. Although many fruits fall to the ground after ripening, mature fruits of common native shrubs (Coprosma sp., V. reticulatum, and S. tameiameiae) may remain on the plants for many months. Both native and alien grasses reach peak flowering in May-June, with seed set complete by July-September.

Game Bird Distribution and Abundance

Ring-necked Pheasants were present along Transects 2 through 4 while Chukars, encountered at somewhat higher elevations, were recorded on Transects 1 through 3 (Table 2). The abundance of these game bird species varied within census periods, elevations, and seasons. Breeding season estimates for the number of pheasants ranged from 17.9 birds/100 ha to 94.4 birds/100 ha, with the peak occurring at T3. Population estimates for this species during the nonbreeding season ranged from 16.7 to 44.4 birds/100 ha.

Chukars were sparse (11.1 birds/100 ha) at T1 and absent at T4 (Table 2). The greatest number of Chukars recorded during the breeding and nonbreeding censuses was along T2, 77.4 birds/100 ha and 160.7 birds/100 ha respectively. At T3, abundance during the breeding season was dramatically lower than at T2 (5.6 birds/100 ha); abundance was high (100.0 birds/100 ha) along this transect during the nonbreeding season. Greater variability was recorded among counts of Chukars during the nonbreeding census than for pheasants, perhaps reflecting a tendency of Chukars to be more gregarious.

Food Habits of Game Birds

Although diets of individual birds were varied and often dominated by only a few species, the composite diets of pheasant and Chukar were similar (Fig. 1). Five of the six most abundant food items in the crops of game birds and six of the ten most frequently recorded food items in crop samples were shared by both game bird species (Table 3). Both species consumed predominantly native, woody dicot fruits and alien, herbaceous dicot leaves and flower parts.

The pheasant diet consisted of 41.1% material derived from native species of plants and animals, 52.8% of material from alien species, and 6.1% of plant and animal material of uncertain classification (Fig. 2). The Chukar diet was comprised of 57.1% material from native species, 31.2% from alien species, and 11.8% of uncertain classification. For pheasants and Chukars, the native component was dominated by fruits of shrub species (93.7% and 82.5% respectively). The alien component consisted primarily of leaves, stems, and stolons of Trifolium repens and Medicago lupulina (39.8% and 34.9% for pheasants and Chukars respectively), of flower buds, leaves, and stems of Hypochoeris (25.0% and 74.0%), and of unidentified dicot flower buds (25.3% and 44.2%).

Berries of Vaccinium reticulatum were the most common food item for both pheasants (17.3%) and Chukars (24.2%) (Table 3). Together with drupes of Styphelia and Coprosma ernodeoides these native fruits comprised 37.0% and 44.3% of the Ring-necked Pheasant and Chukar diets respectively (Fig. 2 and Table 3). Pheasants consumed the low-growing, black-fruited Coprosma ernodeoides about eight times more frequently than the taller, orange-fruited Coprosma montana (Table 1). Chukars consumed almost four times more C. ernodeoides than C. montana fruit. This pattern of consumption occurred despite the fact that C. montana was two to five times more abundant than C. ernodeoides in the locations where birds were sampled for crop contents. C. montana fruits were often found more than 1 m above the ground and were often retained on the branches until drying began. These facts probably made them more difficult to obtain than C. ernodeoides fruits which were available near ground level.

Alien herbaceous dicots (Hypochoeris radicata, Trifolium repens, and Rumex acetosella) made up approximately one third of the pheasant (32.9%) and Chukar (36.5%) diets despite comprising less than three percent of the vegetation cover (Table 1 and 3). Although alien clovers are rare in the study area and largely confined to roadsides and other disturbed sites, they comprised 21.0% of the pheasant (Trifolium and Medicago lupulina) and 10.9% of the Chukar (Trifolium only) diets.

Alien grass seeds (especially Holcus) were taken by pheasants more frequently than by Chukars. Although only one third of the pheasant crops contained grass seeds (5.8% of the average pheasant diet), five individuals collected at 2070-2130 meters had crops containing 24.5% to 80.7% alien grass seeds. Native grass seeds were rare in the pheasant diet (< 0.5% of the average pheasant diet); nevertheless, two individuals collected near T2 where native grasses are common took 5.8% and 8.1% native grass seeds. Nine (47%) of the Chukar crops contained grass seeds (all alien), but grass seeds made up less than 0.9% of the average Chukar diet.

Pheasants consumed more than four times the amount of arthropods (mostly alien) as Chukars, with pheasants favoring isopods and Chukars favoring ladybird beetles (Coccinellidae) (Table 3). Five pheasant crops held more than 13% arthropods and two contained more than 50%. Snails, typically a minor component of the pheasant diet, may be taken in large numbers by females as a source of calcium during the reproductive season (Schwartz & Schwartz 1951). We collected two female pheasants during the breeding season whose crops contained 20% and 27% snails. Overall, mean crop content of animal matter was low in both adult pheasant (7.3%) and Chukar (1.3%).

Adult pheasant and Chukar diets were not significantly different between males and females. The pheasant diet remained similar between the breeding and nonbreeding seasons, while Chukars took more dicot seeds and arthropods (Mann Whitney U Test, $p < 0.05$) during the nonbreeding season (September to January). Nine pheasant chicks were collected during the study, but most crops were only partially full. Hypochoeris stems and flower buds (8 crops) and arthropods (5 crops) dominated the chick diets.

Seed Germination from Game Bird Droppings

Six native and seven alien species germinated during the two years following the start of the experiment (Fig. 3). Eleven species (with 733 individuals) germinated in the ten flats containing pheasant droppings. Eight species (with 115 individuals) germinated from the two flats with Chukar droppings. Native germinants outnumbered alien germinants by almost five to one. Styphelia tameiameiae, Vaccinium reticulatum, and Coprosma ernodeoides comprised 47.0%, 41.0%, and 5.7% of the total native germinants respectively. Of these three species, only Vaccinium reticulatum germinated from the Chukar droppings.

Alien grass and herbaceous dicot species germinated quickly; 85.9% of the alien germinants appeared within the first three months of the experiment (Fig. 3). Only 37.8% of the native germinants appeared within the first three months. Approximately 75% more grass seedlings (16) germinated during the first month in the Chukar flats than in the pheasant flats (9). Almost ten times the number of grass seedlings per flat germinated in the two Chukar flats (8) than in the ten pheasant flats (0.9). Three species, Silene gallica (Caryophyllaceae) (alien), Oenothera biennis (Onagraceae) (alien), and Geranium cuneatum (Geraniaceae) (native) also germinated in low numbers (1 to 5 individuals for all flats) during the first three months of the experiment; only Geranium occurred in both pheasant and Chukar droppings.

Eleven of the thirteen species had germinated within the first three months after the start of the experiment. Styphelia seeds began germinating in March 1989, nine months after the start of the experiment; the total number of Styphelia seedlings germinating through June 1990 was 328, and many Styphelia seeds remained ungerminated. Styphelia seedlings were still appearing three years after the experiment began.

Seeds of four species were found in the crop analysis, but did not appear in the germination experiment: Machaerina gahniaeformis, Medicago lupulina, Sophora chrysophylla, Trifolium sp. Seeds of three species among the germinants were not found among food items in the crop analysis: Euphorbia peplus, Geranium cuneatum, and Poa pratensis. Most of these species were not common in either the game bird diet or the germinants. The most notable absences in the germinants may be those of Hypochoeris and Rumex, perhaps due to low seed viability and/or high digestibility of their seeds. Although Holcus lanatus seed heads comprised 10.9% of the pheasant diet, relatively few Holcus seedlings (25) germinated from droppings in the greenhouse flats.

DISCUSSION

Distribution and Population Size

Our population estimates of 17-94 pheasants per 100 ha for T3 and 28-44 pheasants per 100 ha for T4 exceed those reported by Conant and Stemmermann (1979) for west slope habitat (15-25/100 ha). However, our estimate of 18-30 pheasants per 100 ha on T2 fits well with their estimate for west slope habitat. Schwartz & Schwartz (1951) estimated 10-20 pheasants/100 ha as representative of high-elevation shrubland on Maui. Estimates obtained in this study are in the lower range of maximum densities (52-150/100 ha) reported for Haleakala Crater by Conant and Stemmermann (1979).

Pheasants were not observed on T1 while Chukars were present only during the breeding season with an estimated density of 11 birds/100 ha (Table 2). Pheasants are seen occasionally on Haleakala as high as 2800 m, but are not common above about 2600 m.

Chukars were extremely abundant along Transect 2, with a population estimate of 77-161 birds/100 ha. This elevation is within the optimal Chukar habitat on Haleakala, based on roadside observations as well as transect data. Chukars were less abundant (6-100 birds/100 ha) at Transect 3 and were uncommon on Haleakala's relatively moist northwest slope below 2200 m elevation; no Chukars were observed along T4 during our study. The highest estimates of Chukar density (22-50/100 ha) in Haleakala National Park were for the Kalapawili Ridge grasslands at ca. 2500-2600 m (Conant & Stemmermann 1979). They also recorded Chukars within the park in Kaupo Gap as low as 1200 m elevation.

Our observations on Haleakala suggest an average initial pheasant brood size of 7-9, with 3-4 chicks the brood average for the advanced juvenile stage just prior to flight. Schwartz & Schwartz (1951) found 6-11 eggs in a sample of 55 pheasant nests in the Hawaiian Islands with the average number of young observed from 49 broods at 3.0.

Game Bird Food Habits

The food habits of pheasants in Hawai'i differ from those in the continental United States due to differences in available vegetation and climate (Schwartz & Schwartz 1951). Nevertheless, our results are generally consistent with those from other studies which have found that Ring-necked Pheasants consume a broad range of both plant and animal foods. Schwartz & Schwartz (1951) recorded 97 plant and 55 animal foods from a sample of 191 pheasants collected throughout the Hawaiian Islands. Only three pheasants in their study were collected in habitats typical of our study area. Our data add 12 plant and animal foods to these totals and indicate that some food items are consumed in greater amounts than was reported by Schwartz & Schwartz (1951). The adult pheasant diet is dominated by plant food (75-98%) based on our data and data from other studies (see Schwartz & Schwartz 1951) from Hawaiian high elevation areas; Ferrel et al. (1949) from the Sacramento Valley of California; and five other studies reported in Schwartz & Schwartz (1951)).

Pheasant and Chukar generally select food items according to their relative availability and probably would fill their crops with only one food item if sufficiently abundant (Munro 1944). Consequently, considerable variability exists when crop contents are compared statistically. Nevertheless, these species appear to select certain food items in greater abundance than reflected by their presence in the habitat, suggesting factors other than abundance influence diet choice by game birds (Tables 1 and 3). Foliage and flowers of alien herbs, Hypochoeris radicata and Trifolium sp. and fruits of native shrubs, Coprosma ernodeoides and Vaccinium reticulatum, were taken in higher percentages than expected based on vegetation analyses. Styphelia tameiameiae and the native grasses Deschampsia nubigena and Trisetum glomeratum appear underrepresented in the game bird diets. Although present in areas where native grass seeds were available, Chukar took few grass seeds (< 1%) while pheasants selected predominantly alien grass seeds (about 6%). These differences may reflect greater moisture content, nutrient content, digestibility of these items, or simply local availability.

Game bird chicks were found to depend mainly on animal material (primarily arthropods) in the few studies that succeeded in obtaining samples (see Schwartz & Schwartz 1951). Ferrel et al. (1949) obtained a sufficiently large sample of chicks to indicate changes in the diet during their first four months of life. They found that animal food comprised nearly the entire diet of chicks during the first week of life but declined gradually until the age of 12 weeks, after which the diet of young birds was essentially the same as that of adult birds. The chicks consumed a wide range of insect taxa, apparently based on availability. Hill & Robertson (1988), working in England and Ireland, further emphasized the importance of arthropod food to chick survival during the first three weeks of life. Adult Heteroptera and larval Lepidoptera were judged to comprise the optimal diet for chick survival. Using radiotracking of broods by fitting hens with small radiotransmitters, they demonstrated that broods feeding in areas with few arthropods had larger home ranges and suffered heavier mortality than those feeding in areas where arthropods were more abundant. Although the number of chick collections was small in our study (n=9) and their crops were only partially full, the data suggest that animal matter is a more important diet item for juveniles than for adult pheasants.

Studies in temperate areas of Europe and the United States suggest dramatic seasonal variation in pheasant diets (see Hill & Robertson 1988). However, the diets of game birds from high-elevation shrubland in the Hawaiian islands show relatively little seasonal variation. This observation is consistent with the relatively minor annual variation in temperature at 20^{0}N latitude, the persistence of fruits on native shrubs, and the year-round presence of new growth on alien herbaceous species such as Hypochoeris radicata, Rumex acetosella, and Trifolium repens.

What factors control game bird population size on upper Haleakala?

Mongooses, rats, feral cats, feral pigs, and "fire ants" (Solenopsis sp.) are possible locally important predators on pheasants in Hawaii (Schwartz & Schwartz 1951). Although they were able to obtain very little evidence of any significant predation by any species, Schwartz & Schwartz (1951) considered the mongoose to be the most important pheasant predator. Nevertheless, they noted comparable pheasant densities for islands with and without mongooses. Predation control programs implemented by Haleakala National Park to protect the endangered Nene and Dark-rumped Petrel may have reduced densities of potential game bird predators (including the mongoose) on the west slope of Haleakala volcano. Traplines located throughout the west slope are continuously monitored to maintain a low predator abundance. Although a large number of traps are set regularly, captures of predators are infrequent, suggesting that the densities of potential game bird predators are low and that the control program has been successful. Despite extensive field work in the study area by park scientists and resource management personnel during the last five years, few observations or signs of mammalian predation on game birds in the high-elevation shrubland have been recorded. Although present in the study area, the Hawaiian owl (Asio flammeus sandwichensis) feeds primarily on rodents rather than birds, based on our field observations and the examination of pellet contents. Schwartz & Schwartz (1951) suggested that pheasant populations in Hawaii are probably not regulated by predators or parasites, but by factors such as food, cover, water, and climate. Field observations during this study support the view that game birds are probably not regulated by predators. Hunting may contribute to the regulation of game bird populations outside park boundaries, however.

Impact of introduced game birds on the endemic biota of upper Haleakala

1. Effects on Native Invertebrates

Analyses of crop contents suggest that populations of the Ring-necked Pheasant or Chukar are not significantly depressing populations of native invertebrate species in the study area, especially in comparison to the highly significant threat posed by rodents (Cole et al. unpubl. data) and by alien invertebrates such as the Argentine ant (Cole et al. 1992). Endemic arthropods were virtually absent from the crop samples for both game-bird species. Adult birds took small amounts of animal matter (invertebrates). The invertebrate species taken were overwhelmingly dominated by alien taxa -- sowbugs, ladybird beetles, slugs, garlic snails, and earthworms. Young birds, especially during their first weeks of life when animal food dominates their diet, may have more of an effect on native invertebrate species than the adults do. Although serious impacts on native arthropod populations appear unlikely, a definitive determination of the impact of game birds on populations of rare, endemic arthropod species in high-elevation shrubland of Haleakala (Beardsley 1980) would require further study.

2. Competition with Nene

Baldwin (1947) noted the close

similarity in food preferences of the Nene or Hawaiian Goose (Branta sandvicensis), the California quail, and the pheasant in Hawai'i Volcanoes National Park, but, because of low populations of all three species doubted that the introduced birds exert a negative influence on populations of the Nene. In an analysis of Hawaiian Goose droppings, Baldwin found that the alien herb Hypochoeris was the second (after Deschampsia nubigena) comprising 7.0% of the identifiable volume. Seeds (and fruit parts) of Styphelia tameiameiae, Vaccinium reticulatum, and Coprosma ernodeoides were also a part of the diet, comprising 5.4% of the identifiable volume. These food items were also found to be important components of game bird diet in our investigation (Table 3).

At Haleakala National Park, Nene number only 131-150 birds and are localized in several small patches within about 2000 ha of potential habitat (Hodges 1991). Although food habits of the pheasant and Chukar appear similar, the restricted Nene distribution within the park and the abundance of favored food items throughout the study area suggest that food quantity is not limiting Nene abundance. Consequently, we believe that interspecific competition between pheasant and Nene for food items is not intense, although this hypothesis remains to be tested.

3. Role in Seed Dispersal and Germination of Native and Introduced Plant Species

Swank (1944) found that Ring-necked Pheasants in West Virginia are a significant disperser of seeds, particularly very small ones and those with very hard seed coats. Although a high percentage of ingested seeds, even those with hard coats (such as wild grape), were digested, many passed through the birds' digestive tracts intact. These intact, but scarified, seeds had high viability and were found to germinate more quickly than seeds not exposed to such treatment (Swank 1944).

Lewin & Lewin (1984) found that a primary food of another game bird introduced to the forests on Hawaii island, the introduced Kalij Pheasant (Lophura leucomelana), is banana poka (Passiflora mollissima) and that the Kalij Pheasant is probably a major disperser of that aggressive weedy vine. The Kalij Pheasant is not established on Maui, where banana poka is still confined to a relatively small area. The Ring-necked Pheasant occurs in relatively dry, non-forest habitats and has not been shown to serve as an important vector for dispersal of any of the most aggressive weeds of the Hawaiian Islands.

Styphelia tameiameiae, one of the native shrub species that germinated frequently from game-bird droppings in greenhouse trials in this study, is known as a notoriously difficult species to germinate. Wooliams (1976), in a presentation emphasizing the difficulties encountered by Hawaiian botanical gardens in rare plant conservation, stated: "I know of no one who has successfully germinated 'pukiawe' -- Styphelia tameiameiae -- yet this plant is one of the most common low to high elevation plants. Possibly the fruit passes through a bird."

Results from this study suggest that pheasants and Chukars are important dispersal agents for several native shrub species of Haleakala's high-elevation shrubland. Alien plant species are also dispersed by game birds, but to a lesser extent; many of the alien seeds prominent in the diet (such as Holcus) were much less prominent among the germinants from droppings, and were probably digested. At the other extreme in the germination experiment, seeds of Styphelia, a native species with hard, thick coats, were still germinating after three years in the germination trays.

Recent research has revealed the richness of the Hawaiian avifauna prior to colonization by Polynesians (Olson & James 1982). Whereas only 10 endemic Hawaiian species of land birds were known historically from Maui, analysis of bird bone subfossils from a single cave in the lowlands of Maui has increased the island's known avifauna to 29 species (James et al. 1987). There can be little doubt that Ring-necked Pheasants and Chukars are at least partially occupying a niche in Maui's high-elevation shrublands and fulfilling a role in seed dispersal (and perhaps enhancement of germination) once held by now-extinct or rare, in the case of the Nene, birds. Olson & James (1991) give descriptions of at least two extinct species, known from subfossils found in lava tubes, which may have formerly (prior to Polynesian arrival in the 4th century A.D.) been seed dispersers in Haleakala's high-elevation shrubland -- a flightless goose-like duck (Ptaiochen pau) and a flightless goose (Branta hylobadistes). The bills of these species have serrated edges that are thought to have been adapted for grinding seeds. Although there is no reliable historical record of Nene from Maui, bones of the species (Branta sandvicensis) have been found, although rarely, in East Maui lava tubes (Olson & James 1991).

4. Potential Role as Buffer Species for Alien Predators

Mammalian predators (mongoose, feral cat, rats, and occasionally feral dogs) and the sole avian predator, the Hawaiian Short-eared Owl (Asio flammeus sandwichensis), probably have little effect on the size of game bird populations; factors other than predation appear to regulate game bird abundance in the high-elevation shrubland. Nevertheless, mammalian predators are the primary known limiting factor for the remnant population of the Hawaiian Dark-rumped Petrel (Pterodroma phaeopygia sandwichensis) that survives near the summit of Haleakala volcano (Simons 1985) as well as one of the factors that may threaten the long-term survival of the Nene (Branta sandvicensis) in natural habitats of Hawaii (Banko & Manuwal 1982; Stone et al. 1983). These predators may be able to persist for longer periods in the high-elevation shrublands of Haleakala by preying on game birds, especially eggs and immatures, which act as buffer species (see Giles 1978). Use of game birds as buffer species may be most critical during March and April when alternative prey items (house mouse) are scarce (Cole et al., unpublished data). One of us (ACM) has observed several carcasses of female pheasants that were killed by predators during the spring in Haleakala's Kalapawili grasslands. We doubt that adult game birds are common prey for mammalian predators, but some individuals may be taken opportunistically; all evidence of depredation on adult game birds by mammalian predators, although limited, has been noted during the spring. It is unlikely that populations of mammalian predators living on the west slope of Haleakala volcano rely on game birds as a major food source throughout the year.

We speculate that mammalian predators have a relatively reliable food supply from

May through December. Black rat populations are small in size but largely stable throughout the year; house mouse populations on upper Haleakala generally fluctuate from a low in late winter and spring to a high in fall; and populations of ground-dwelling arthropods are abundant in late spring and throughout the summer (Cole et al., unpublished data). Game-bird eggs and chicks are available from late February until August. January-April is the period likely to be most difficult for survival of vertebrate predators in the high-elevation shrubland. Environmental conditions are most extreme at this time and rodents, possibly their most important food resource, are scarce. Although some arthropod species are common in March and April, these species do not appear to be important food items for mongooses and cats. However, game birds begin breeding in late February, so that by March and April, eggs and chicks are common, potential food items. Mongooses or cats that wander into the high-elevation shrublands from habitats at lower elevations might be sustained by game bird prey during March and April. The presence of game bird prey might reduce mortality rates for these predators during this critical period, and ultimately aid them in moving to high elevations where Dark-rumped Petrel colonies are located or into Haleakala Crater where the majority of Nene nests are found.

5. Role of Game birds as a Reservoir or Vector of Disease and Parasites

Banko & Manuwal (1982) have appropriately suggested that introduced game birds need to be evaluated as reservoirs of disease, particularly for the Nene which shares habitat with both Ring-necked Pheasant and Chukar on upper Haleakala volcano. Two diseases believed to pose particularly severe threats to Hawaiian bird life are avian pox (a viral disease) and malaria (a disease caused by a protozoan, Plasmodium relictum capistranoae) (van Riper & van Riper 1985). Although both diseases may have been influential in the decline of the Hawaiian forest birds, neither of these diseases, nor other blood parasites, have been found to be prevalent in game birds (Gassmann-Duvall, Olinda Endangered Species Captive Propagation Facility, Dept. of Land and Natural Resources, Hawaii, pers. comm.). Nevertheless, Warner (1968) suggests the possibility that introduced game birds such as the Ring-necked Pheasant and the California quail may play significant roles in carrying and spreading these pathogens.

Although apparently largely free of pox virus and malaria, the Ring-necked Pheasant and other Hawaiian game bird species appear to comprise a major reservoir and vectors for parasites which may affect the Nene (e.g., gapeworm (Nematoda: Syngamus bronchialis; Gassmann-Duvall 1987). Lewin and Holmes (1971) found a strikingly high incidence of parasitism by helminths in Ring-necked Pheasant and six other species of game birds on Puuwaawaa Ranch, Hawaii. Schwartz & Schwartz (1951) and van Riper & van Riper (1985) cite a large number of parasites recorded from Ring-necked Pheasants in the Hawaiian Islands, including nematodes (10 spp.), trematodes (1 sp.), mites (2 spp.), feather lice (8 spp.), and hippoboscid flies (1 sp.). Recent parasitological surveys of six Ring-necked Pheasants from East Maui (five from Olinda, one from Haleakala) showed Coccidia sp., Capillaria sp., Heterakis sp., and Syngamus trachea, the latter a new parasite record for Ring-necked Pheasants in Hawaii (Gassmann-Duvall unpubl. data). Coccidia and Heterakis, among other parasites, were found on individuals in the captive Nene flock near Pohakuloa (Gassmann-Duval 1987) and in a Nene breeding pair near Haleakala National Park Headquarters (Gassmann-Duvall unpubl. data), strongly suggesting that Ring-necked Pheasants may serve as vectors which facilitate transmission of parasites to the Nene. Heavy parasite loads may in turn reduce Nene reproductive success and survival, thereby hampering restoration efforts. We could find little information on parasites or diseases of Chukar in Hawaii. Studies on Lanai conducted by the Hawaii Bureau of Game in the late 1950's found that Chukars were heavily infested with ecto- and endoparasites (Ron Walker, personal communication). Cecal worms occurred in almost 40% of the birds examined and eyeworms in over 15%. Lice or mites were found on almost 50% of the birds. In related work on Hawaii Island, the Hawaii Bureau of Game collected no Chukar with internal parasites and only a few specimens had lice. Evidence of disease was scarce in these studies; coccidiosis was suspected in only one Chukar collected on Lanai, but no confirming microscopic examination was made.

Importance of Game Birds to the Conservation of Native Hawaiian Ecosystems

Game birds present in the high-elevation shrublands of Haleakala National Park occupy a niche at least superficially similar to that of extinct or highly reduced (in the case of the Nene) bird species. The pheasant and Chukar diets appear consistent with speculated diets for extinct species and roughly similar to that of the Nene. In addition, habitat requirements of pheasant and Chukar are similar to those of the Nene. These game birds may play a similar role to that of extinct or rare (Nene) avifauna in dispersing native plant species (see Temple 1977). Scarification of seeds by birds may be necessary for germination of some native species. Based on results of the germination experiments, game birds may also disperse seeds of alien as well as native species.

The role of these alien birds in dispersal of seeds of native shrub and sedge species seems beneficial in restoring, for conservation purposes, ecosystems degraded for nearly two centuries by feral ungulates. The game birds appear not to be significant competitors with the Nene (which is rare as a result of other factors). Also, their impact on native inverte brates appears to be minimal. However, these game-bird species may provide a significant seasonal food source (buffer species; see Giles 1978) for alien carnivorous mammals (mongoose, feral cat) that also prey on the endangered Nene and Dark-rumped Petrel (Pterodroma phaeopygia sandwichensis). In addition, Ring-necked Pheasants and Chukars may comprise important reservoirs or vectors for various bird parasites that may threaten native Hawaiian avifauna, particularly the Nene (Gasmann-Duvall, Olinda Endangered Species Captive Propagation Facility, Dept. of Land and Natural Resources, Hawaii, personal communication). Further study is needed before a definitive assessment of the role of the Ring-necked Pheasant and Chukar in the high-elevation shrubland ecosystem of Haleakala National Park will be possible.

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Table 1. Estimated percent cover of plant species on four elevational transects (2860-2900m [T1], 2640-2660m [T2], 2430-2450m [T3], and 2070-2130m [T4]) based on cover estimates from four 10-m x 10-m quadrats per transect. A species is included in the table if its mean cover value exceeded 0.5% on at least one transect. Species observed near but not in the sample plots are indicated by +.

Species	Transect 1	Transect 2	Transect 3	Transect 4
Native Dicots				
Styphelia tameiameiae	6.2	3.0	24.0	31.2
Vaccinium reticulatum	0.2	6.2	16.0	13.8
Sophora chrysophylla	---	2.8	3.4	9.0
Coprosma montana	---	5.0	4.2	1.8
Coprosma ernodeoides	---	---	0.8	0.8
Dubautia menziesii	0.5	0.2	0.6	---
Santalum haleakalae	---	---	2.0	+
Geranium cuneatum	---	0.5	6.0	---
Tetramolopium humile	0.8	---	---	---
Alien Dicots				
Hypochoeris radicata	1.0	4.0	1.0	2.0
Rumex acetosella	0.2	1.0	1.0	---
Danthonia pilosa	---	---	0.4	1.8
Native Monocots				
Deschampsia nubigena	1.0	11.5	1.0	---
Trisetum glomeratum	0.8	1.0	1.0	0.5
Agrostis sandwicensis	1.0	---	---	---
Carex wahuensis	---	+	1.0	0.5
Luzula hawaiiensis	---	0.2	0.8	0.2
Alien Monocots				
Holcus lanatus	---	2.5	8.0	8.8
Anthoxanthum odoratum	---	---	1.0	7.8
Poa pratensis	---	2.0	0.2	---
Native Fern				
Pteridium aquilinum	---	5.0	1.0	4.0
Bare ground and litter	89.5	53.7	25.0	14.2

Table 2. Relative abundance estimates (no./100 ha) of Ring-necked Pheasant and Chukar at four different elevations (2860-2900 m [T1], 2640-2660 m [T2], 2430-2450 m [T3], and 2070-2130 m [T4]) based on censuses during April-May (breeding) and November-January (nonbreeding) periods. Data represent means (± 1 SE) of three censuses for each period. Comparison of means between seasons for each transect were made using Mann Whitney U Tests. Statistical differences ($p < 0.05$) are indicated by an asterisk.

Transect	Pheasant		Chukar	
	Breeding	Nonbreeding	Breeding	Nonbreeding
1	0.0	0.0	11.1 ± 11.1	0.0
2	17.9 ± 10.3	29.8 ± 21.5	77.4 ± 21.5	160.7 ± 81.2
3	94.4 ± 30.9*	16.7 ± 0.0	5.6 ± 5.6	100.0 ± 50.0
4	27.8 ± 27.8	44.4 ± 24.2	0.0	0.0

Table 3. Fifteen most common diet items for Ring-necked Pheasant and Chukar ranked by mean percentage (± 1 SE) of total crop contents (by mass). Frequency of occurrence for a specific food item is expressed as thepercentage of the total crops sampled. Native species are indicated by an asterisk.

Pheasant n=43

Food Item	Percent of Diet	Freq. (%)
Vaccinium reticulatum fruit*	17.3 ± 4.9	49
Trifolium sp. leaf	15.9 ± 4.1	40
Coprosma ernodeoides fruit *	12.7 ± 4.2	35
Hypochoeris radicata flower bud	8.3 ± 2.1	70
Styphelia tameiameiae fruit*	7.0 ± 2.5	47
Holcus lanata seed head	5.8 ± 2.5	23
Unidentified plant matter	5.1 ± 2.5	47
Isopoda (*Porcellio laevis*)	4.8 ± 2.2	47
Hypochoeris radicata stem	3.7 ± 1.2	37
Medicago sp. leaf	3.2 ± 1.8	9
Rumex acetosella leaf	3.1 ± 1.4	33
Trifolium sp. stolon	1.9 ± 1.1	5
Coprosma montana fruit*	1.5 ± 1.1	7
Slugs (*Milax* sp.)	1.5 ± 0.8	21
Unidentified monocot sp	0.8 ± 0.4	21

Chukar n=19

Food Item	Percent of Diet	Freq. (%)
Vaccinium reticulatum fruit*	24.2 ± 6.7	68
Hypochoeris radicata flower bud	12.7 ± 2.9	100
Coprosma ernodeoides fruit*	10.9 ± 5.5	21
Trifolium sp. leafl	0.9 ± 3.2	68
Styphelia tameiameiae fruit*	9.2 ± 4.2	58
Hypochoeris radicata leaf	6.1 ± 2.7	58
Unidentified dicot sp. seed	4.8 ± 2.0	89
Hypochoeris radicata stem	4.3 ± 2.7	58
Unidentified monocot sp	3.3 ± 2.7	16
Unidentified plant matter	3.0 ± 1.0	16
Coprosma montana fruit*	2.8 ± 2.1	11
Rumex acetosella leaf	2.5 ± 2.1	42
Beetles *(Hippodamia convergens)*	1.3 ± 0.4	80
Cerastium vulgatum seed head	0.7 ± 0.3	53
Hypochoeris radicata seeds	0.5 ± 0.3	74

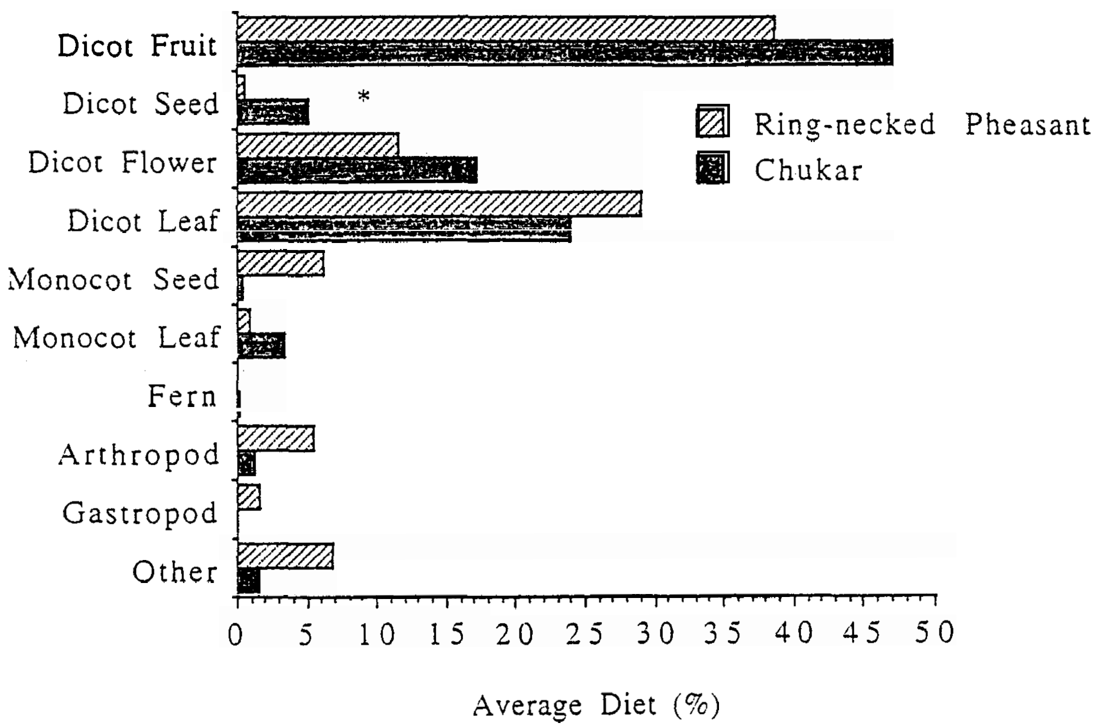
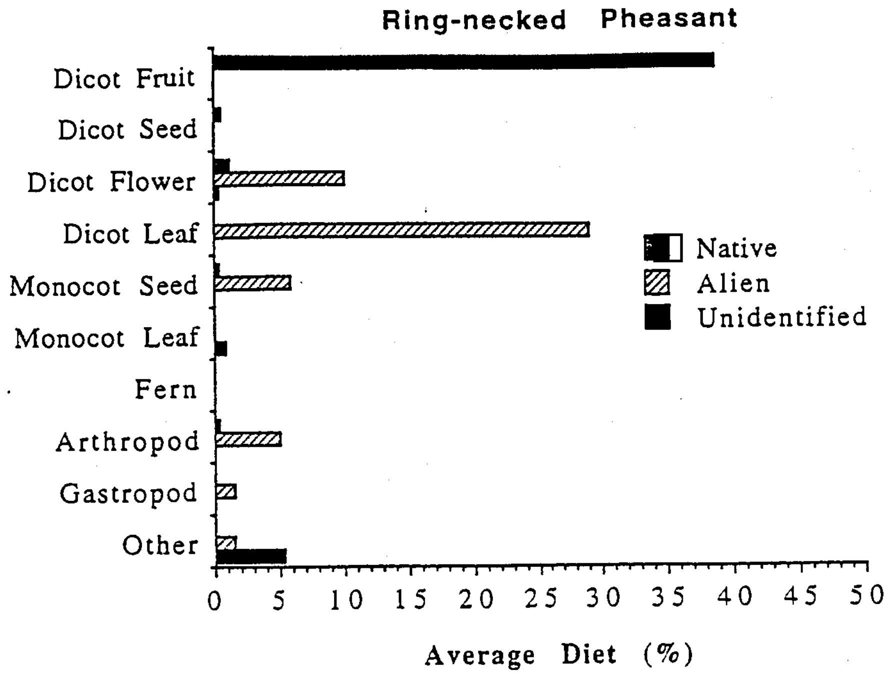


Figure 1. Crop contents of Ring-neck Pheasant (n=43) and Chukar (n=19) collected in the shrublands of Haleakala National Park between 2030 m and 2900 m elevations. Bars represent percentage of the average diet. Statistical significance is indicated by an asterisk (Mann Whitney U Test, $p < 0.05$).



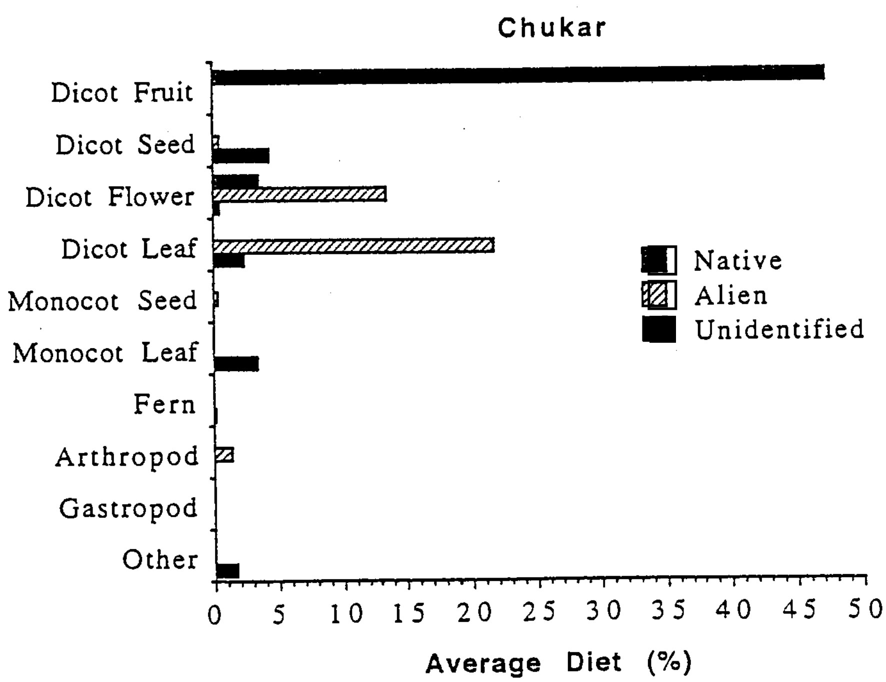


Figure 2. Native, alien, and unidentified food items taken by Ring-necked Pheasant (n=43) and Chukar (n=19) collected in the shrublands of Haleakala National Park between 2070 m and 2900 m elevations. Bars represent percentages of the average diet.

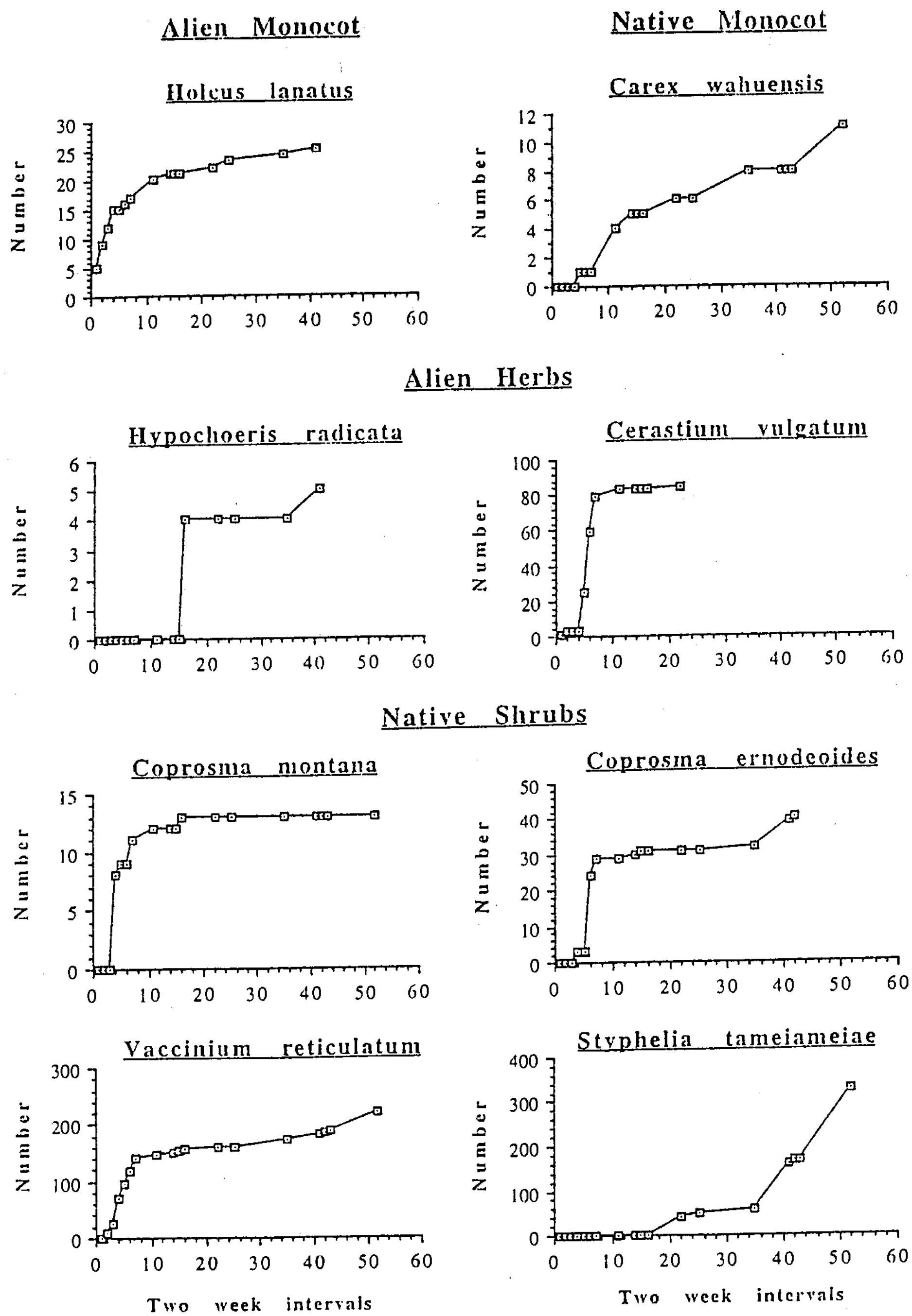


Figure 3. Germination patterns for seeds of eight species occurring in Ring-neck Pheasant droppings. An alien grass (Holcus lanatus), alien herbaceous dicots (Cerastium vulgatum and Hypochoeris radicata), a native sedge (Carex wahuensis), and native shrub species (Vaccinium reticulatum, Coprosma montana, C. ernodeoides, Styphelia tameiameiae) are shown. Data points represent the cumulative number of new germinants at two week intervals for up to two years.