Ecology and behavior of reintroduced Hawaiian Geese

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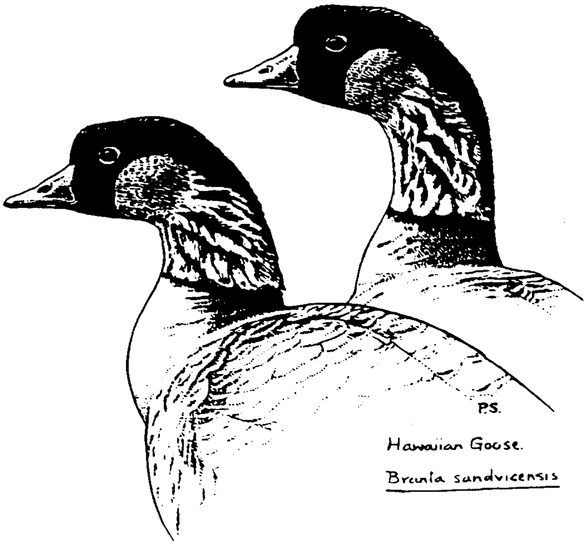
Dedicated to the many people that are working together to save the Hawaiian Goose from extinction



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ZUSAMMENFASSUNG

Von August 1994 bis März 1996 habe ich die Ökologie und das Verhalten von ausgewilderten Hawaiigänsen (*Branta sandvicensis*) im Hawaii Volcanoes National Park untersucht, um daraus Managementvorschläge zur Erhaltung dieser bedrohten Art zu entwickeln. Zusätzlich standen mir seit 1960 gesammelte Wiedersicht- und Brutdaten zur Verfügung.

Beobachtungen über das Brutverhalten und die Habitatwahl verdeutlichen, daß die Gänse, nachdem die Brutterritorien in Nähe der Auswilderungsgehege besetzt waren, vor allem in spärlich bewachsenen Buschländern in mittlerer Höhenlage brüteten. Jungtiere, die in der Wildnis oder in offenen Gehegen aufgezogen wurden, verpaarten sich früher als Jungtiere, die in geschlossenen Gehegen aufwuchsen. Der Kontakt zu den Eltern war nicht nur während des Aufwachsens sondern auch nach der Auswilderung für die Entwicklung des Sozialverhaltens wichtig. Ich empfehle daher, Jungtiere mit den Eltern auszuwildern.

Die anhand von Wiedersichtdaten individuell markierter Hawaiigänse durchgeführten Untersuchungen über die Gruppenstruktur, Verteilung und die Wanderungen der im Hawaii Volcanoes National Park ausgewilderten Hawaiigänse zeigen, daß die Gruppenzusammensetzungen von Jahr zu Jahr variierten. Innerhalb eines Beobachtungsjahres nutzten einige Tiere nur zwei oder drei Gebiete, andere hingegen viele. Um die gesamte Population zu stützen, sollte Gebietsmanagement daher weiträumig sein.

Die saisonalen Verteilungsmuster der Gänse veränderten sich mit der Nahrungsverfügbarkeit in den Busch- und Grasländern. Die Phänologie der Futterpflanzen variierte im Jahresverlauf, zwischen den Studiengebieten und mit der Höhenlage. Das Zeitmuster der Wanderungen und des Brütens war auf die lokale Verfügbarkeit des Futters abgestimmt. Diese Unterschiede sollten beim Habitatmanagement berücksichtigt werden.

Zur Untersuchung des Freßverhaltens von Hawaiigänsen in verschieden Graslandgebieten innerhalb des Hawaii Volcanoes National Parks und der zeitlichen Nutzung dieser Habitate wurden zwei von Gras überwucherte Gebiete gemäht und mit seit längerer Zeit gemähten und bereits von den Gänsen beweideten Grasländern verglichen. Hawaiigänse weideten verstärkt in Gebieten mit proteinreichen Futterpflanzen. Die Nahrungsqualität der Futterpflanzen in den neu gemähten Gebieten war relativ schlecht und die meisten Gänse blieben in den schon vorhandenen Gebieten. Meine Empfehlung ist deshalb, durch regelmäßiges Mähen, Bewässern in Trockenperioden und gezielte Düngung die Verfügbarkeit von Futterpflanzen das ganze Jahr hindurch zu verbessern.

Auf Maui legten Hawaiigänse deutlich größere Gelege als auf Hawaii. Dies könnte daran liegen, daß auf Maui im Haleakala National Park mehr Niederschlag fällt, was die Qualität der Futterpflanzen verbessert und den Gänsen erlaubt, mehr Energiereserven für das Eierlegen anzulegen. Auf Maui wurden durchschnittlich jedoch nicht mehr Junge flügge, was darauf hindeutet, daß andere Faktoren, wie z.B. Prädation, in allen Gebieten eine starke Rolle spielten. Der Bruterfolg von Gänsen, die in prädatorensicheren Gehegen mit Futter nisteten war deutlich höher als der in der freien Wildbahn. Mit einem Wildtier verpaarte Tiere hatten einen höheren Bruterfolg als Paare, die sich aus zwei ausgewilderten Tieren zusammensetzten. Ich empfehle daher, die wilde Population mittels Graslandmanagement und verstärkter Prädatorenkontrolle zu stützen.

Die Anzahl der pro Gelege geschlüpften Jungen stieg zunächst mit dem Alter der Gänse und der Partnerdauer an, nahm aber ab dem neunten Lebensjahr wieder ab. Detaillierte Verhaltensbeobachtungen während sogenannter 'Triumphzeremonien' ergaben, daß das Paarverhalten vom Alter, der Größe und der Dauer, die die Partner zusammen waren, abhängig war. Paare hatten eher ein Gelege, wenn das Männchen weniger stark als das Weibchen triumphierte. Wenn das Weibchen das Triumphverhalten des Männchens ignorierte, hatten Paare einen geringeren Schlupferfolg. Da im Hawaii Volcanoes National Park jedes Jahr nur wenige Junge flügge werden, haben junge Gänse nur eine begrenzte Auswahl an Partnern, was zu suboptimalen Paarbindungen führen könnte.

ABSTRACT

This study investigates the ecology and behavior of reintroduced Hawaiian Geese (*Branta sandvicensis*). Results of the study are used to make recommendations for the management of the species.

After release, Hawaiian Geese established breeding populations around rearing and release pens, but after the maintenance of lowland pens was discontinued, birds moved away and colonized new breeding habitats. New breeding habitats were mainly located at mid-altitude volcanic scrublands with little vegetation cover. Wild-bred goslings and goslings reared by free-flying parents inside predator proof pens paired and bred earlier than foster-reared goslings and goslings reared by parents in closed-top pens. Parental contact was apparently important to development of social skills not only during rearing but after release, suggesting that young should be released with their parents.

The distribution of individual Hawaiian Geese varied between years. Some birds were faithful to a restricted number of areas but others ranged more widely, suggesting some individuals were predisposed to movement whereas others were not. In order for habitat management to be beneficial to a large proportion of the population it should be large scale.

The phenology of food plants varied between sites, rainfall and with elevation. Individually marked Hawaiian Geese timed their movements and nesting according to local food availability. Generally, geese that nested earlier in the season, when food availability was high, tended to be more successful in rearing young but other events, such as predation, caused some early breeders to fail. These local differences should be considered when planning management.

Two overgrown grasslands were mowed and compared with established grasslands that had previously been mowed or grazed by livestock. Sites differed in plant species composition and quality, seedhead production, grass height and rainfall. Hawaiian Geese grazed more in sites that had plants of high nutritional quality. Over time, the variation in rainfall explained a large part of the differing grazing pressure, suggesting that geese used grasslands less during dry periods. Hawaiian Geese remained in established sites and did not move to newly managed sites. To encourage feeding opportunities, my results suggest that grasslands could be managed at a height below twelve centimeters, irrigated in drought periods and fertilized.

Since 1960, 366 goslings were known to have fledged in the three release regions, classified in two breeding situations: 196 in the wild and 161 in or around pens. Perhaps due to higher rainfall and better foraging conditions, clutch size at Haleakala was greater than on Hawaii. Birds in pens had more offspring than those in the wild, reflecting reduced predation and enhanced feeding opportunities. When paired to a wild bird, released birds were more successful than when paired to another released bird. Parent-reared birds in large open top pens, which eventually flew from the pens after fledging, reproduced most successfully. Species management should therefore concentrate on the wild population, through managing grasslands and increased predator control. Large sanctuaries surrounded by predator-proof fences could provide safe breeding grounds for wild birds.

In captivity, clutch size and the number of eggs hatched initially increased with age in males and females, then leveled off and declined for older birds. The number of hatched eggs initially increased with pair duration, but eventually decreased. Body size did not affect reproductive success. Hawaiian Geese were compatible with their partners to a varying degree. The behavioral fine-tuning in social displays in pairs varied in relation to the relative age, size and pair duration of partners. Pairs in which the male display was less intense than the females' displays were more likely to have a clutch. Pairs in which the females did not respond to the males' display advances had a lower hatching success. Concentration of management efforts in a few core areas would ensure that enough birds are recruited every year to allow optimal mate choice.

Schlagworte: Hawaiigans, Verhaltensökologie, Habitatmanagement
Key Words: Hawaiian Goose, Behavioral Ecology, Habitat Management

TABLE OF CONTENTS

Chapter 1: General introduction, background and methods

1. GENERAL INTRODUCTION

In spite of major conservation efforts, the Hawaiian Goose, or 'Nene' (*Branta sandvicensis*), is still among the most endangered waterfowl species in the world. When Captain Cook discovered the Hawaiian Islands in 1778, the population was estimated at around 25,000 individuals (Baldwin 1945, Kear and Berger 1980). Through hunting, habitat loss and introduced predators like dogs, pigs, cats, rats and mongooses, the wild population was reduced to fewer than 30 individuals by 1945 (Smith 1952). These last birds were seen at high elevation on the Big Island of Hawaii, on the slopes of Mauna Loa and Mauna Kea (Elder and Woodside 1958). Populations on other islands had already disappeared.

To save the species from extinction, the State of Hawaii initiated a captive breeding program at Pohakuloa on the island of Hawaii in 1948. A year later, Sir Peter Scott from The Wildfowl & Wetlands Trust started to propagate Hawaiian Geese in Slimbridge, England (Kear and Berger 1980). Since 1960, over 2200 birds have been released on the islands of Hawaii, Maui and Kauai (Fig. 1). The Hawaiian Goose reintroduction program has often been praised as a 'success story' for conservation, but these claims are premature. Few of the released birds survived or succeeded to rear young (Banko 1992, Black *et al.* 1997). When releases were temporarily reduced in the late 1970s, the wild populations declined sharply from more than 875 individuals in 1977, to about 400 in 1980 (Devick 1981, Black *et al.* 1991). Releases had kept the wild population artificially high (Devick 1981, Banko 1988, Stone and Stone 1989; Fig. 2).

The 'Nene Recovery Initiative' - Research against extinction

To identify causes of low survival and productivity of released birds, the 'Nene Recovery Initiative' was launched in 1990 including a comprehensive five year research plan (Black 1990). The Wildfowl & Wetlands Trust in the U.K. teamed up with Hawaii conservation partners including the U.S. National Park Service, the Hawaii State Division of Forestry and Wildlife (DOFAW), the U.S. Fish and Wildlife Service, the University of North Dakota and the Smithsonian Institution. Research included studies on potential limiting factors such as inbreeding, disease, loss of adaptive skills after release, predator detection and nutrition deficiency (Table 1). Six factors are likely to still be limiting recovery of the species (Table 1). Although demographic problems of small population size are often of greater importance than genetic considerations (Simberloff 1988, Craig 1991), inbreeding was found to be potentially limiting in Hawaiian Geese through lowering fertility and survival (Rave *et al.* 1999). Birds reared without parents lost adaptive skills by being less vigilant towards predators and integrating into a flock more slowly than parent-reared birds (Marshall and Black 1992).

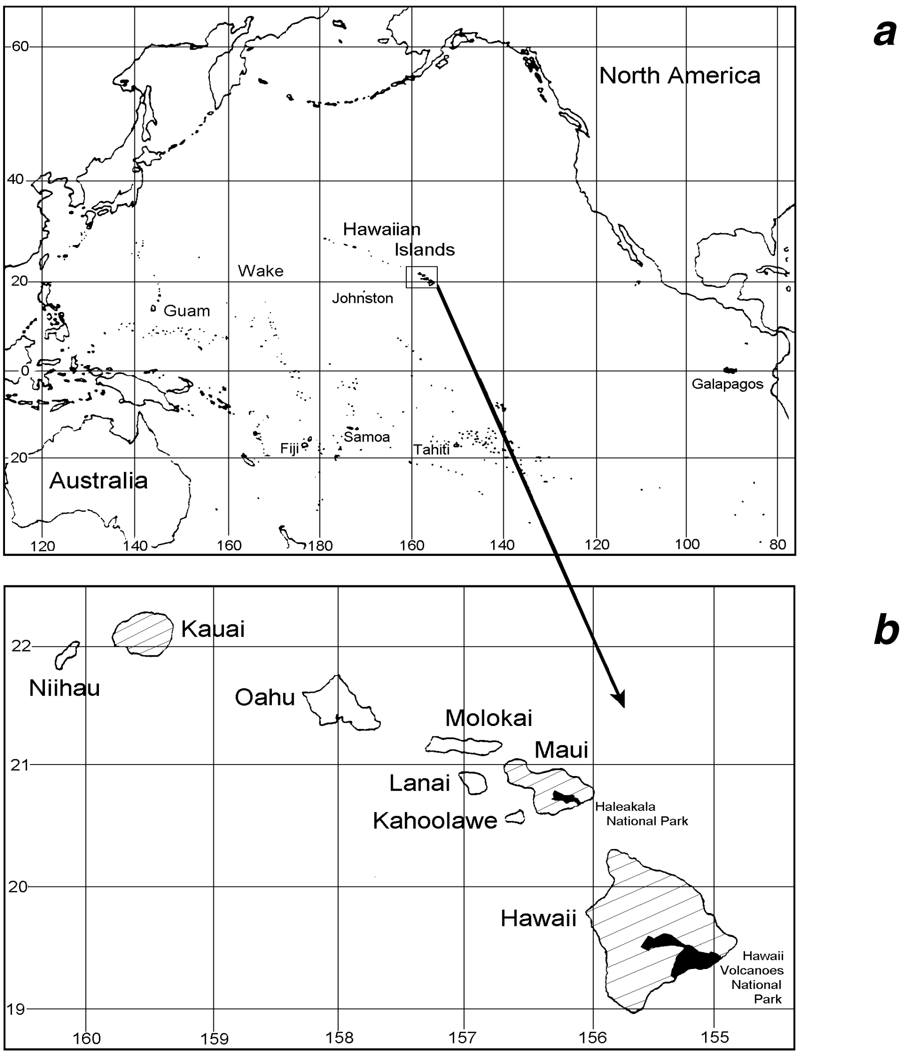


Fig. 1a: Location of the Hawaiian Islands in the middle of the Pacific Ocean. **b:** The main Hawaiian Islands, with Hawaii Volcanoes National Park on Hawaii and Haleakala National Park on Maui (wild Hawaiian Goose populations occur on hatched islands).

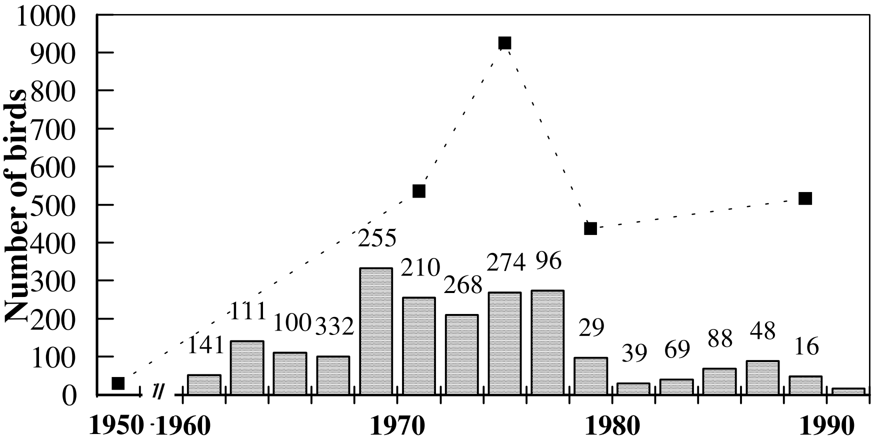


Fig. 2: The trend in numbers (estimates) of Hawaiian Geese in the wild (upper line) and the numbers that were released (lower histogram). Numbers in the histogram are two year sums. From Black *et al.* (1991).

Birds released into upland areas had lower survival rates possibly because the carrying capacity of the habitat in terms of food availability was insufficient and predation levels were high (Black *et al.* 1997). Poor food availability and predation by introduced mammals are thought to be major obstacles on the route to recovery for the Hawaiian Goose (Banko 1992, Black and Banko 1994, Black 1995).

Table 1: Limiting factors, proposed by Stone *et al.* (1983), that were assessed in the Nene Recovery Initiative research program, 1990-1996. From Black (1998a).

Potential limiting factors	Limiting?	Explanation	Recommendation	S
Inbreeding	Yes	Potential low fertility and survival	Optimize genetic diversity in flocks with few founders and emigration	h i l
Disease/parasites	No	Low infestation levels	Research on avian pox	g
Loss of adaptive skills foraging social predator detection	 No Yes Yes	Foraging skills after release sufficient for survival parent-reared birds are best	Research on methods for training prior to release	f d j
Diet/nutrition deficiency	Yes	Exotic plants are a bonus but not enough high-quality food available	Habitat management required	f k
Predation	Yes	40% of nests destroyed by mongoose, lowlands worse than highlands	Intensive predator control	a c e
Poaching/road kills	Yes	Isolated events	Further education	m
Inadequate funding	Yes	Shoe-string budget	Further fundraising and collaboration	b

Sources: a) Hoshide *et al.* (1990), b) Banko and Elder (1990), c) Banko (1992), d) Marshall and Black (1992), e) Black and Banko (1994), f) Black *et al.* (1994), g) Bailey and Black (1995), h) Rave *et al.* (1994), i) Rave (1995), j) Rojek and Conant (1997), k) Black *et al.* (1997) l) Rave *et al.* 1999, m) unpublished anecdotes.

By integrating current research findings into future recovery planning, the problems outlined above may be addressed. Genetic diversity could be increased through translocation of eggs and adults, captive-reared goslings could be trained to avoid predators prior to release, intensive habitat management would allow birds to acquire adequate fat and nutrient reserves and predator control could increase productivity (Banko 1992, Black and Banko 1994, Black *et al.* 1994, 1997, Black 1995, 1998a).

Our knowledge of the species' biology has increased dramatically in the last 30 years (Black 1995), and several factors that limit recovery have been identified. But for species recovery, research into the effectiveness of reintroduction techniques and habitat requirements remains vital. Before committing large funds for state-wide programs, we need to know exactly how and when to manage habitats.

My thesis sets out to increase our knowledge of the species' biology in relation to reintroduction parameters and to test some management actions at a local level in order to make state-wide recommendations.

2. BIOLOGICAL BACKGROUND

The Hawaiian Goose is a medium-sized, black and brown goose endemic to the Hawaiian Islands (Fig. 1a, b). Like most geese of the genera *Branta* and *Anser*, Hawaiian Geese are herbivores and pair for life. They have adapted to live on land throughout their annual cycle. Courtship, copulation and rearing of young takes place entirely on land. Morphological changes to their body include reduced webbing between their toes which may be an adaptation to walk and climb on rugged lava flows. Leg muscles are proportionally more developed than in other goose species and wing muscles are reduced (Miller 1937), but birds are fully capable of flight. Having evolved in the isolation of the Hawaiian Islands, the geese do not exhibit migratory behavior that is typical of all other northern goose species. Conditions on the islands support the birds year round. The Hawaiian Goose population is the most isolated goose population in the world.

Historic range and ancestors

Sub-fossil remains of Hawaiian Geese have been discovered on all main islands except on Oahu (Olson and James 1991), but today Hawaiian Geese are only found on the islands of Hawaii, Maui and Kauai (Fig. 1b). Based on mitochondrial DNA evidence and geologically calibrated estimates of time, Hawaiian Geese diverged from a modern, large subspecies of the Canada Goose 0.82 - 1.08 million years ago (Paxinos 1998). Occasional sightings of Canada Geese (*Branta canadensis*) are not uncommon in Hawaii today. Sub-fossil bones of at least ten more goose species have been described of which at least seven were flightless (Olson and James 1991). It is hard to imagine what habitats these species lived in and what niche Hawaiian Geese may have occupied. The distribution of the sub-fossil records suggests that many of the large extinct goose species lived in rainforest habitat at different elevations but Hawaiian Goose bones have been found along an elevational gradient in more sparsely vegetated, open habitat (Helen James pers. comm.).

Breeding biology

In the late 18th century, naturalists reported that Hawaiian Geese bred primarily in the lowlands and then moved to higher elevations with their fledglings (Henshaw 1902, Perkins 1903, Munro 1944). From 1960 onwards, nests have been found from sea level up to 2300 m high, in ecological zones ranging from coastal lowland to sub-alpine (Müller-Dombois 1976), but an altitudinal migration pattern cannot be observed today. Hawaiian Geese nest in the usually wet winter months, between September and April, when food is more abundant, using a variety of habitats. Typically, the female scrapes a shallow nest bowl in open lava deserts under shrubs such as Pukiawe (*Styphelia tameiameiae*), Aalii (*Dodonaea viscosa*), small Ohia trees (*Metrosideros collina*) or *Sadleria* ferns. The volcanic, open scrubland desert habitats usually have lower predator densities, but are far away from food. Some geese use more dense cover like the mixed grassy scrub around Paliku in Haleakala Crater, whereas others nest along cliffs or in fresh burns with virtually no vegetation cover (Banko 1988). Hawaiian Geese are determinate layers, the female produces an egg every 2 days (Kear and Berger 1980, Banko 1988) and lines the nest with down when starting incubation. Incubating females can be recognized by a bare patch on their lower chest, known as the brood patch. Males do not incubate, but guard the nest and their mate, usually from a slightly elevated position. Eggs are large in relation to female body weight and clutches are relatively small (range 2 - 6 eggs), which is typical for island waterfowl species (Lack 1968). With an average of 30 days, the incubation period is the longest in any goose species. Large eggs and long incubation periods are thought to increase the maturity and mobility of goslings (Lack 1968), which is important for Hawaiian Geese as young usually hatch far from suitable food and have to travel over rugged lava to rearing areas, which are typically pastures (Stone *et al.* 1983, Hoshide *et al.* 1990). Parents leading goslings are very vigilant and have, on some occasions, been observed to defend their offspring against introduced ground predators (Banko 1988), such as the mongoose (*Herpestes auropunctatus*). Goslings fledge after 10 - 12 weeks, but typically stay with their parents until the next breeding season (Kear and Berger 1980).

In summer, birds give up the territorial behavior they exhibited throughout the winter whilst breeding and aggregate in flocking areas. This is where young birds are thought to choose their mates.

3. GENERAL METHODS

The study areas

The Hawaiian archipelago is located in the middle of the Pacific Ocean more than 3800 km west of North America and over 6200 km east of Japan (Fig. 1a). The island chain ranges over 2500 km and comprises more than 132 volcanic islands. Over 99% of the land area is located on the eight southeasterly islands: Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Niihau and Kauai (Fig. 1b). Hawaiian Geese became extinct on all the islands except Hawaii, but today reintroduced populations are found on Maui and Kauai. In 1997, about 885 wild Hawaiian Geese were estimated in the Hawaiian Islands, as follows: 393 on the island of Hawaii, 236 on Maui and 256 on Kauai (Banko *et al.* in press). Most of my work concentrated on the Hawaiian Goose population in Hawaii Volcanoes National Park (19°15'N, 155°15'W) on Hawaii. The Park comprises an area of 85,000 ha ranging from sea level to 4164 m on the summit of Mauna Loa. Hawaii is one of the geologically youngest land masses on earth and its' volcanoes are still active. Lava flows, cinder fields and ash prevail; most soils are young. Depending on the age of the soils and local rainfall patterns, succession of plants is at different stages. The vegetation is stratified altidudinally and pastures are scattered between forest and scrubland areas.

Vegetation composition has changed dramatically within the range of the Hawaiian Goose, especially in lowland and mid-elevation areas that are believed to have been open woodland before human settlement (Cuddihy and Stone 1990). Through human alteration such as farming, large areas of open woodland have become pasture consisting primarily of introduced grass species which are readily eaten by the geese (Black *et al.* 1994). In the morning birds often fly to pastures, but at night they typically roost in open lava deserts. In general, Hawaiian Geese prefer open areas where they can see potential predators approaching.

Documenting reintroduction

It is crucial that birds are adequately monitored after release so that an evaluation of the success of a reintroduction program can be carried out (Black 1991, Kleiman *et al.* 1994). Only if released birds produce sufficient offspring to equate with mortality in the wild population, can a reintroduction program be deemed successful. Throughout the Hawaiian Goose reintroduction program, released birds and many of their offspring were marked with individual leg bands and subsequently resighted. Recently, the Nene Recovery Initiative collated data collected throughout the program into a comprehensive database (Hunter and Black 1995), making an analysis of the long-term data and a long-term assessment of the reintroduction program possible. The database contains six main files including information on banding, bird measurements, resighting, nesting, predators and death. The two main files which I analyzed were the resighting and nesting records. The banding file was also used to identify the sex and parentage of a bird, its' age, and rearing and release history.

1. The island-wide nest-record database

Data compiled in the nest-record database included information on laying dates of individual birds, clutch size, number of fertile and infertile eggs, number of eggs predated per clutch, number of eggs hatched and number of goslings fledged. Since the beginning of the reintroduction program, the number of nesting pairs located each year fluctuated considerably, probably mainly due to unquantifiable differences in observer effort, both in terms of area covered and man-hours spent in the field (Fig. 3). Most nests were found on Hawaii (465 in Hawaii Volcanoes National Park with relatively constant observer effort and 256 from the rest of the island) and 170 nests were recorded on Maui, resulting in a total of 890 records with known nesting locations. Since the release of Hawaiian Geese on Kauai, birds have successfully bred there, and today the population is estimated at around 200 birds (Banko *et al.* in press).

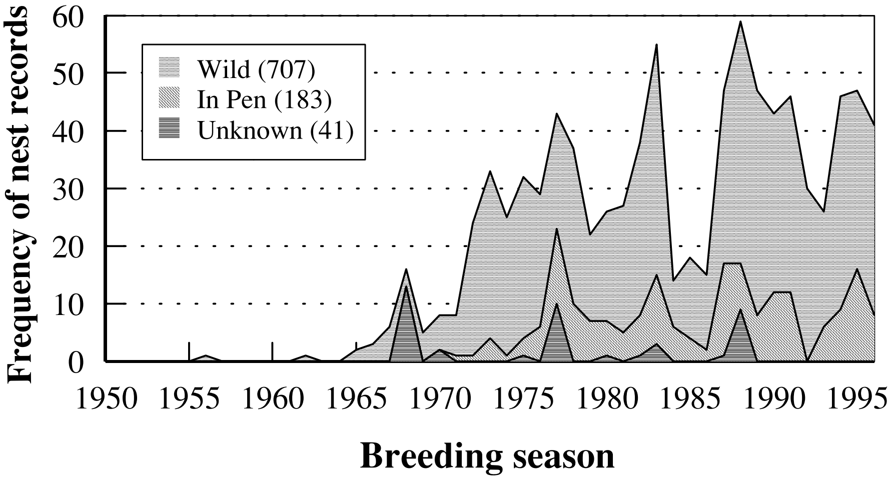


Fig. 3: Annual number of Hawaiian Goose nesting pairs recorded in the wild and in breeding pens (1950 = 1950/51 breeding season), total nest records n = 931 from Hawaii and Maui. Breeding pens were open-top or closed-top (for locations see Chapters 2 and 6)

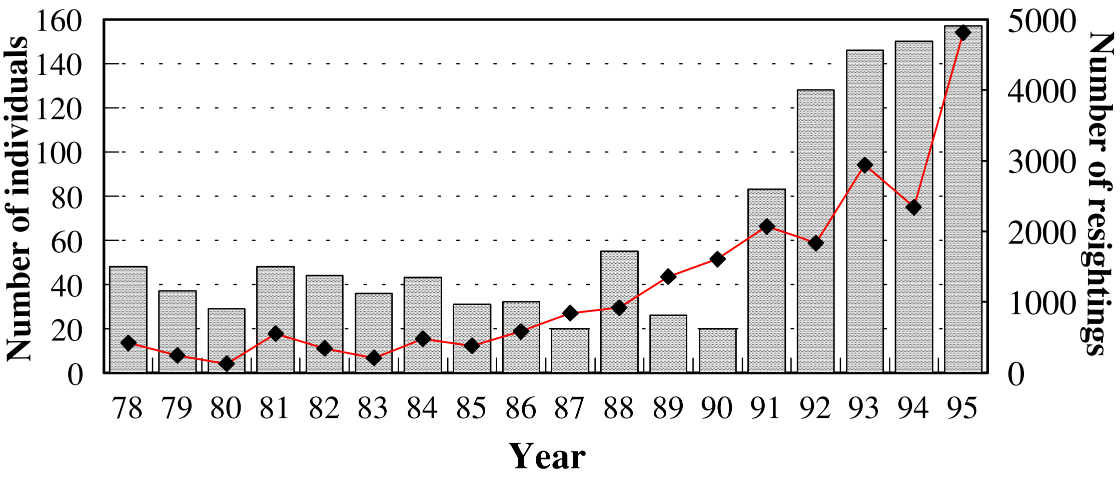


Fig. 4: Number of individuals seen annually, as identified by their leg bands (indicated by bars, left axis) and annual resighting data collected between 1978 and 1995 (diamonds, right axis) in Hawaii Volcanoes National Park. Data from 1996 were incomplete and are therefore not presented.

2. The Hawaii Volcanoes National Park resighting database

Although resighting data were available from other areas, I concentrated my analysis on data collected from Hawaii Volcanoes National Park. Most areas known to be used by Hawaiian Geese were searched at least monthly and band number, location, date, time of day, flock size, mate and number of associated goslings were noted. The database encompasses over 23,600 resighting records of 479 individually marked birds resighted between 1978 and 1996. On average, individual birds were resighted 14.6 times a year and were seen for an average of 4.25 years. Some birds were sighted in all 18 consecutive years of the study. Figure 4 shows how many individuals (identified by their leg bands) were seen each year and the total annual number of resightings.

THESIS OUTLINE

Reintroduction of captive-bred animals can be viewed as an experiment in conservation, and in my thesis I report some of the results of this large-scale, outdoor experiment which has been running for over 40 years. I hope to demonstrate how long-term data and specifically targeted research projects can be used as a tool for conservation, in assessing the success of the reintroduction program and to fine-tune recovery techniques. The state-wide Hawaiian Goose database is the foundation for Chapters 2, 3 and 6. Chapters 4, 5, 7 and 8 report results from research projects I specifically designed.

At Hawaii Volcanoes National Park, Hawaiian Geese were released into an area that was devoid of a wild population. In Chapter 2, I describe reasons for the natal dispersal pattern observed from several rearing and release sites. I then look at the effect of rearing and release techniques on the age at first pairing and describe where birds found their mates. In Chapter 3, the flock structure of Hawaiian Geese in Hawaii Volcanoes National Park is described; distribution patterns and movements of individual birds over the years are also assessed. In Chapters 4 and 5 I consider what factors may cause distribution patterns. Chapter 4 deals with annual habitat use and how bird distribution and timing of nesting in scrublands was related to rainfall patterns and subsequent food plant phenology. Using a combination of behavioral and ecological field methods, Chapter 5 provides new information on foraging behavior and temporal use of grasslands, outlining the implications for grassland management.

Only if released animals reproduce in the wild will a reintroduction program be successful. In Chapter 6, I look at how a bird's rearing and release history affected reproductive success. By following a bird's success throughout the reproductive cycle, I pinpoint stages where problems may occur. Determining the variation in reproductive parameters between different rearing and release styles enables me to test the significance of social learning to future performance of individuals.

Predation pressure and food availability are among factors which are difficult to control for in the wild. Captive animals may provide research findings that, whilst controlling for these factors, can assist the wild population. Research for Chapters 7 and 8 was conducted on a captive population of Hawaiian Geese at The Wildfowl & Wetlands Trust in Slimbridge, U.K. In Chapter 7, I study the effect of age and size parameters on reproductive success and by looking at how the age and size of a partner may affect success, I try to find evidence for assortative pairing. I conclude my thesis with a detailed study of pair compatibility and provide some evidence for measurable behavioral differences between individuals and their mates.

Hawaiian Geese are rare and, unlike many other geese, they do not nest in colonies but in a dispersed fashion. Consequently their nests are hard to find. Where other goose studies can rely on very large sample sizes (e.g. Snow Goose or Barnacle Goose studies; Cooke *et al.* 1995, Owen and Black 1991) sample sizes in some of my comparisons are rather small, but this problem is intrinsic when studying endangered populations.

To facilitate publication, chapters are written in paper format. Because chapters stand on their own, invariably some background information and central ideas are repeated.

Chapter 2: Natal dispersal and pairing in Hawaiian Geese: colonization of new habitats and the importance of parental contact after release

INTRODUCTION

Recent research highlights the great variety of natal dispersal patterns found not only between different species but also between populations of the same species (e.g. Martin and Hannon 1987, Robinson and Oring 1997). There is considerable individual variation in natal dispersal which may be an expression of different evolutionary strategies (Cooke and Abraham 1978, Robinson and Oring 1997). It is unlikely that all individuals in similar environmental conditions will make the same choices. Individuals who stay in a good habitat will be rewarded, whereas those who move into unknown, new habitats take a risk. The lack of prior knowledge of good feeding areas and predators might be disadvantageous. In social animals like geese, individuals that move to new areas will have to reestablish their position in the rank order of a flock, which might involve aggressive encounters with risk of injury (Black 1998b). However, philopatry may be costly if the natal habitat deteriorates (Cooch *et al.* 1993, Rockwell *et al.* 1993, Williams *et al.* 1993, Robinson and Oring 1997, Spear *et al.* 1998) or is limited (Drent *et al.* 1998) and it might be adaptive for animals to leave their natal area.

Female ducks, geese and swans tend to nest in areas where they were reared and their male partners typically follow them to these sites (reviewed by Anderson *et al.* 1992). Female Hawaiian Geese have been seen to return to their natal area for breeding, whereas male juveniles are thought to disperse (Banko and Manuwal 1982, Banko 1988). When breeding pairs colonize new habitats, however, the female philopatry and male dispersal mechanism must not be operative (Black 1998b). In the initial phases of the reintroduction program, Hawaiian Geese were released into an area devoid of a wild population and subsequently colonized new habitats. The choice of breeding habitat was not learned from wild birds. As the population grew and with the first offspring produced in the wild, an increasing number of nesting territories became occupied (Banko 1988).

In the wild, young geese stay with their parents until the next breeding season. During this period goslings are thought to learn various traits from their parents, such as location of feeding habitats and social skills (Black and Owen 1987, Marshall and Black 1992). They might encounter their future mate during this time and form a pair bond for life (Choudhury and Black 1993). Throughout the reintroduction program, many Hawaiian Geese have been reared and released without their parents and hence lack this early experience. Goslings reared without their parents were less vigilant and integrated slower into a flock than goslings reared with parents (Marshall and Black 1992) and their mortality after release was higher (Black *et al.* 1997). In Hawaii Volcanoes National Park, all goslings were reared with their parents but were released either with or without them. Parental contact after release from the rearing pens may be important for a bird's procurement of mates, food and other resources.

My objectives in this chapter are to: (1) describe the colonization of new breeding habitats; (2) compare natal dispersal distances between the sexes, and in relation to bird origin (Hawaii Volcanoes National Park, Pohakuloa or the wild), rearing and release history and (3) describe how the age at first pairing varies with rearing and release techniques employed, and how this influences the age at first breeding, dispersal distance and a bird's reproductive success. Understanding how the different release techniques affected a birds' dispersal patterns, mate choice and initial breeding attempts might guide future management of limited genetic stock and reintroduction strategies.

STUDY AREA AND METHODS

Hawaii Volcanoes National Park (19°15'N, 155°15'W) comprises an area of 85,000 ha ranging from sea level to 4164 m on the summit of Mauna Loa. In an attempt to establish a wild, self-sustaining Hawaiian Goose population, captive propagation within the National Park was initiated in 1972, concentrating on low to mid elevations (Hoshide *et al.* 1990). Figure 1 shows the study area and locations of the breeding and release pens. Captive breeders and their offspring were provided with commercial chicken food and water. Predators in the area around the pens were controlled.

Banding and resighting

Throughout the reintroduction program, released birds were fitted with unique leg bands. During the later stages of the program, when the first released birds started to nest in the wild, the majority of their offspring were caught and banded before fledging (also see Chapter 3, 4 and 6). Most areas known to be used by Hawaiian Geese were searched at least monthly and band number, location, date, time of day, flock size, mate and number of associated goslings was noted at each visit. Since the first releases in 1974 (Hoshide *et al.* 1990), the population within the National Park has grown to about 200 individuals in 1998 (Banko *et al.* in press).

Nest searches

Nest searches were carried out throughout the breeding season between October and March for most years from 1976 onwards (see Chapter 6 for details in methodology). The large size of the breeding areas and the length of the breeding season made a constant search effort difficult and some nests may have remained undetected. With regard to natal dispersal, incomplete data may bias our recorded age of first breeding but will probably not affect the location of the nest as the majority of Hawaiian Geese are philopatric to a chosen nesting area (Banko 1988).

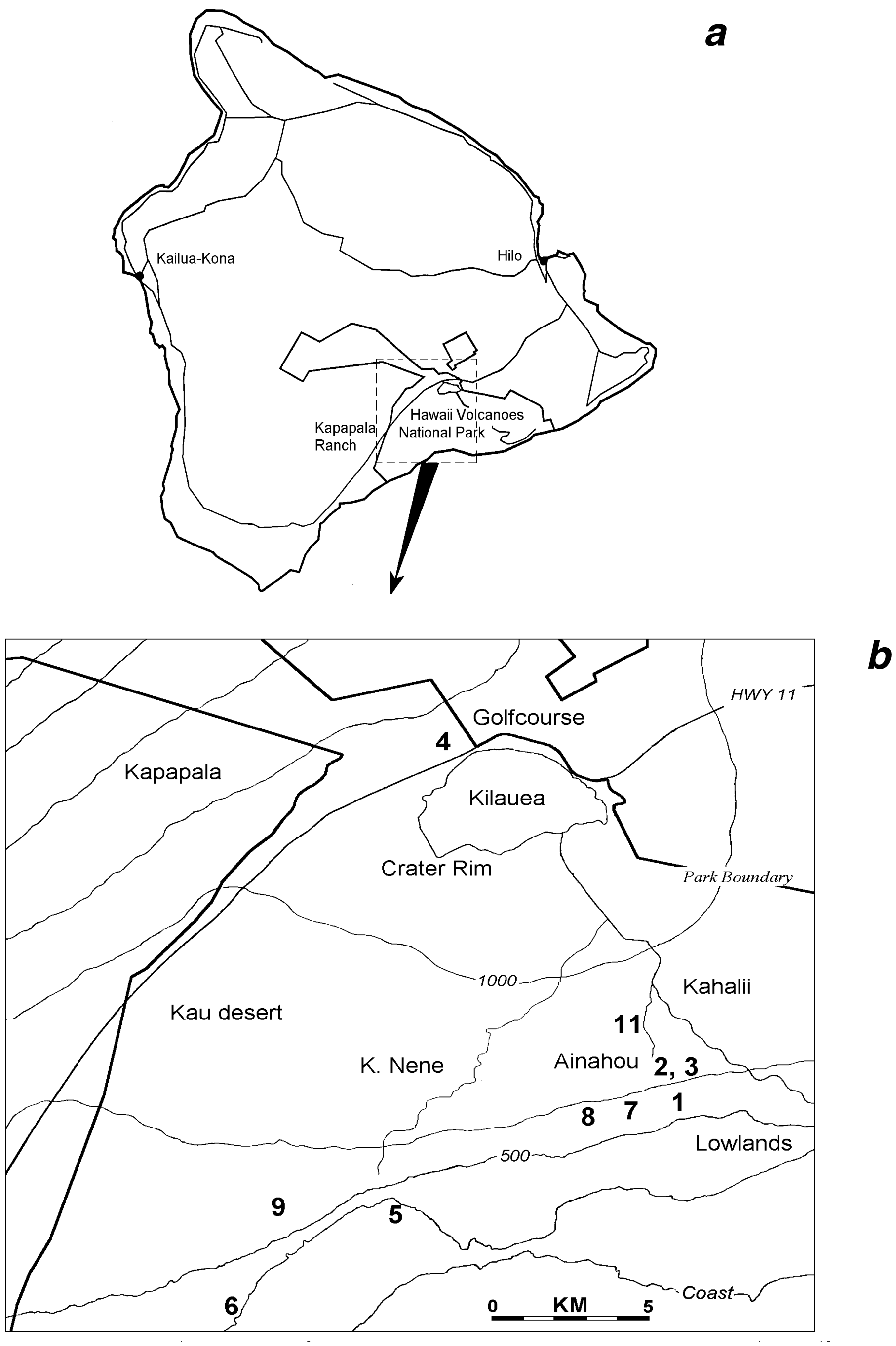


Fig. 1a: Hawaii island with Hawaii Volcanoes National Park and b: location of breeding and release pens (contours in 250 m intervals).

Bird origin

I distinguished three types of birds: (1) National Park birds (referred to as 'HAVO') that were usually reared in and released from the pen in which they hatched. These include a few birds that were translocated to a different pen for release; (2) birds from the Pohakuloa Endangered Species Breeding Facility run by the State of Hawaii were released from the pen in which they were foster-reared in (referred to as 'State' birds); and (3) offspring from released birds were regarded to have originated from the wild (referred to as 'wild'). The above classifications were further subdivided according to the specific rearing and release technique employed.

Rearing and release techniques

In the National Park, birds were reared by their parents until fledging. The majority of the Pohakuloa birds were fostered to captive parents in the National Park between 3 - 6 weeks of age. In the National Park, captive parents nested either in closed-top or open-top breeding pens (OP-PCnF: Open Pen, parents cannot fly). Closed-top pens were small (approx. 25 m^2) whereas open-top pens were larger (between 0.3 and 1.5 ha). Some wild parents voluntarily nested inside open-top breeding pens (OP-PCF: Open Pen, parents can fly), taking advantage of the supplemental feed and predator protection. Most young were released by allowing them to fly from their release pens at their natural time of fledging (see Chapter 6), when they were between 2 - 4 months of age (n = 203); 17 birds were released at an older age.

'Hatching site' includes rearing site. 'Release site' includes birds that were released from their hatch site and birds that were transferred to a different pen for release. 'Natal area' refers to the pen or area in which young hatched or were released. 'Natal dispersal' relates to dispersal from the hatch and release site to the site of first breeding. Breeding pens were often used as release pens and some birds bred in release pens.

Data analysis

Distances from the hatching and release site to the first recorded nest site were measured on a map to the nearest kilometer. Distance data were skewed and therefore log transformed. As most partners in a pair originated from different hatch and release sites, male and female dispersal distances were regarded independently. Data were classified according to management period. The early period between the 1973/1974 and 1983/1984 breeding seasons was characterized by propagation in low and mid-elevation breeding pens. During the later period (1984/1985 - 1995/1996) birds were only bred at mid-elevation at Pen 7 (730 m) and Pen 11 (850 m). Habitats were classified into three types: open scrubland, grassy scrub and grasslands. Scrublands were open, volcanic desert with scattered bushes. Grasslands were managed pastures with predominantly grass cover. Grassy scrub was a mixture of shrubs and unmanaged tall grasses.

To test the effect of sex, origin, rearing technique, management period and chosen first breeding habitat on natal dispersal distance, a general linear model was developed using GLIM

(NAG 1993). All variables and interaction terms were fitted to the initial model. Progressive removal of the variables that explained the least variance in natal dispersal distance produced the most parsimonious model (Crawley 1993).

Timing of pair formation was calculated by subtracting hatching date from date of first sighting with a partner. The majority of birds were sighted at least once a month, hence I expressed the timing of pair formation in months. Only birds that were seen together for at least 10 times were considered to be a pair. I tested the effects of rearing technique and release age on the timing of pair formation. I then tested if the age at first pairing explained first breeding age, whilst controlling for possibly confounding factors including management period, distance moved to first breeding site, habitat first bred in and rearing technique. I followed the modelling procedure described above. Age at first pairing was fitted as a continuous variable with a Poisson error. Some of the data were overdispersed and consequently the constraints imposed by the declaration of a Poisson error distribution were modified by adjustment of the scale parameter. This was achieved by dividing the Pearson Chi-square statistic by the residual degrees of freedom (Crawley 1993).

The total number of fledglings produced from first breeding until death or up to 1997 was taken as a measure of an individuals' overall productivity and analyzed with a Poisson error structure for each sex separately, controlling for potentially confounding variables. Data was too limited to control for longevity and thus results have to be interpreted with caution. Age and distance data were fitted as continuous explanatory variables and squared terms tested as well. To further elucidate natal dispersal distance, I grouped it into four categories: 1) No movement, 2) moved 1 - 5 kilometers, 3) moved 6-10 kilometers and 4) moved more than 10 kilometers. I then summarized fledgling production in the four categories. Frequencies were compared by using G-tests (Crawley 1993), which are equivalent to non-parametric chi-square tests and allow the testing of small samples (Fisher's exact).

RESULTS

Individual natal dispersal events

Individual natal dispersal events, for males and females reared within the National Park (41 males and 38 females; Fig. 2 and 3), and for birds fostered to National Park breeding pairs from Pohakuloa (19 males and 16 females; Fig. 4), reveal a large variety of dispersal patterns. The maps are ordered by dispersal from specific rearing and release pens (Pens 1 - 11) and from the wild. Most birds hatched and reared in the National Park were released from the pens in which they were reared in (n = 63; solid arrow, dot indicates breeding at the hatch and release site) or were wild (n = 3), but some were translocated to a different pen for release (n = 17; dotted arrow: start of arrow indicates rearing site; the second pen along the arrow indicates the release site). Translocation from the hatch site did not affect dispersal distance from the release site (F = 0.006, df = 1, P >0.05). From the data presented in the maps it is not possible to conclude that translocation prior to release affected a bird's first breeding site. Some birds moved into the National Park from surrounding areas (Fig. 4, bottom; n = 22). These included 15 birds released from Keauhou (between 2 and 23 km) moved between release site and first breeding record), 4 birds from Keauhou II (47 - 65 km), 2 birds from Kahuku (26 km) and one bird from Kipuka Ainahou (30 km). A summary of the natal dispersal events presented in the maps and distances dispersed from the release pens in Hawaii Volcanoes National Park is given in Tables 1 and 2. Some birds did not disperse to breed but nested at their release pen (Table 1). For example, a breeding tradition was established at Pen 7 where breeders took advantage of the supplemental food provided.

Table 1: Number of birds (males and females are pooled) and areas they moved to nest for the first time in relation to their release area and pen. Only birds with known hatch and release site are presented (including Pohakuloa birds). Area codes: A-l = Lower Ainahou, A-u = Upper Ainahou, Kah = Kahalii, K.-N. = Kipuka Nene, Rim = Crater Rim (includes Devastation), GC = Golfcourse, Kau = Kau desert, Kap = Kapapala Ranch, Low = Lowlands.

Release		Release	**First nest recorded at:**									
Area	**Pen**	Pen	A-l	A-u	Kah	K.-N.	Rim	GC	Kau	Kap	Low	***Total***
A-l	1		2	1	1		1	1	1			***7***
	5	2	1		2		1					***6***
	6	4	1		1					1		***7***
	7	10	1	5	1	8	7		3	1	1	***37***
	8	1	5	1	1	2			2			***12***
	9		1			1	1					***3***
A-u	2	1	3	3		2	1	1	1			***12***
	3		4				1	2				***7***
	11		3	5	5	2	2		2		1	***20***
GC	4		1			1		1		1		***4***
Total		***18***	***23***	***15***	***11***	***16***	***14***	***5***	***9***	***3***	***1***	***115***

Table 2: Natal dispersal distances by release pen for 60 male and 58 female Hawaiian Geese with known hatch and release site (see Figs. 2, 3 and 4).

	Males					Females				
Release	Distance moved (km)									
Pen	0	≤ 1	≤ 2	≤ 3	> 3	0	≤ 1	≤ 2	≤ 3	>3
1				2	1		1			3
2		1	1	1	2	2	1		1	3
3				3			1			3
4		1			2					1
5	1				2	1				2
6	2				2	2				1
7	2	1	1	4	12	7	1			9
8		1	2		3	1		1	1	3
9					3					5
11		3	4	1	2		2	2	1	1
Wild							2			
Total	5	7	8	11	29	13	8	3	3	31
Average distance	-	*0.94*	*2.0*	*2.64*	*10.6*	-	*0.94*	*2.0*	*2.67*	*9.26*

Most birds moved more than one kilometer to their first nest site. Difference in natal dispersal distances between the early and late period, between the sexes and with other parameters are described below.

Change in natal dispersal distance over time

Natal dispersal distances changed throughout the reintroduction program (Fig. 5). In the early phase of the program, 33% of the birds undertook their first nesting attempt in and around their natal breeding pen. From 1984 onwards, the number nesting in and around pens dropped to 9% and most birds dispersed to new breeding areas.

Colonization of new breeding habitats

In the wild, the first natal dispersal events over more than two kilometers occurred in the 1981 breeding season with one first breeding attempt at Kipuka Kahalii and one in the Kau desert (Table 3). In the same season, two nests were recorded at Crater Rim from two birds that moved over 14 kilometers into the National Park from the State Sanctuary at Keauhou. Birds released from the National Park started breeding there in the following year. No substantial wild breeding population was established at Lower Ainahou. Most birds breeding there made use of supplemental feed in the breeding and release pens and moved away after the breeding pens and associated supplemental food there were phased out (see below). Breeding around the Golfcourse ceased after the breeding pen and associated supplemental food there was phased out. Between 1995 and 1998, one pair nested at the end of the Chain of Craters road at sea level. Prospecting breeders have been reported recently from an area east of Mauna Ulu,

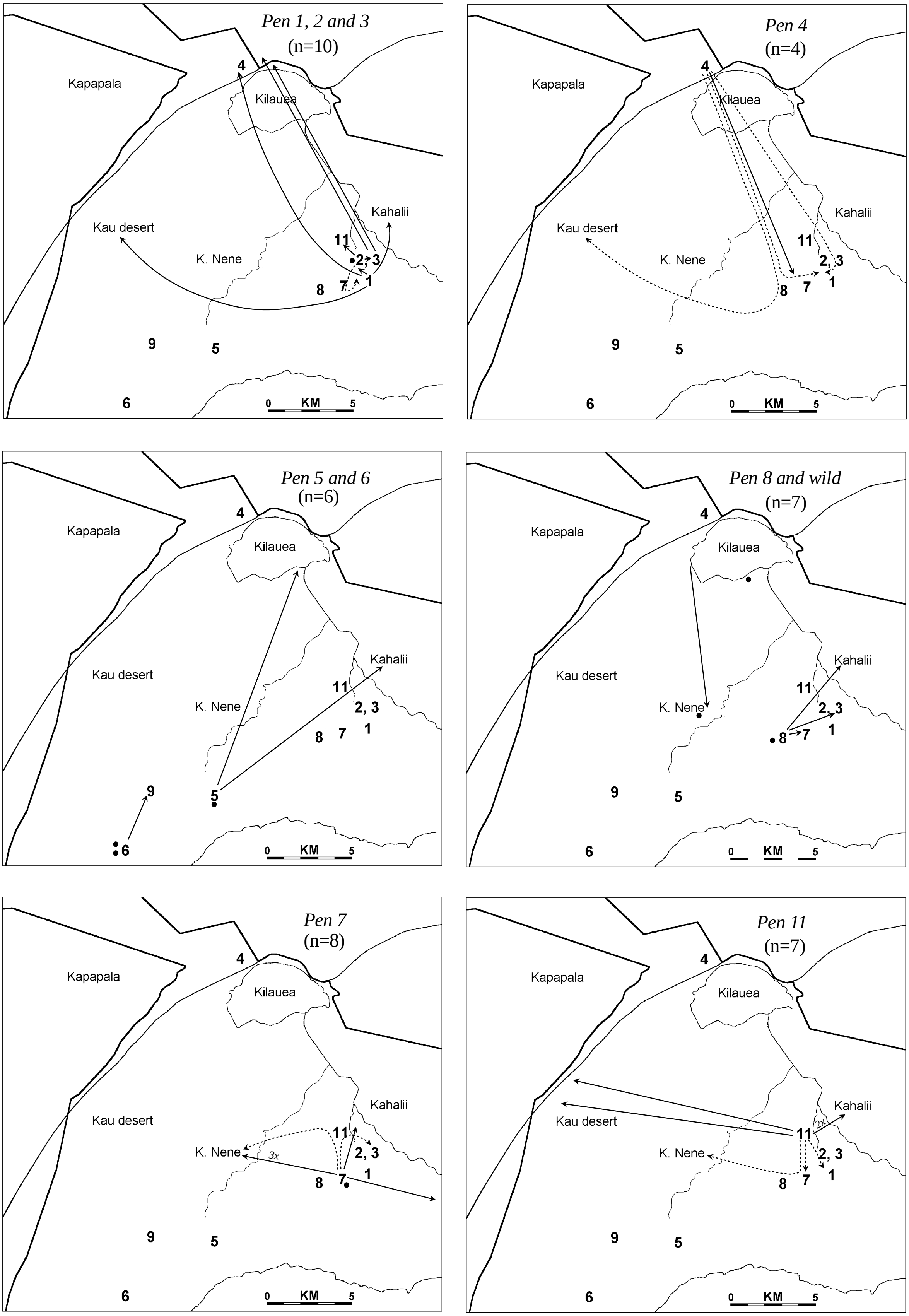


Fig. 2: Female dispersal from the hatch site in Hawaii Volcanoes National Park between 1977 and 1997. Unless indicated otherwise (e.g. 3x = 3 birds), one line refers to one bird (solid line where release site equals hatch site, dotted line indicates a transfer to a release site different from the hatch site). Dots represent breeding in the natal area.

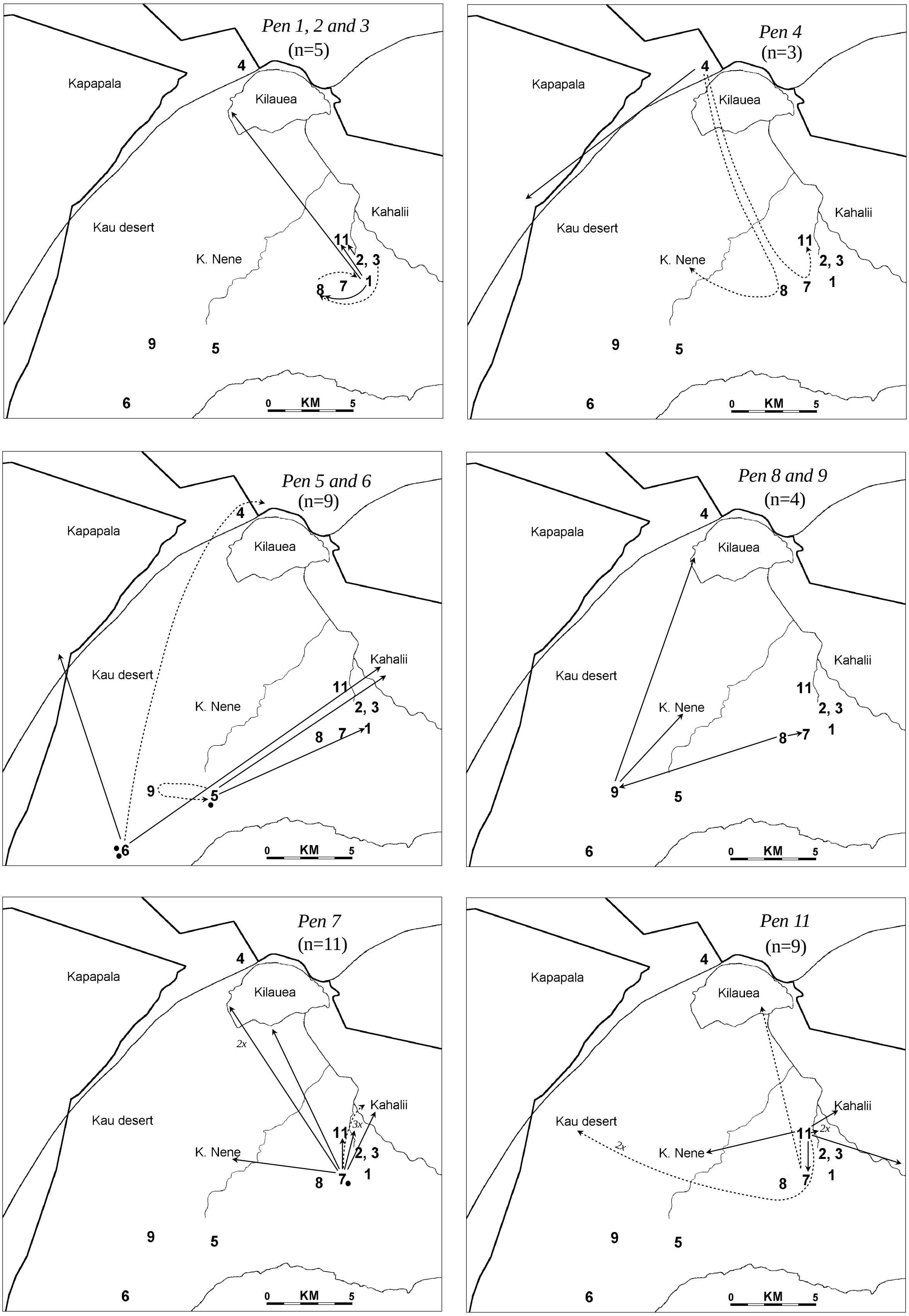


Fig. 3: Male dispersal from the hatch site in Hawaii Volcanoes National Park between 1977 and 1997. Unless indicated otherwise (e.g. 3x = 3 birds), one arrow refers to one bird (solid line where release site equals hatch site, dotted line indicates a transfer to a release site different from the hatch site). Dots represent breeding in the natal area.

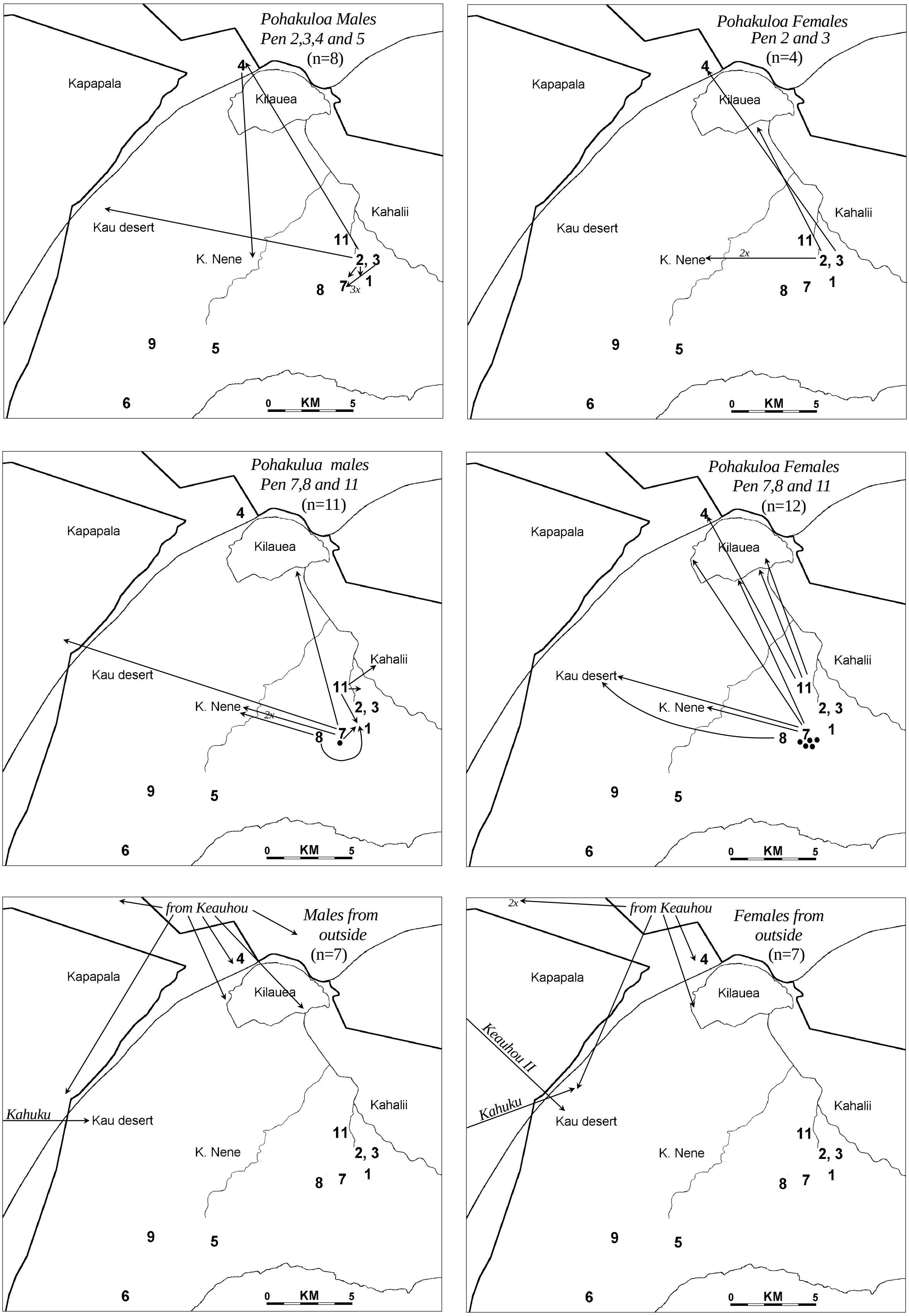


Fig. 4: Male and female dispersal from the release site in Hawaii Volcanoes National Park of birds reared at Pohakuloa between 1975 and 1997. Dots represent breeding in the natal area.

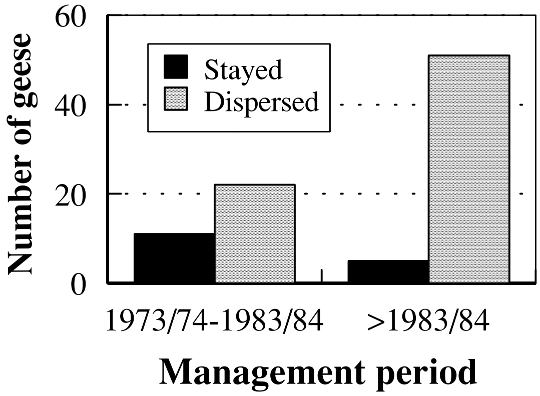


Fig. 5: Number of natal philopatric and dispersing geese in the early and later stages of the reintroduction program. More birds dispersed in the later stages of the program (G = 8.14, df = 1, P < 0.005; 1973/74 = breeding season between October 1973 and March 1974)

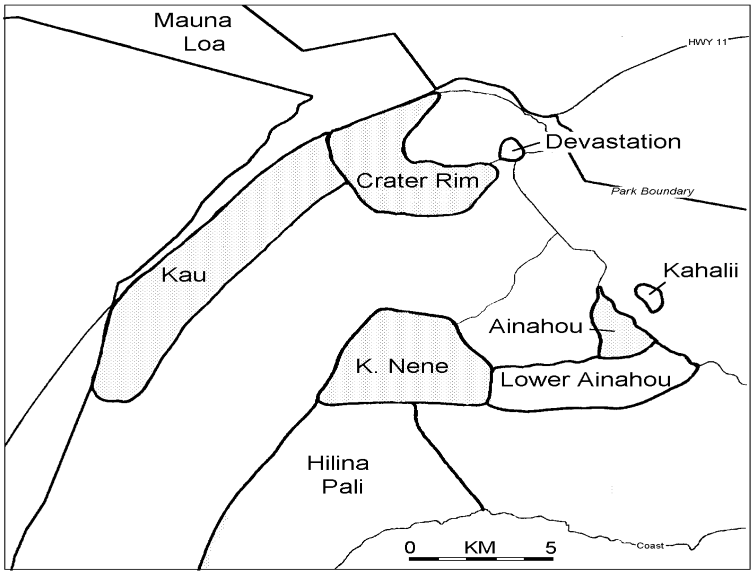


Fig. 6: Nesting areas in Hawaii Volcanoes National Park (main areas shaded)

which illustrates that the colonization process is ongoing. Colonization of the wild habitat was apparently not affected by elevation (Table 3). Figure 6 gives an overview of the current breeding areas.

Table 3: Location and season of first breeding events (natal dispersal) for captive-reared females released in Hawaii Volcanoes National Park, nesting in the wild and in breeding pens between 1977 and 1997 (excluding birds in the captive breeding stock, e.g. pinioned birds); e.g. 1977 = 1976/1977 breeding season. Nesting area codes: A-u = Upper Ainahou, A-l = Lower Ainahou, GC = Golfcourse, Kah = Kahalii, Kau = Kau desert, Rim = Crater Rim, K.-N. = Kipuka Nene.

		A-u	A-l	GC	Kah	Kau	Rim**	K. - N.
Elevation (m)		*850*	*730*	*1214*	*920*	*880*	*1120*	*880*
Total released *		21	33	1	-	-	-	-
Year of first nest record	*pen*	1977	1978	1978	-	-	-	-
(= colonization)	*wild*	1980	1988	1983	1981	1981	1982	1984
Total natal dispersal events to	*pen*	7	17	2	-	-	-	-
(= first nests)	*wild*	4	6	1	7	7	9	12
Nests except first nests	*pen*	1	8	-	-	-	-	-
	wild	20	5	5	2	35	53	32
Sub total	*pen*	8	25	2	-	-	-	-
	wild	24	11	6	9	42	62	44
Grand total		32	36	8	9	42	62	44

* *females with known hatch and release site*

** *two birds released outside the National Park bred in this area in 1981*

Type of breeding habitat

The majority of birds that hatched in and were released from habitats with high cover (grasslands and grassy scrub) dispersed to nest in more open scrubland habitat (Fig. 7). This preference for open scrubland was responsible for the change of primary breeding habitat between the two management periods (Fig. 8).

After release, the majority of birds nested uphill or stayed at a similar elevation, only few birds nested downhill (Fig. 9). This trend was similar in females and males ($G = 0.28$, $df = 1$, $P > 0.1$) and when comparing birds originating from the National Park and the State ($G = 0.24$, $df = 1$, $P > 0.1$). Seventeen natal dispersal events were recorded for birds that moved into the National Park from high elevation sites, mainly from the State Sanctuary at Keauhou (1860 m). Fourteen of these movements were downhill.

Natal dispersal distance

More females than males nested at their release site (15 females out of 65, 7 males out of 73; $G = 5.02$, $df = 1$, $P < 0.05$). However, dispersing captive-reared females did not move smaller distances than dispersing captive-reared males (Fig. 10 a, b). When grouping distance data into four categories (see methods: no movement, 1 - 5 kilometers, 6-10 kilometers and more

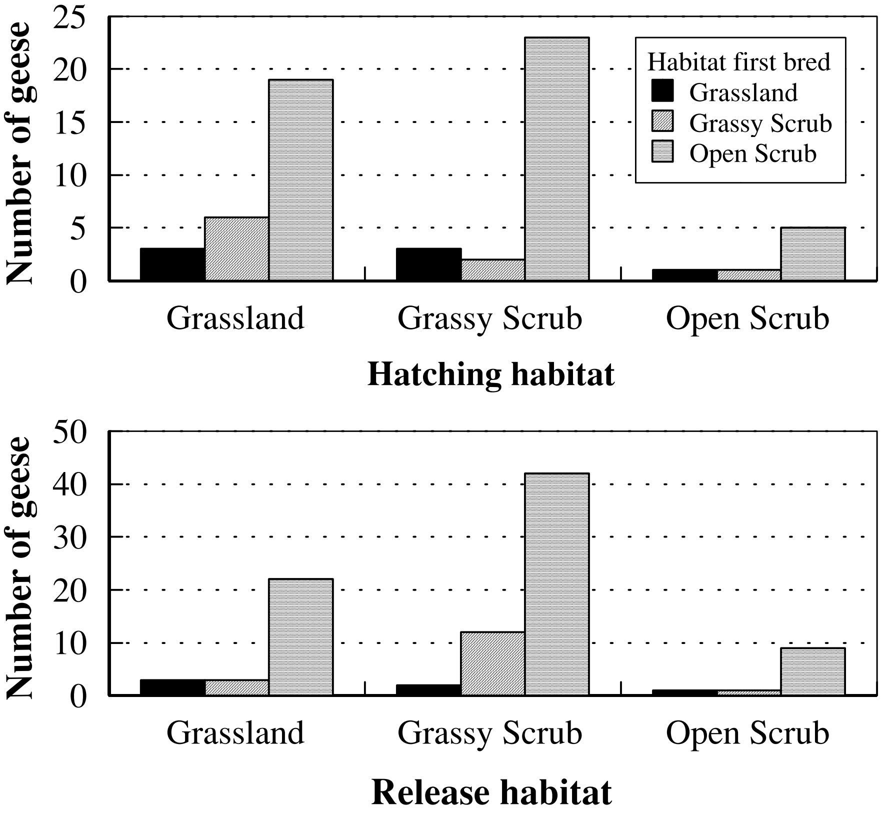


Fig. 7: The number of geese that bred in each habitat type in relation to hatching (upper graph) and release habitat (bottom graph). Most birds moved from hatching and release sites with high cover (grasslands, grassy scrub) to more open habitat (open scrublands). Not all birds were released in their hatching habitat.

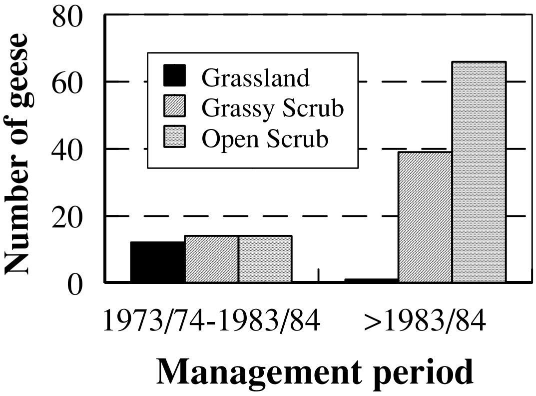


Fig. 8: Habitats that first-time breeders' nests where found in during the early and later stages of the reintroduction program (includes birds nesting in and around pens). In the later stages of the program, more birds nested in open scrub (G = 29.0, df = 2, P < 0.0001).

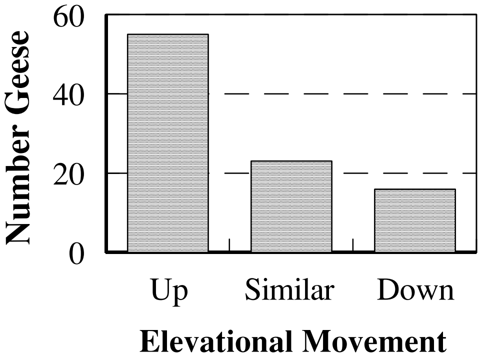


Fig. 9: Elevational movement to first breeding site (includes wild nests and those that nested voluntarily in breeding or release pens). Most birds moved uphill, or stayed at a similar elevation, only few birds moved downhill.

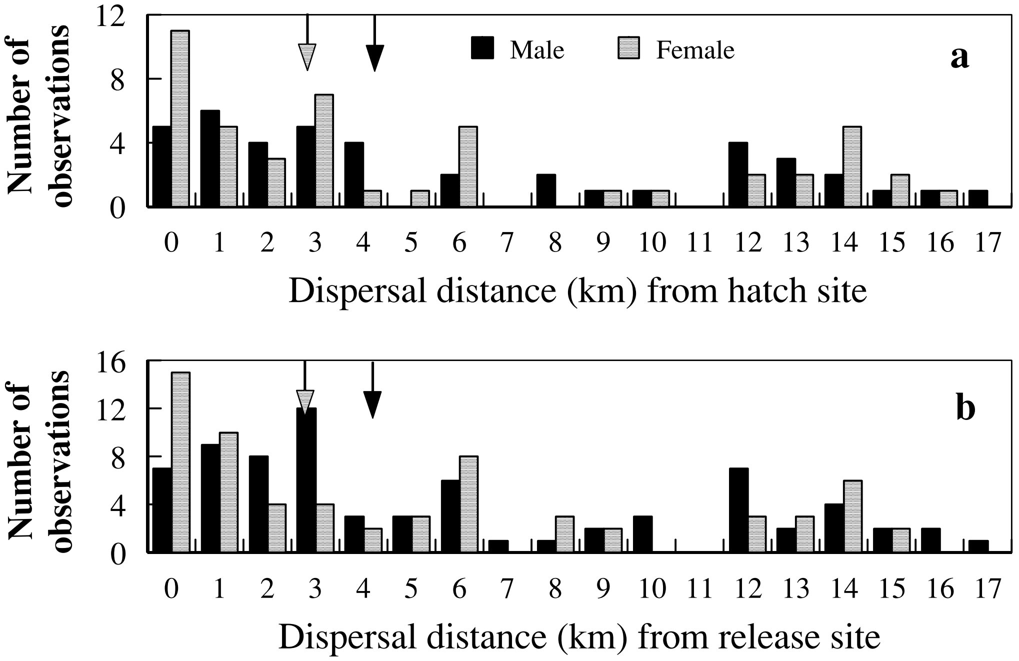


Fig. 10: Distribution of dispersal distances of captive-reared males (solid bars) and females (grey bars) between a) hatch site and site of first breeding record ('HAVO' birds only) and b) distance between release site and site of first breeding record (includes birds reared at Pohakuloa, which were subsequently released at Hawaii Volcanoes National Park. Median dispersal distances for males (black arrows) and females (grey arrows) are indicated.

than 10 kilometers), males and females dispersed similar distances from the hatch site ($G = 2.3$, $df = 3$; $P > 0.05$) and from the release site (G 5.05, $df = 3$, $P > 0.05$).

Birds nesting voluntarily in and around pens moved significantly less from their release site than birds dispersing to wild nesting areas (Fig. 11). Subsequently, I analyzed the two groups separately. In the earlier phases of the reintroduction program, natal dispersal distances of birds nesting in the wild were larger than in the later phases (Fig. 12a). Birds of wild origin moved less than birds originating from the National Park breeding pens (HAVO) or Pohakuloa (State; Fig. 12b). Birds that moved into open scrubland moved the largest distances (Fig. 12c; for statistics see Table 4).

Table 4: Model of natal dispersal distance in relation to management period, origin, first breeding habitat and sex of birds nesting in the wild.

Explanatory variable	F-value	Δ df	P-Value <
management period	6.79	1	0.01
origin	5.08	2	0.01
habitat	8.9	2	0.001
sex	-	-	n.s.

Pairing in relation to hatch and release site

The hatch site of both partners in a pair bond was known in 36 cases. Of these, 92 % were paired with a mate that had hatched in a different area. Only three pairs from the same hatch site formed permanent pair bonds and they were all either same year or previous year siblings. One sibling pair from within the National Park was known to have successfully nested but did not fledge any young.

The release site of both partners in a pair bond was known in 124 cases. Of those, 80 % paired with a partner from a different release site or a partner of wild origin, 13 % paired with a partner from the same release site and 7 % paired with a partner from a release pen located within 500 m distance.

Timing of pair formation

The timing of pair formation was influenced by the rearing history of the birds (Fig. 13). Wild birds paired the earliest, followed by birds that were hatched in open-topped pens by fully-winged parents. Young of captive parents generally paired later and young of parents in close-top pens showed the largest variation in first pairing age (Fig. 13).

In the early phase of the reintroduction program, 18 % of the birds formed a pair bond under the age of 12 months, whereas this rose to 44 % in the later period (compared to birds pairing at above 12 months of age: $G = 10.46$, $df = 1$, $P < 0.005$). Most birds originating from

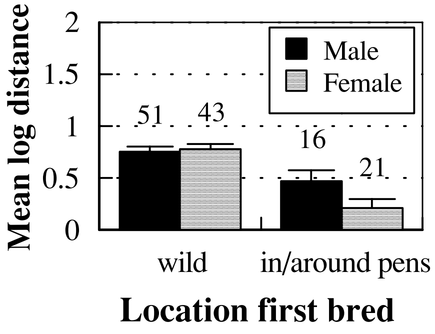


Fig. 11: Mean log natal dispersal distance (for first breeding) in males and females nesting in the wild and in/around pens. Standard errors and sample sizes are indicated. Birds nesting in the wild dispersed over larger distances (F = 5.12, df = 1, P < 0.05).

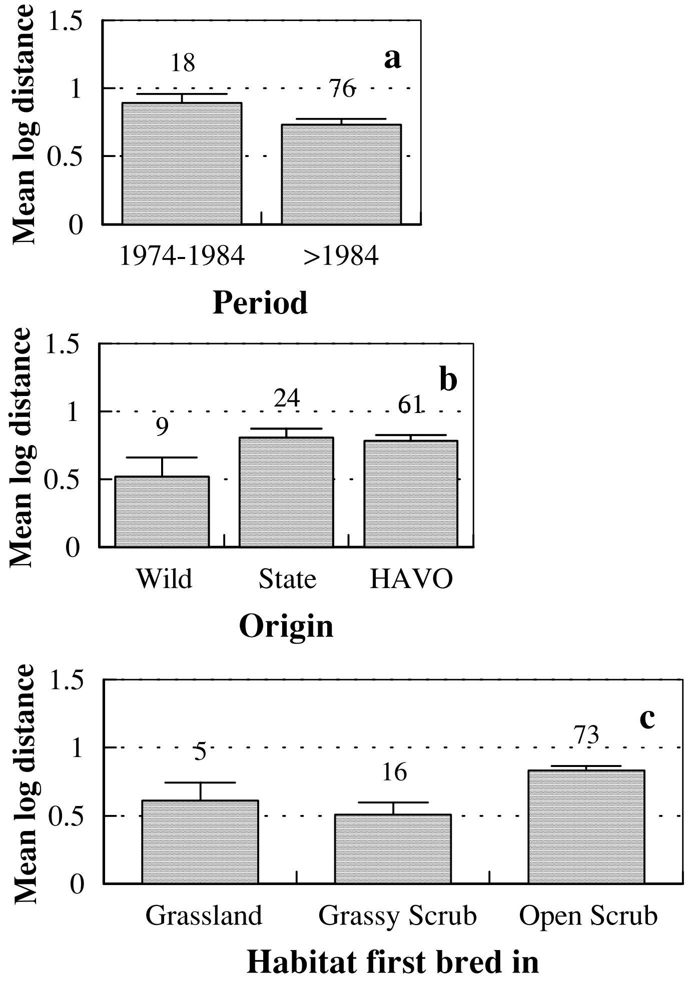


Fig. 12: Mean log dispersal distance to breeding areas in the wild by a) period, b) origin and c) habitat first bred in. Standard errors and sample sizes are indicated. For statistics see Table 4. Origin: 'State' = birds reared at Pohakuloa, 'HAVO' = birds reared at Hawaii Volcanoes National Park.

the wild formed a pair bond in their first year (86 %), followed by birds reared in open and close-top pens in the National Park (32 %); but only 12 % of the birds fostered from the Pohakuloa State breeding facility paired in their first year (compared to birds paired at above 12 months of age: G = 24.12, df = 2, P < 0.0001). Most birds first bred between 2 and 4 years of age. In males and females, age at first breeding was best explained by age at first pairing (Fig. 14).

Reproductive success in relation to natal dispersal distance and age at first breeding

In terms of the number of offspring fledged, birds nesting in the wild were more successful when dispersing (Fig. 15). Females nesting at their natal pens successfully reproduced whereas males did not (Fig. 15). In an analysis of variance, however, natal dispersal distance or age at first breeding did not influence the cumulative number of fledglings produced in neither males (dispersal distance:χ^2 = 0.29, df = 1, P > 0.05; age at first breeding: χ^2 = 0.23, df = 1, P > 0.05) or females (dispersal distance:χ^2 = 0.2, df = 1, P > 0.05; age at first breeding: χ^2 = 0.18, df = 1, P > 0.05).

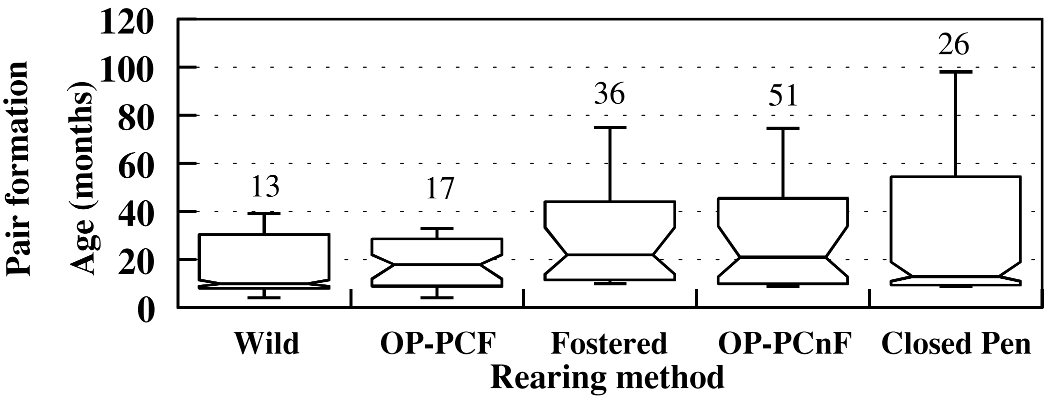


Fig. 13: Age at pair formation (months) in relation to rearing technique (OP-PCnF: Open Pen, parents cannot fly; OP-PCF: Open Pen, parents can fly). Fostered birds were mainly reared with OP-PCnF. The timing of pair formation depended on the rearing history of a bird (χ^2 = 25.7, df = 4, P < 0.0001) and an interaction term between rearing history and management period (χ^2 = 15.2, df = 3, P < 0.005). Displayed is the median and range of the data, notches represent the interquartile range, whiskers define the outlying 5% of the data values. The number of birds in each category is indicated.

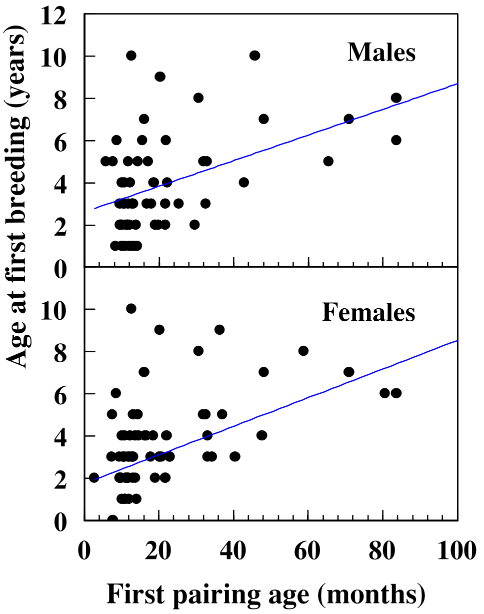


Fig. 14: Age at first breeding was best explained by age at first pairing (females: F = 16.7, df = 1, P < 0.0001, males: F = 8.9, df = 1, P < 0.01). An interaction term between age and rearing technique was significant in males ($\chi^2 = 25.1$, df = 9, P < 0.005), but not females. Possibly confounding factors such as management period, first breeding habitat, bred around pens or in the wild and distance moved were fitted to the same model but were all non-significant.

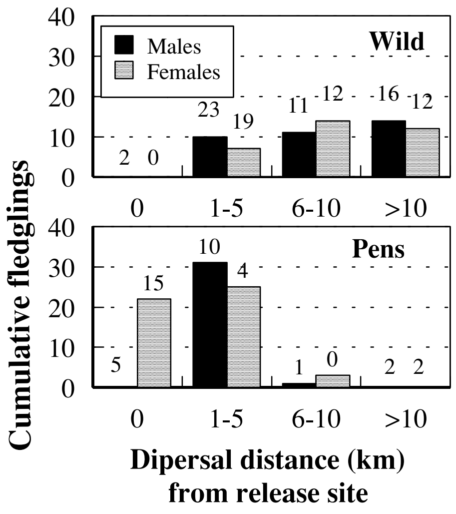


Fig. 15: Cumulative number of fledglings produced by captive-bred male and female Hawaiian Geese between 1973 and 1997 in relation to the distance (km) they dispersed from the release site of birds nesting in the wild or in/around pens (see methods). Males and females produced most young when staying close to their natal pen, but both sexes were successful at larger dispersal distances when moving to wild breeding habitats (males: G = 38.7, df = 1, P < 0.0001; females: G = 58.7, df = 1, P < 0.0001).

DISCUSSION

Natal dispersal - distance moved and habitats colonized

In the early stages of the reintroduction program, the majority of Hawaiian Geese reared and released in the low to mid-elevation breeding pens at Hawaii Volcanoes National Park nested close to their rearing and release area. They moved further away and ventured into new habitat when bird density around the pens increased. Banko (1988) described territorial fights in and around the breeding pens during this period of increasing density (for annual population estimates see Chapter 6, Fig. 5). The dry grassy scrub around the lowland pens provided little natural food and when the pens were phased out, no more supplemental food was available and birds were forced to leave. The majority of birds colonized open scrubland habitat and moved considerable distances to do so. Predator density in open scrubland is lower than in grasslands and scrub with higher vegetation cover, lowering the risk of egg and gosling predation.

Most breeding areas that were colonized were at mid-elevations. Mid-elevation sites receive more rainfall than low or high elevation sites and therefore tend to have more food (see Chapter 4), which probably explains why most birds from the lowlands moved uphill and most birds from the upland sanctuaries moved downhill to establish new breeding territories.

Sex-biased differences in natal philopatry

In geese, females are thought to defend a familiar territory whereas males are thought to defend mates (Owen and Wells 1979, Mineau and Cooke 1979, McKinney 1986). This often leads to female philopatry and male dispersal (see Introduction). In this study, not all males dispersed but some set up their first nesting territory at their natal pen. Females that nested at their natal pen successfully reproduced whereas males did not. Females paired to philopatric males dispersed to the natal site of the male and were thus on unfamiliar territory. Judging from their higher reproductive success, philopatric females around pens may have had an advantage over females moving in from the outside. Perhaps residential females had established dominance in the site familiar to them and so secured access to supplemental food. Lessels (1985) suggested that the ability to exploit information on brood rearing areas may be an important selection pressure favoring female philopatry in wildfowl. The low success of philopatric males may explain why most males disperse.

Pair formation

The majority of Hawaiian Geese paired with a mate from a different release pen, showing a high degree of outbreeding. This is in contrast to Barnacle Geese which preferentially paired with birds familiar from early life (Owen *et al.* 1988, Choudhury and Black 1993). A few sibling matings occurred, but only in the early stages of the program when the number of possible mates was low. In Canada geese, no pairings among siblings or parents and offspring were observed (Raveling 1978). Pairing among siblings is thought to be effectively inhibited by behaviors during pairing (Fischer 1965, Lorenz 1966). At the National Park, the potential for sibling mating has been actively reduced by releasing progeny of captive pairs from different pens each year (Banko 1988). It is therefore unclear whether the observed pairing pattern was a result of these translocations. In later years, however, when this practice was discontinued and siblings were readily available to pair with, the majority of geese still paired with mates from different rearing and release pens.

First pairing age and age at first breeding in relation to rearing and release technique

Before 1984, few birds under the age of 12 months formed pairs and this might reflect a low availability of potential mates in this period. Consequently the age at first breeding was higher in birds which paired before 1984 than in birds paired later. Late pairing and breeding could potentially reduce a bird's life-time reproductive success (Owen and Black 1989). For a reintroduction program to be successful, a sufficient number of potential mates has to be available (see also Chapter 8).

Most birds released with their parents and birds reared in open-top pens paired earlier than birds reared in close-top pens. The difference in pairing age might be explained by differences in social experience. Wild geese often flew into open-top pens and mingled with goslings there (Banko 1988), enhancing the young birds' social experience. Goslings reared in closed-top pens lacked this experience in early life which may have delayed pairing and subsequent first breeding age. When fledglings left their breeding pen with their parents they enhanced their social experience by using a larger number of sites, thus increasing their likelihood of encountering a potential mate.

In geese, dominance rank is typically highest in families, followed by pairs and single individuals rank lowest (Raveling 1970, Black and Owen 1989). Therefore, young released with their parents would be dominant over young released without parents and this may be to their advantage later in life. Young learn aggressive skills and may assume their parents' dominance rank (Black and Owen 1987). The most dominant birds have the best access to resources, in many cases this results in better breeding success (Collias and Jahn 1959, Lamprecht 1986 a, b).

Natal dispersal in relation to the availability of nest sites and dominance rank

Like Lesser Snow Geese (Cooke *et al.* 1975), individual Hawaiian Geese displayed differences in their degree of philopatry. Wild females tended to be more philopatric than released ones but more data on wild birds are needed to elucidate natal dispersal strategies in a habitat that has been colonized and is no longer void of a wild population. In Hawaii Volcanoes National Park, good breeding sites are rare (Black *et al.* 1994) and spread over large distances. If nesting habitats close to a mother's territory do not support additional breeding pairs, females that try to be philopatric might not breed unless they disperse. Non-breeding may be a successful strategy when queuing for a territory (Ens *et al.* 1995). Geese are long-lived and so may be able to delay breeding if the territory they expect to get is better than a territory immediately available.

In social species, natal dispersal might be influenced by dominance rank. For example, dispersing coyotes were low-ranking and philopatric individuals were high ranking (Gese *et al.* 1996). Although this needs further study, it may be that in Hawaiian Geese a few dominant pairs defend the best breeding territories but subordinate pairs have to disperse to less suitable sites. Typically parents would be expected to be dominant over their offspring. Parent geese have been observed to chase away their offspring when the breeding season starts (personal observations, also: P.C. Banko, H. Hoshide pers. comm.). Given these dominance relationships, it is likely that mothers will hold a better breeding territory than daughters that try to nest close-by. Local resource competition between mother and daughter are likely in *Anseriformes* (Pöysä *et al.* 1997) but there is little information available about the actual mechanisms of competition between parents and offspring (Gowaty 1993). The low availability of good nest sites in terms of food resources and high interference experienced around those sites might explain why some Hawaiian Goose pairs still disperse to prospect for potentially new breeding sites.

Management implications

The immediate habitat in which birds were released did not support a wild population. Birds were mobile and colonized breeding habitats some distance from their original release sites. Birds reared by wild parents paired earlier than young of captive parents, which may have increased their potential life-time reproductive success under environmentally favorable conditions. Offspring from free-flying parents probably learned the location of feeding sites from their parents, where they mingled with other birds and subsequently increased their social experience. Wild parents should be encouraged to nest in predator-free enclosures in wild habitat, where goslings grow up under natural conditions and can fly out of the pens with their parents. Fostering additional goslings into families where both parents can fly could be explored as a way of increasing the wild population where necessary. Whereas previous studies have shown that parental contact was important during rearing (Black and Owen 1987, Marshall and Black 1992) this study suggests that parental contact is also influential after release. Concentration of management efforts in a few core areas would ensure that enough birds are recruited every year to avoid sibling pairings and to allow optimal mate choice.

Future research

More data are needed about the individual variation of natal dispersal distances in Hawaiian Geese, which may be life-history adaptations to fluctuating environmental conditions. The effect of unpredictable or changing habitats may be an important consideration for predicting natal dispersal in this species.

SUMMARY

Hawaiian Geese established breeding populations around rearing and release pens, but after the maintenance of lowland pens was discontinued, males and females moved away and colonized new breeding habitats. New breeding habitats were located mainly at mid-altitude in volcanic scrublands with little vegetation cover. Released birds typically paired with birds from a different release pen or with wild birds. Goslings bred in the wild and goslings reared by free-flying parents inside predator proof breeding pens paired earliest. Goslings reared in closed-top breeding pens showed the largest variation in first pairing age. First pairing age explained most of the variation in first breeding age. Parental contact was apparently important not only during rearing but after release, suggesting that young should be released with their parents.

Chapter 3: Hawaiian Goose flock structure in Hawaii Volcanoes National Park - the distribution and movement of individuals

INTRODUCTION

Goose flocks are thought to contain subdivisions, each of which is faithful to feeding and roost areas (Raveling 1969, Percival 1991). Raveling (1969) suggested that these subdivisions or sub-flocks are maintained throughout the year and reflect cohesion of breeding units, but this hypothesis has yet to be proven. Individual Barnacle Geese appear to be consistent in using the same wintering, spring staging and breeding grounds over a number of years (J. M. Black pers. comm.). Individual variation in the degree of site fidelity, or conversely the frequency of movements between sites also has been described for Barnacle Geese (Percival 1991, Ganter 1994, Black 1998b). Sub-flocks may express local habits of individuals rather than social group behavior.

Hawaiian Geese stay within Hawaii Volcanoes National Park throughout the year. They do not migrate over large distances but are known to move around within the National Park. It has been previously suggested that individual birds belong to distinct sub-flocks, which are characterized by the use of the same areas or combination of areas (Hoshide *et al.* 1990). In this chapter I will outline how the geese were distributed within the National Park between 1989 and 1995. I will identify the extent to which individual birds used single and/or multiple areas (systems) and how faithful birds were to a 'core' area. I will determine if sub-flocks occurred by using cluster analysis and will describe any changes in the groupings of birds between years. In an attempt to identify movement patterns within the National Park, I will analyze annual, seasonal and monthly movement patterns of individual geese.

STUDY AREAS

Several major breeding, brooding, molting and summer flocking areas have been described within Hawaii Volcanoes National Park (Hoshide *et al.* 1990). Most Hawaiian Geese nest in open volcanic scrubland (see Chapter 1). After hatching, parents typically lead their young to adjacent grasslands, where food is more abundant. After molt, large numbers of geese aggregate in summer flocking areas (Hoshide *et al.* 1990). Figure 1 gives an overview of areas that are utilized by the geese in Hawaii Volcanoes National Park.

Birds breeding in the desert around 'Kipuka Nene' lead their goslings to pastures at the Kipuka Nene Campground. Those nesting at 'Kipuka Kahalii' and the lava flow east of the former Ainahou ranch lead their young to the pastures around the 'Ainahou' breeding pens. Birds nesting along the southeast of the 'Crater Rim' tend to lead their goslings to the Volcano 'Golfcourse', and those nesting in the northeastern part of the 'Kau' desert lead their young to

'Kapapala' Ranch (Stone *et al.* 1983). Birds nesting around Keanakakoi Crater (which is part of the 'Crater Rim') are not utilizing grasslands to rear their young. They forage on native and introduced vegetation at 'Devastation'. Kipuka Kahalii is one of the most important summer flocking areas (see Chapter 4). Vegetation composition of the scrublands is described in Chapter 4, the grasslands are described in Chapter 5.

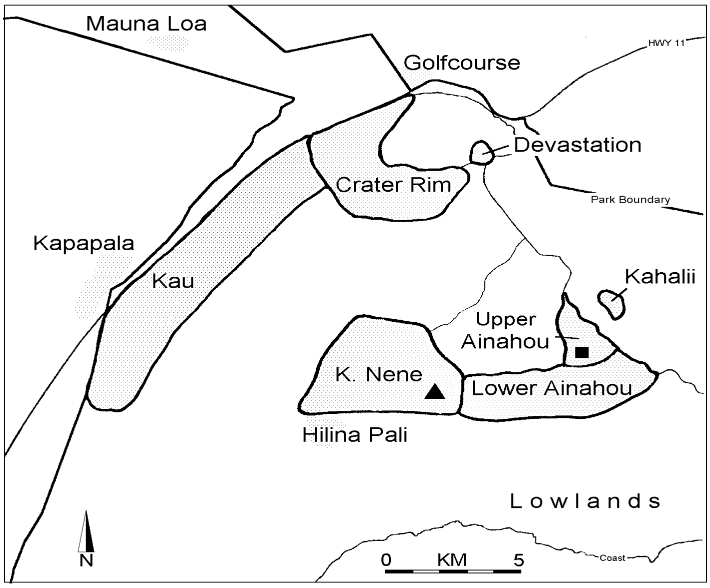


Fig. 1: Main areas used by Hawaiian Geese in Hawaii Volcanoes National Park.
= Kipuka Nene Campground, ■ = Ainahou breeding pens

METHODS

Banding and Resightings

Throughout the reintroduction program, released birds were fitted with unique leg bands. During the later stages of the program, when the first released birds started to nest in the wild, the majority of their offspring were caught and banded before fledging (see also Chapter 2, 4 and 6). Whenever geese were seen, information on date, time, location, flock size, band number, partner's band number and number of associated goslings was recorded. Resighting data were usually collected between 8.00 hours and 16.00 hours and do not include overnight roosting areas.

Social Status

To avoid including trial partnerships, birds were considered paired when they had been seen with their mate at least ten times. Paired birds generally maintain a closer distance to each other and exhibit distinct behaviors, such as coordinated preflight signaling, coherence during aggressive encounters and triumph ceremonies (Black *et al.* 1996). Single birds were typically young, but some older birds remained unpaired. Birds in short-term trial partnerships (< 10 observations) were regarded as singles. Data on families were limited and are not considered.

Cluster analysis: Individual resightings by area

Cluster analysis is a multivariate procedure for detecting groupings in the data, e.g. individuals that use similar area combinations will be grouped in one cluster. I included all birds that were resighted at least 30 times throughout the reintroduction program and I grouped resightings into years. Rather than calendar year, I used years between breeding seasons (e.g. 1989 = October 88 - September 89). A bird had to be seen at least 10 times annually to be included. Any records for which the ring had not been read with certainty have been discarded from the analyses. If birds where seen more than once in a day, only one randomly selected record was included. Birds taken into captivity or wild birds paired to captive birds in open-top pens were excluded from the analyses. Single birds were excluded as they were typically juvenile birds and may have had different flock associations than paired adult birds. To avoid pseudoreplication, only data from adult, paired females were analyzed and those from their mates were ignored.

Some areas were visited more often than others, thus increasing the likelihood of seeing birds. I therefore weighted the data so that the number of resightings in any area was a direct proportion of the number of ringed individuals seen using an area in a given year (Percival 1991). An example of how sightings of an individual bird were weighted is given below:

Total number of resightings of all individuals in an area in a given year (October to March) = ***nS***
Number of ringed birds using the area in a given year = ***nR***
Weighting factor for that year = ***nR/nS***
Weighted number of resightings of the individual in each area = actual number of resightings of the individual in each area x weighting factor.

For each year a matrix was constructed with individual birds as the row labels and areas as column labels. Cluster analyses of the weighted resightings of individuals in each area were carried out for each year separately using the median method in SPSS (Percival 1991, SPSS 1998). I explored different linking methods, but clusters were similar regardless of the method used, especially if allowing a large number of clusters. I chose eight clusters to represent sub-flocks. Some clusters only had a few birds in them, but these typically separated early in the analysis and were not a result of choosing too many clusters. After each bird had been assigned a cluster by SPSS, I calculated the proportion of resightings at different locations for birds within that cluster. This gave me an indication of 'core' areas and a range of areas used by birds in different clusters.

Movement analysis

Consecutive resightings of an individual were classified either as 'stayed' in an area or as 'moved'. Only birds that had been seen at least 30 times were included in the analysis of annual, seasonal and monthly movement.

Movement data were analyzed using a binomial error structure in GLIM, with the number of movements ('moved') defined as the response variable and the total number of observations (moved and stayed) as the binomial denominator. Movement was then expressed as a proportion of the total number of observations, including number of resightings with and without movement (Crawley 1993). I tested if the proportion of resightings with movement varied between years (e.g. whether birds moved more in some years than in others), seasons (e.g. whether birds moved more in the breeding or non-breeding season), months and with social status (e.g. paired, single male or single female). Some of the data were overdispersed and, because the denominators were unequal, this was controlled by using William's procedure (Crawley 1993). After adjusting for overdispersion, F-values were used instead of χ^2-values (Crawley 1993).

RESULTS

Colonization of new habitats

The annual number of individuals using different areas and the proportion that they represented of the total population changed over the years (Fig. 2). Initially, birds were mainly seen around their release areas, such as Upper and Lower Ainahou and the Golfcourse. From 1981 onwards, birds started to colonize new areas, such as Kipuka Kahalii, Kipuka Nene, Devastation and Crater Rim. Birds continued to use release areas, even after releases there stopped. Geese released from the Keauhou State Sanctuary were seen at Mauna Loa and in the Kapapala area.

Annual sub-flocks

Hawaiian Geese used eight principal areas within the National Park: Lower Ainahou, Upper Ainahou, Kipuka Kahalii, Kipuka Nene (including Hilina Pali), Devastation (including Puu Puai), Crater Rim (including Keanakakoi Crater), the Golfcourse and Kapapala Ranch (Fig. 1). Cluster membership indicated the distribution of individuals in sub-flocks or flock associations which were characterized by their proportional number of resightings in an area (Fig. 3). Distribution patterns of sub-flocks varied between years. Within a given year there appeared to be two main strategies: some birds used only one or two principal areas whereas others used a larger combination of areas. Area combinations used in one year were not always used in the next. Annual patterns of use were classified into birds using four main area combinations (systems): The Ainahou system (including Kipuka Kahalii), the Kipuka Nene system, the Golfcourse system (including Devastation and Crater Rim) and the Kapapala system. In a given year, only a few birds used one system exclusively: the majority of birds was seen in other systems as well.

Most birds using Lower Ainahou were seen at Upper Ainahou and Kipuka Kahalii but some birds used a combination of only two of the above areas. Kipuka Nene birds used a

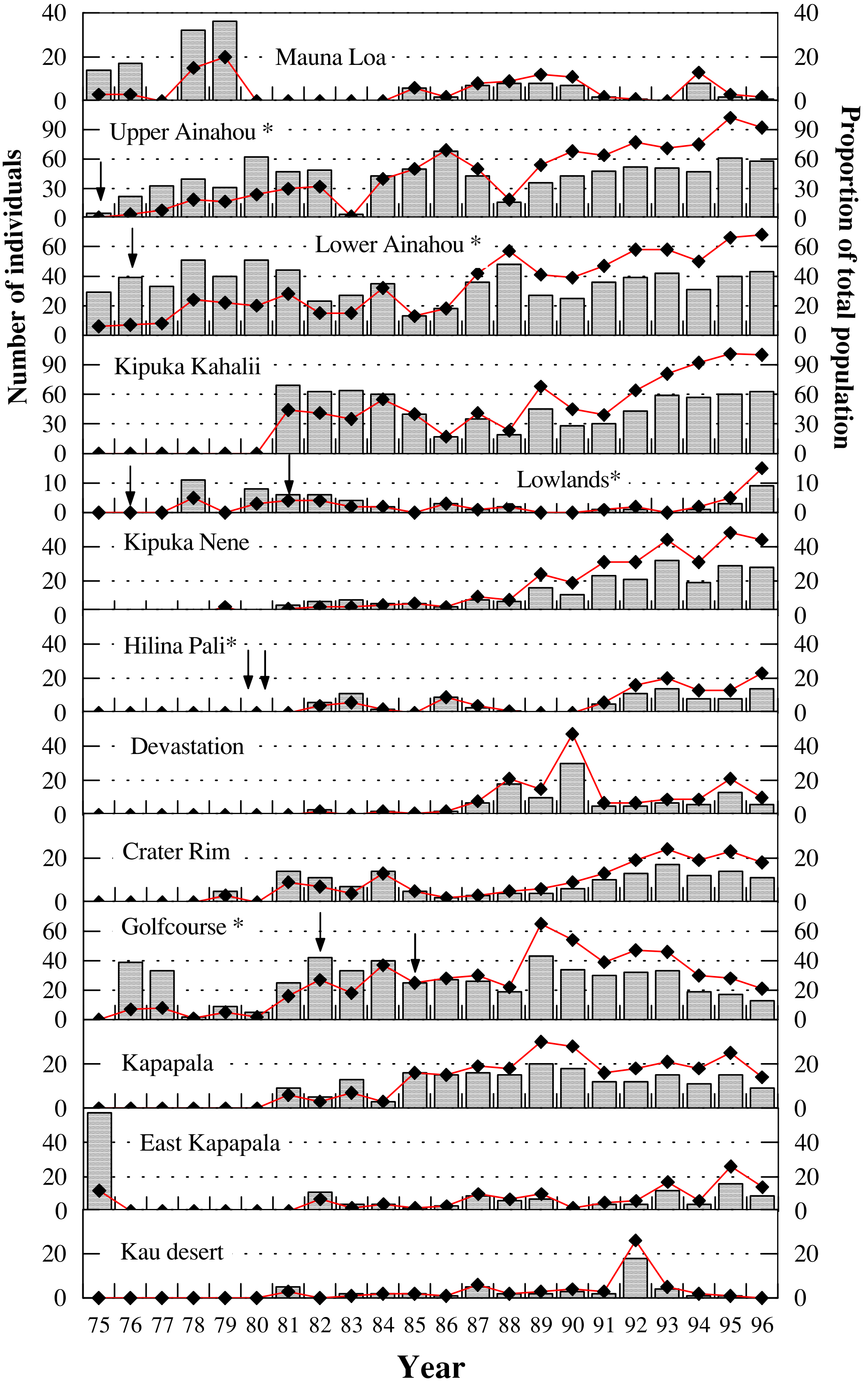


Fig. 2: Number of individuals (as identified by their leg bands) using various areas within Hawaii Volcanoes National Park since reintroduction (diamonds and lines) and the proportion that these birds represent of the total marked population (bars). * = release area. Arrows indicate start and/or end of releases in an area (ongoing at Upper/Lower Ainahou in 1996).

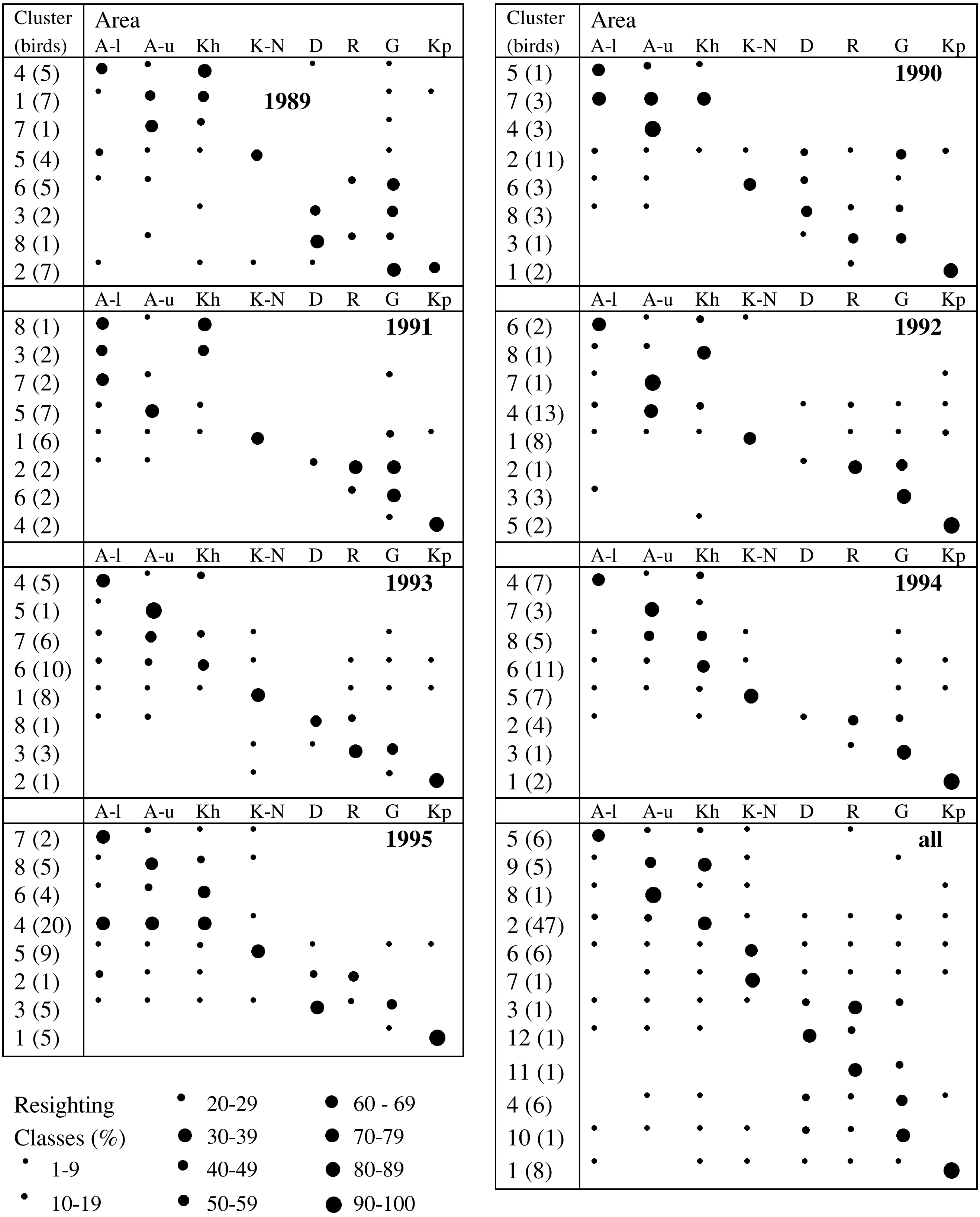


Fig. 3: Proportion of resightings of paired females by cluster group in eight areas within Hawaii Volcanoes National Park between 1989 and 1995 (1989 = October 88 - September 89). Numbers in brackets indicate numbers of birds in a cluster. Large dots are areas mainly used by that cluster of birds. Adjacent areas are listed next to each other. A-u: Upper Ainahou, D: Devastation, A-l: Lower Ainahou, R: Crater Rim, Kh: Kipuka Kahalii, G: Golf course, K-N: Kipuka Nene, Kp: Kapapala.

large number of areas, most were seen in the Ainahou/Kahalii system and parts of the Golfcourse and Kapapala system. Devastation and Crater Rim birds were usually associated with the Golfcourse, but not all Devastation birds used Crater Rim and not all Crater Rim birds used Devastation. Kapapala birds appeared to be a distinct group in most years, with some birds using the Golfcourse system occasionally.

Pooling all resighting data collected between 1989 and 1995 revealed that 56% of the birds used a large number of areas whereas others concentrated their area usage, e.g. 14% were mainly seen in the Ainahou/Kahalii system, 8% in the Kipuka Nene system, 12% in the Golfcourse system and 10% in the Kapapala system (Fig. 3, bottom right).

Individual differences in area usage

Between 1989 and 1995 most birds used a combination of 3 - 5 areas, only few birds used more areas (Fig. 4).

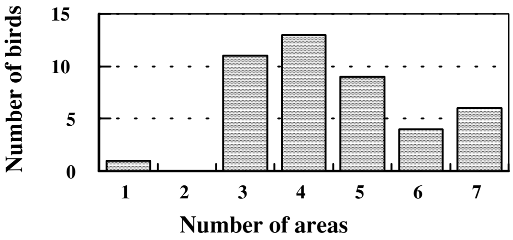


Fig. 4: Number of areas used by individual Hawaiian Geese within Hawaii Volcanoes National Park. Only birds that were seen at least ten times annually in at least three consecutive years are presented.

Between 1989 and 1995, the area combinations used were consistent for some individuals, but not for others (Fig. 5). For example, birds 788, 660 and 661 consistently used a combination of Upper Ainahou, Lower Ainahou and Kipuka Kahalii, but the annual proportion of resightings varied, e.g. in some years their 'core' area was Upper Ainahou, in others Lower Ainahou or Kipuka Kahalii. Birds 608, 626, 696, 703 and 704 mainly used Kipuka Nene, but were also seen in a variety of other areas, that were not consistent between individuals or between years. Birds 682, 684 and 453 are examples for individuals with a large within and between-year range of area usage.

Arranging birds by their annual cluster membership (Fig. 3, Fig. 5) revealed that some birds were seen in long-term associations (Table 1). For example, the siblings 661 and 660 were assigned to the same cluster between 1990 and 1992. Birds 601, 788 and 520 were associated in the Ainahou/Kahalii system between 1993 - 1995. They had all hatched in 1984. Hatch year and parentage did, however, not affect other cluster associations. Birds 608, 626, 610, 704 and 696 were unrelated and hatched in a variety of years, but were associated in clusters characterized by the use of Kipuka Nene. The pen that birds were released from did not affect their cluster associations (Table 1). Bird associations persisted between years, even when birds changed or expanded their use of areas.

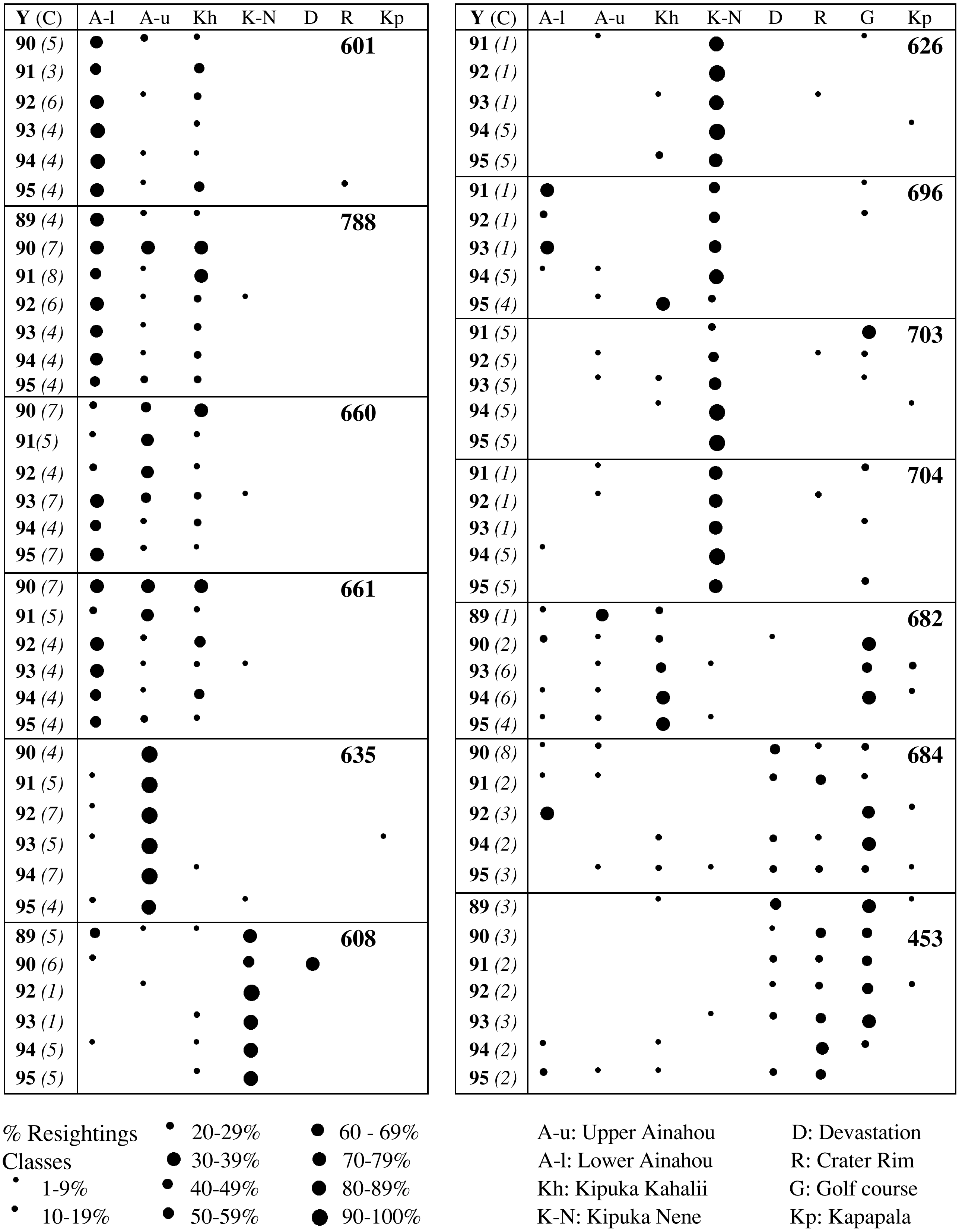


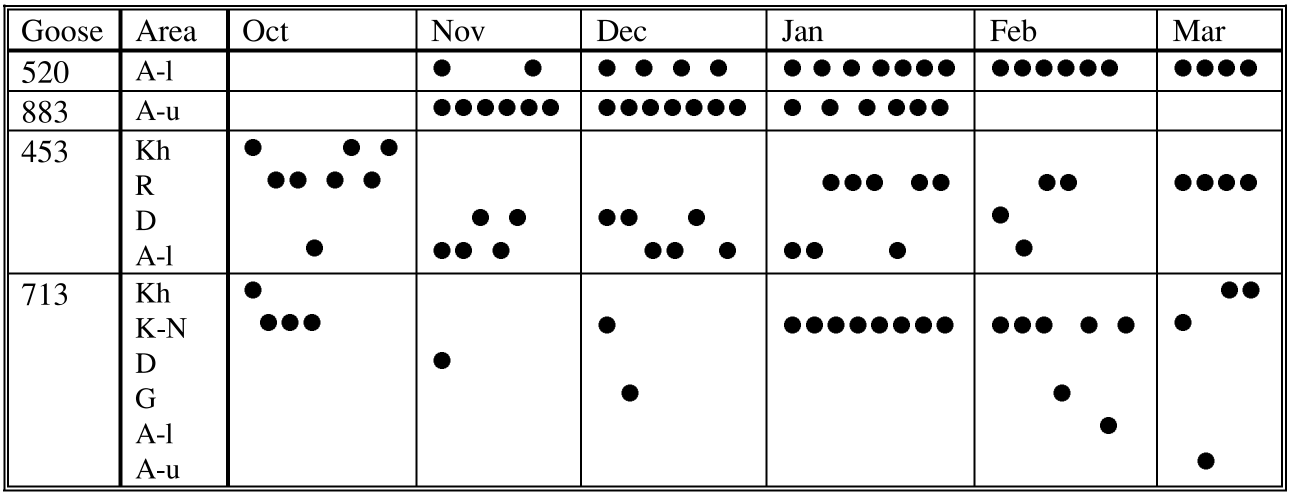
Fig. 5: Annual proportion of resightings of individual paired females in eight areas within Hawaii Volcanoes National Park. Individual identification codes are indicated in the upper right hand corner of each square. Only birds that had been seen in at least five years are presented. Y = Year, C = cluster membership (see Fig. 3), adjacent areas are listed next to each other. Large dots represent areas mainly used by an individual goose.

Table 1: Bird associations between years (cluster membership is indicated by numbers). Only birds that had been seen in at least 5 years are included. Shading indicates sub-flocks. 1 = Ainahou/Kahalii sub-flock, 2 = Kipuka Nene sub-flock.

Band ID	**89**	**90**	**91**	**92**	**93**	**94**	**95**		Hatch Year	Release Pen	***ID Mother***
601	-	5	3	6	4	4	4	*1*	84	8	*917*
788	4	7	8	6	4	4	4		84	7	*8089*
520	1	-	-	4	4	4	4		84	8	*416*
661	-	7	5	4	4	4	4		86	7	*917*
660	-	7	5	4	7	4	7		86	7	*917*
635	-	4	5	7	5	7	4		85	3	*151*
703	-	-	5	5	5	5	5	*2*	90	7	*609*
610	5	6	1	1	-	-	5		84	7	*8089*
608	5	6	-	1	1	5	5		85	2	*P-30*
626	5	6	1	1	1	5	5		84	7	*P-43*
704	-	-	1	1	1	5	5		90	7	*609*
696	-	-	1	1	1	5	4		89	7	*P-43*
682	1	2	-	-	6	6	4		88	7	*151*
684	-	8	2	3	-	2	3		88	7	*8089*
453	3	3	2	2	3	2	2		81	5	*917*

Movement pattern

Between 1989 and 1995, the proportion of resightings of individuals that involved movement was similar between years (F = 1.43, df = 6, P > 0.05) ranging between 23% and 32% annually. The proportion of resightings with movement was also similar between the breeding (24%) and non-breeding seasons (26%; F = 1.06, df = 1, P > 0.05). Some birds did not move throughout the year, whereas others moved between sites in different months (Fig. 6). This was not related social status. Pairs, single males and single females moved to a similar extent (F = 2.06, df = 2, P > 0.05) with 27%, 27% and 23% respectively. The proportion of resightings with movement varied significantly between months in 1992 and 1995 but there was no consistent pattern between years (Fig. 7). After using Bonferroni adjustments for multiple comparisons, there were no significant differences between cluster groups in the proportion of resightings involving movement in a given year (before adjustments: 1989: F = 0.8, P > 0.02, 1990: F = 1.9, P > 0.02, 1991: F = 1.4, P > 0.02, 1992: F = 1.8, P > 0.02, 1993: F = 1.6, P > 0.02, 1994: F = 2.4, P < 0.05, 1995: F = 2.17, P < 0.05).



Goose	Area	Oct	Nov	Dec	Jan	Feb	Mar
520	A-l		● ●	● ● ● ●	● ● ● ●●●●	●●●●●●	●●●●
883	A-u		●●●●●●	●●●●●●●	● ● ● ●●●		
453	Kh	● ● ●					
	R	●● ● ●			●●● ●●	●●	●●●●
	D		● ●	●● ●		●	
	A-l	●	●● ●	●● ●	●● ●	●	
713	Kh	●					●●
	K-N	●●●		●	●●●●●●●●	●●● ● ●	●
	D		●				
	G			●		●	
	A-l					●	
	A-u						●

Fig. 6: Individual resightings of four female Hawaiian Geese in the 1994/95 breeding season. Each dot represents one resighting. For area codes see Figure 3.

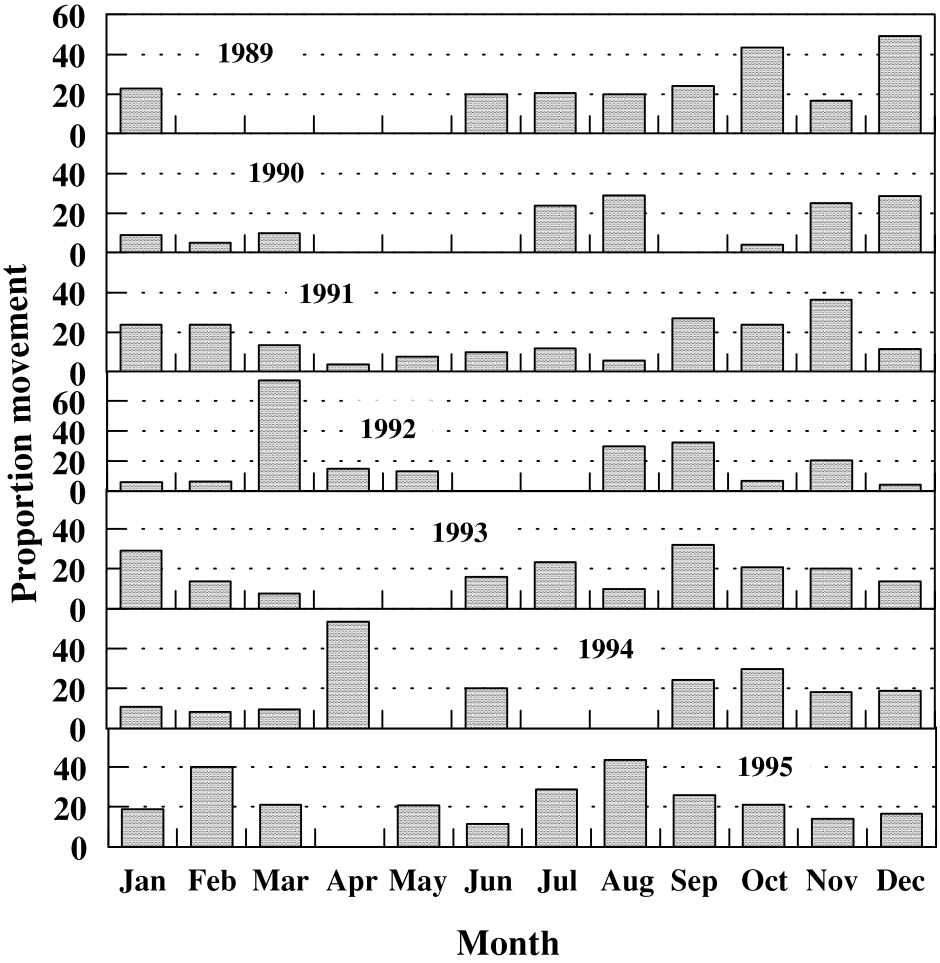


Fig. 7: Monthly mean proportion of resightings showing individual movement between 1989 and 1995. Only birds that had been seen at least five times a month were included. Movement varied significantly between months in 1992 (F = 3.18, df = 11, P < 0.001) and 1995 (F = 2.24, df = 11, P < 0.01).

DISCUSSION

The Hawaiian Goose population in Hawaii Volcanoes National Park showed a discernible spatial structure. Individuals exhibited a large variation in distribution patterns; some were faithful to a small number of areas whereas others ranged more widely. It appears that birds may have different individual strategies in their area usage, responding differently to variable food availability and quality, predators and encounters with other geese. Distribution patterns identified through cluster analysis were not random, but changed between years. Some birds were seen in long-term flock associations, but others changed their associations between years. This suggests that sub-flocks existed, but that they were not static.

During a seven-year period, the majority of birds was seen in a large number of areas, but some concentrated their site usage to only 2 - 3 areas. For example, some birds regularly used Ainahou, others Kipuka Nene, the Golfcourse or Kapapala. This suggests that some birds belonged to stable flock associations, whereas others changed between flocks.

I observed that individuals differed in the amount of interference that they experienced at a site, which depended on other geese present. Repeated use of an area increases experience in that site, which may contribute to the dominance status there (Sutherland and Parker 1985). Birds that are faithful to an area may have a high dominance status there and not tolerate competitors, whereas those using a larger number of areas may be lower ranking. Foraging efficiency in a good area may be low for a subordinate individual if aggressive encounters reduce total feeding time. It might pay subordinates to leave good areas and move to lower quality areas in which they experience less interference. In times of localized food abundance interference will be higher than when food is readily available in large areas. The non-random distribution may minimize aggressive encounters and maximize food intake (Raveling 1978).

For some individuals, site quality may be sufficiently predictable within years to make frequent changes between sites not worthwhile, but between years, unpredictable localized rainfall and subsequent localized differences in food availability may explain why some animals did not specialize in defending any one area over a number of years.

Paired and single geese moved to a similar extent and age did not affect the likelihood of movement. Single Hawaiian Geese were rarely seen alone but typically followed other groups of birds which may explain the similar likelihood of movement. This is in unison with some authors' findings (Ganter 1994), but in contradiction to others (Boyd 1955, Raveling 1969). Paired birds are usually older and more dominant than single birds and would therefore be expected to move less. Young and single birds would be expected to undertake more exploratory flights. I did not detect any differences in the extent of movement between singles and pairs presumably because some pairs moved a lot.

Social interactions, as outlined above, are likely to influence association patterns, and more research is needed to elucidate how dominance, aggression and kinship influence the observed patterns.

The lack of a monthly movement pattern between years may be a result of variable rainfall patterns, which cause variable food availability and quality. In chapters 4, 5 and 6 I will investigate the distribution of geese in more detail and study the role of rainfall in influencing food availability.

SUMMARY

The flock structure, distribution and movement of released Hawaiian Geese in Hawaii Volcanoes National Park were studied throughout the reintroduction program using resightings of individually marked birds. Distinct groups of birds were identified using cluster analysis. The distribution of individuals varied between years. Within years, some birds were faithful to a restricted number of areas but others ranged more widely. Clustering resighting data for all years combined (1989 - 1995) by area, revealed that some birds had used a large number of areas whereas others concentrated their site usage. The likelihood of an individual to move between sites was similar between years and seasons. There was no consistent monthly movement pattern. Single birds and pairs moved to a similar extent. The observed distribution and movement patterns are likely to be a result of a combination of factors such as food availability and quality, predators and social behavior. Individuals appear to use different strategies of site selection.

Chapter 4: Distribution and timing of nesting in Hawaiian Geese in relation to food phenology and rainfall in scrublands

INTRODUCTION

Food availability is thought to be one of the main factors governing animal distribution (Krebs 1978, Newton 1980). Herbivores track the quality of their food and when resources are depleted they switch sites, diet or both (Drent and Prins 1987). The reproductive success of arctic geese is influenced by the availability of food in the winter and spring staging grounds (Ankney 1977, Ankney and MacInnes 1978, Raveling 1978, Ebbinge 1989, Prop and Deerenberg 1991). Geese are thought to time their nesting so that food plants in their nesting habitat are most nutritious and abundant when goslings hatch (e.g. Ely and Raveling 1984, Sedinger and Raveling 1986). In the tropics and subtropics, many fruit and nectar-feeding birds migrate locally according to food availability (Sick 1968, Wolf 1970, Leck 1972).

There are few historic accounts of seasonal habitat use in Hawaiian Geese or how, when and where they foraged. Some authors suggest that Hawaiian Geese, before their near extinction, bred and molted in the lowlands (below 400 - 700 m) where they fed on fresh plant growth in the wet winter months, but migrated to higher altitudes when food resources became scarce during the drier summer months (Henshaw 1902, Perkins 1903, Munro 1944, Baldwin 1945, 1947). Today, there is no evidence of such an elevational migration pattern, although birds move between locations throughout the year (Chapter 3).

Since 1974, over 260 Hawaiian Geese have been released in Hawaii Volcanoes National Park and adjacent ranch land. The birds have subsequently dispersed from the release sites into different scrubland and grassland areas (Chapter 2). The diet of Hawaiian Geese varies spatially and temporally and birds preferably feed on plants of high nutritional quality (see also Chapter 5). Prior to nesting, most breeders accumulate fat reserves in grasslands (Black *et al.* 1994). During nesting, birds primarily forage for berries on shrubs that grow on lava flows with little vegetation cover within their breeding habitat, but sometimes birds fly to adjacent grasslands to feed (Black *et al.* 1994). After hatching, parents typically lead their young to adjacent grasslands. These grasslands consist primarily of non-native plant species and are managed either through grazing or regular cutting. Goslings mostly feed on a variety of grasses and herbs but have occasionally been observed to take berries. During the non-breeding season, Hawaiian Geese disperse away from the breeding areas (Banko and Elder 1990) and aggregate in flocking areas. Molting areas are dispersed throughout remote desert areas where there is little or no vegetation. Because birds are secretive at molt and difficult to locate, little is known about their behavior during this period.

There is large geographical, annual and seasonal variation in rainfall in Hawaii that causes fluctuations in food availability for the geese (Banko 1988, Black *et al.* 1994). In summer, the prevailing northeastern trade-winds bring a gradual supply of rain to the windward areas whereas leeward areas remain drier. The winter months are usually wetter which is caused by storms that bring rain from the south (Armstrong 1983). Droughts in the leeward areas are common when the winter storms fail to occur (Armstrong 1983). The climate of high altitude sites is affected by an inversion layer, a meteorological condition in which the layer of air next to the earth's surface is cooler than the overlying air. The layer forms above 1200 - 2400 m and is present for about 70 % of the time (Giambelluca *et al.* 1986), causing areas above it to be arid.

Poor availability of food is thought to be a major bottleneck in the annual cycle of Hawaiian Geese (Baldwin 1947, Stone *et al.* 1983, Banko 1992, Hoshide *et al.* 1990). Understanding how Hawaiian Geese respond to the fluctuations in the abundance of their food plants is crucial for conservation management during the breeding and non-breeding seasons.

The chapter is in three sections: The first deals with the habitat use of the Hawaiian Goose population within Hawaii Volcanoes National Park by comparing monthly resighting frequencies of marked birds in scrublands with other habitats. Secondly, in an attempt to explain variations in goose distribution, I examined seasonal berry availability and young plant growth in scrublands and whether it was influenced by rainfall. Thirdly, I describe the timing of nesting in relation to rainfall and food availability.

STUDY AREAS

Hawaii Volcanoes National Park (19°15'N, 155°15'W) comprises an area of 85,000 ha ranging from sea level to 4164 m on the summit of Mauna Loa. Geese mainly utilize the mid elevation desert scrublands and small grassland patches (600 - 1200 m). A few birds have been seen at sea level whilst others occur as high as 2100 m in the remote vegetation patches surrounded by lava (Kipukas) of the subalpine zone. Eight volcanic, open scrubland areas along an elevational gradient were studied between October 1994 and March 1996, encompassing two breeding seasons and one summer flocking season (Fig. 1). Plant species growing in each of the study areas are listed in Appendix 1, including Latin and common names. Plants are found on three differently structured volcanic substrates: Pahoehoe lava has a smooth, glassy surface; Aa lava consists of rough, sharp-edged boulders; whereas cinder is a fine substrate consisting of small lava pebbles.

'Three Trees Kipuka' is a high altitude site, located on Mauna Loa at the intergrade of the montane and subalpine zones. It is a vegetation island on Pahoehoe lava surrounded by rough, unvegetated Aa lava flows. It has never been reported to hold more than one breeding pair at a time. Because of its' colder temperatures and small size, it appears to be marginal breeding habitat. The main foods available are Pukiawe (*Styphelia tameiameiae*) and

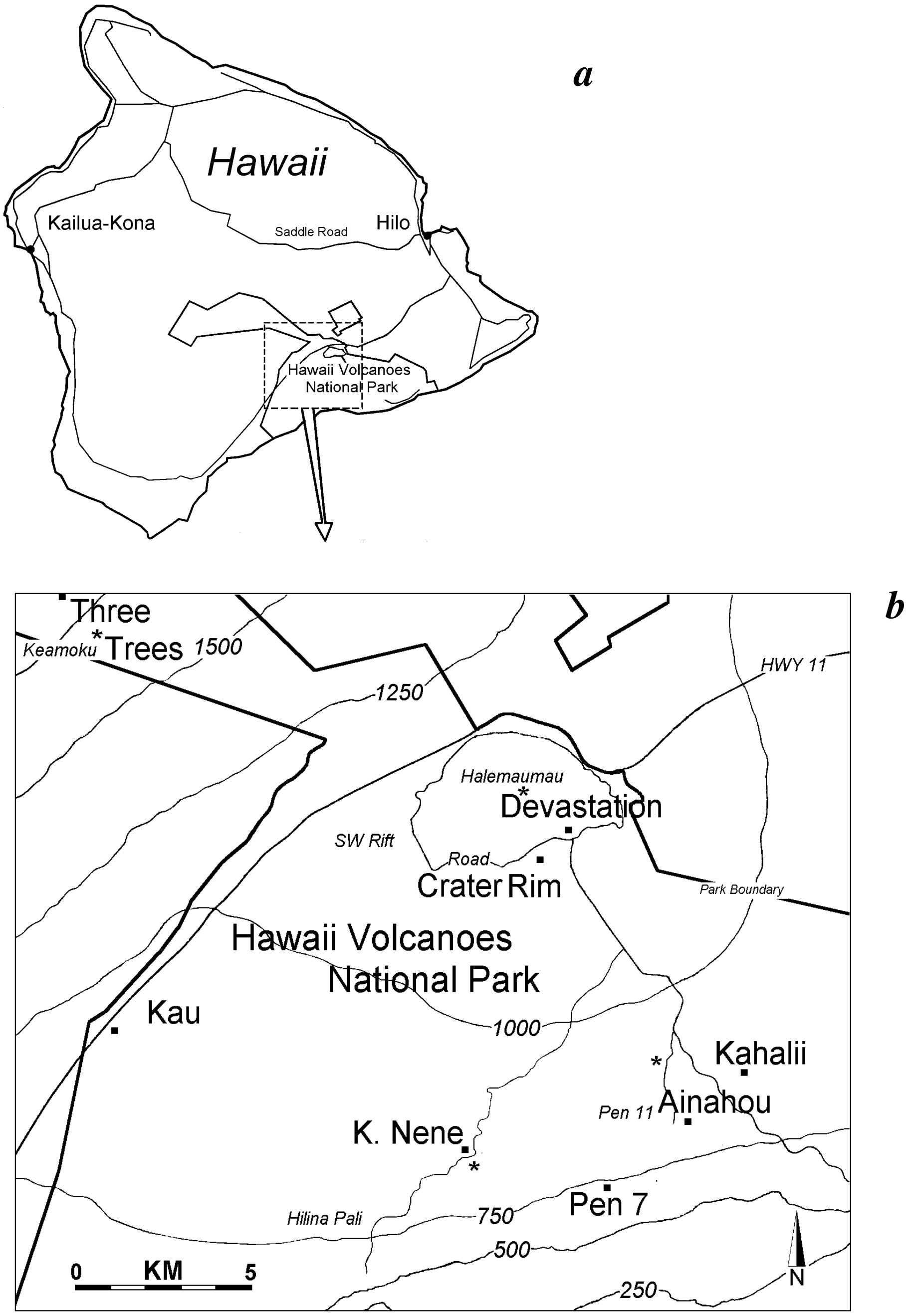


Fig. 1a: The island of Hawaii with Hawaii Volcanoes National Park and **b:** Scrubland study sites (indicated with a square) within the National Park (* = weather stations run by the National Park; contours in 250 m intervals).

Kukaenene (*Coprosma ernodeoides*) berries and Gosmore (*Hypochoeris radicata*), some *Rumex acetosella*, as well as several native and introduced grass species (*Deschampsia nubigena*, *Anthoxanthum odoratum*, *Eragrostis sp.*, *Holcus lanatus*).

'Devastation' and 'Crater Rim' (close to Keanakakoi Crater) are located in the montane seasonal zone with a summer dry climate and both have volcanic cinder substrate. Vegetation cover at the Crater Rim is sparse, including Pukiawe, Ohelo (*Vaccinium reticulatum*) and some introduced grasses along the roadsides. The site is often exposed to wind and volcanic fumes from the nearby Kilauea Crater. In contrast, Devastation is more sheltered by surrounding forest, receives more rainfall and vegetation cover is greater in most parts. Introduced plant species such as *Buddleia asiatica*, *Andropogon virginicus*, Pamakani (*Ageratina riparia*), Blackberry (*Rubus argutus*) and Gosmore grow alongside natives such as *Rumex skottsbergii*, *Dubautia scabra* and Ohelo. Most geese nesting around the southern part of the Crater Rim, including Keanakakoi Crater, lead their goslings to Devastation to forage.

The remaining study sites are situated on the southern slope of Kilauea and have a summer dry climate. The desert around 'Kipuka Nene' is open, mesic scrubland on a Pahoehoe lava flow, dominated by Pukiawe, Aalii (*Dononaea viscosa*) and Ohia (*Metrosideros polymorpha*), with scattered grasses, mainly introduced *Andropogon*, *Melinis minutiflora* and the native sedge *Bulbostylis capillaris*. The Pahoehoe lava flow east of the former Ainahou ranch is dominated by Ohia, Pukiawe, Aalii and scattered Uulei (*Osteomeles anthyllidifolia*), and, compared to the other study sites, has the highest density of introduced grasses such as *Andropogon* and *Melinis*. 'Kipuka Kahalii' is a cinder field surrounded by open, mostly unvegetated Pahoehoe lava flows. Mamaki (*Pipturus albidus*) bushes predominate at this site and grow over 6 feet tall, but geese exploit large parts of the bushes by climbing into them. Other species used by the geese include introduced *Buddleia*, and native *Rumex* and *Dubautia scabra*. The southwestern part of the 'Kau' desert is dominated by Pukiawe and Ohia shrubs with some Aalii, introduced grasses such as *Andropogon* and *Melinis* and the native sedge *Bulbostylis*. 'Pen 7' is a comparatively dry lowland site, in the vicinity of an open-top breeding pen. The main attraction for the geese is probably the supplemental food inside the breeding pen, but natural vegetation is eaten as well. Aalii and Pukiawe are predominant with scattered introduced grasses.

METHODS

Study population

Since the first releases in 1974, Hawaiian Geese in Hawaii Volcanoes National Park have been individually marked with leg bands. In addition, most progeny of released birds have been banded prior to fledging, resulting in over 90% of the population being marked. The bands are made of either aluminum, colored plastic or, most recently, Darvic engraved with a unique letter code, and can be read through a spotting scope or binoculars. By 1996, the population had grown to approximately 160 individuals.

Resighting data

During my study, between October 1994 and March 1996, most areas utilized by Hawaiian Geese were searched and counted at least weekly. During counts, band number, location, date, time of day, mate and number of associated goslings were noted for each goose found. Data were usually collected between 08.00 and 16.00 hours. Resighting data of marked individuals were used to compare differences in habitat use between months.

The largest flock size recorded in a given month (monthly maximum number of geese) in two flocking areas ('Kipuka Kahalii' and 'Devastation') since 1981 was used as an index of habitat use. It was not meaningful to compare maximum goose counts between breeding areas ('Ainahou', 'Kipuka Nene', 'Kau', 'Crater Rim', 'Three Trees Kipuka' and 'Pen 7') because birds were dispersed during nesting and observed goose numbers were low. I therefore only used the combined monthly number of individuals seen at three scrubland sites (Kipuka Nene, Crater Rim and Ainahou). The number of individuals resighted in other areas was low throughout the year (e.g. 4 birds at Kau desert and 2 birds at Three Trees Kipuka) and they were therefore not included.

Nest searches

All nesting areas were surveyed regularly for nesting activity. For a detailed account of the methods used for nest searches and associated data collection see Chapter 6. Clutch size was noted for each nest. Nests were classified as either successfully fledged, or hatched or failed. Lay date was either noted directly in the field, or estimated from the hatch date by subtracting 30 days or, alternatively, estimated from the date when a pair was seen with up to one week old goslings (the G1 stage as described by Hunter 1995) by subtracting 37 days. Known second clutches were excluded from the analysis. In addition to the data collected for this study, long-term nesting data from 1975/1976 onward were available, allowing a long-term analysis of the timing of nesting and seasonal trend in clutch size. Nest initiation dates of individual birds were compared by counting the days between lay dates in consecutive years.

Plant phenology transects

At each site, three parallel transects, each 200 m long and 100 m apart, were set up using measured lengths of twine by following randomly selected compass bearings. Transects were subdivided into ten 20-m sections. Key food plant species were selected according to their known importance in the Hawaiian Goose diet, based on faecal analysis (Black *et al.* 1994) and from personal observations (P. Banko pers. comm., H. Hoshide pers. comm., D. Hu pers. comm.). Within each 20-m section, one of every key food plant species was marked with flagging and a small metal tag with a number. This resulted in 30 individual plants of each species being marked at each site (Table 1). Bushes were selected at random to provide a distribution of sizes available at each sample site. Species included Pukiawe, Ohelo, Uulei, Mamaki, *Rumex skottsbergii*, *Dubautia scabra*, *Buddleia asiatica* and Pamakani.

Kukaenene and Florida Blackberry grew in clumps and in small numbers. I therefore used a different method and, instead of individual bushes, marked 30 individual branches with numbered poultry rings, distributed over 3 - 4 bushes.

Table 1: Study sites with food plant species marked

Study site	Species
Three Trees Kipuka	Pukiawe, Kukaenene
Devastation	Ohelo, Kukaenene, *Dubautia*, *Buddleia*, *Rumex*, Pamakani
Crater Rim	Pukiawe, Ohelo
Kipuka Nene	Pukiawe
Kau Desert	Pukiawe, Uulei
Kipuka Kahalii	Mamaki, *Dubautia*, *Buddleia*, *Rumex*
Pen 7	Pukiawe
Ainahou	Pukiawe, Uulei

Phenological measurements included intensity of vegetative growth or flush, flowering, unripe berries, ripe berries and over-ripe berries. The following categories were used to measure all but the ripe berries (adapted from Bridges *et al.* 1981): A = no occurrence, B = little or occurrence on less than a third of the branches, C = moderate or occurrence on more than a third of the branches and D = heavy or occurrence on more than two thirds of the branches. The number of ripe berries was estimated on bushes and counted on marked branches. All plants were monitored on a monthly basis. Plant density in each scrubland study site was assessed in randomly chosen 10 x 10 m quadrates.

Weather data

Rain gauges and 'minimum-maximum' thermometers were placed in each study area. Weather data were collected on a weekly basis. Prior to my study, from 1988 onwards, rainfall records were available for some nesting areas within Hawaii Volcanoes National Park. To test if rainfall patterns affected the timing of nesting, I assigned rainfall from the various weather stations to the nearest nesting areas as follows: Data from 'Kipuka Nene' (850 m) were assigned to Kipuka Nene and 'Hilina Pali', data from 'Ainahou' (915 m) to the lava flow east of Ainahou and 'Kipuka Kahalii', data from 'Halemaumau' (1100 m) to 'Crater Rim', 'Keanakakoi', 'South West Rift Zone', 'Kau desert' and 'Devastation' and data from 'Keamoku' (1700 m) to 'Three Trees Kipuka' up Mauna Loa. Rainfall before nesting may affect food resources that a female can accumulate prior to laying and therefore affect clutch size. Rainfall during incubation may affect incubation performance and rainfall after hatching may affect plant growth which is important for gosling growth and survival (see Chapter 6). Subsequently, monthly sums of rainfall (mm) were taken before, during, and after the month of nest initiation and classified as either dry (< 100 mm monthly rainfall) or as wet (≥100 mm). I then compared the number of nests initiated in each month with monthly rainfall.

Data analysis

Habitats were classified into three types: open scrubland, grassy scrub and grasslands. Scrublands were open, volcanic desert with scattered bushes. Grasslands were managed pastures with predominantly grass cover. Grassy scrub was a mixture of shrubs and unmanaged tall grasses.

To evaluate differences in habitat use, I compared the proportion of banded birds seen each month in open volcanic scrubland with the proportion they were resighted in other habitat types using a binomial error distribution in GLIM (Crawley 1993). To avoid pseudo replication, I used paired geese and single birds as one unit. If birds were seen more than once a day, one resighting was randomly selected. Resightings in and around breeding pens with access to food were excluded from the analysis. The data were overdispersed and because the denominators were unequal, this was controlled for by using William's procedure (Crawley 1993). After adjusting for over-dispersion, F-values were used instead of χ^2-values. Month was added as a factor and rainfall from a central point in Hawaiian Goose habitat ('Kipuka Nene') was added as a continuous explanatory variable. For plotting purposes, proportion data were arcsine transformed.

To determine the monthly relative abundance of ripe berries, an index was calculated by summing the monthly berry counts on 30 bushes for each site and species separately (Bridges *et al.* 1981). Indices for ripe Blackberries and Kukaenene berries were derived by summing berries counted on the 30 individually marked branches. Because Mamaki bushes were large and berries hard to estimate, phenology of ripe Mamaki berries was assessed by counting the maximum number of berries found on a branch for each bush, and then summing the maximum counts for 30 bushes. To get an index for vegetative growth, the indices for the 30 plants in each study site were summed. Data on flowering, unripe berries and over-ripe berries are not presented except for Blackberries. The phenological measurements provided an index of food availability at the time of measurement. Data dependency between monthly measurements prevented an analysis of correlation between rainfall, berry availability and maximum flock sizes. Time series analysis was not appropriate because phenology measurements were taken over an 18 month period only. My results concerning phenology are therefore mainly descriptive.

A seasonal trend in clutch size was investigated in an analysis of variance in Glim with a normal error distribution (Crawley 1993).

RESULTS

Weather data

Minimum temperatures, which potentially limit plant growth (Begon *et al.* 1996), were lowest at the high elevation site (Three Trees Kipuka) and highest at the low elevation site (Pen 7; Fig. 2). In 1995, January and February were the coldest months, August through October were the warmest (Fig. 2). Annual rainfall was highest at Devastation, the Hawaii Volcano Observatory (HVO), Upper Ainahou and Kipuka Kahalii, intermediate around the Crater Rim, at Kipuka Nene and at the lava flow east of the former Ainahou ranch (Pen 11 measurement) and lowest at the high elevation sites (Mauna Loa, Keamoku and Three Trees Kipuka), low altitude site (Pen 7) and the Kau Desert (Fig. 3).

Between 1988 and 1995, the highest average rainfall was recorded between November and January and the lowest in June (Appendix 2). Monthly rainfall varied considerably between sites (Appendix 3) and years (Appendix 4). Mauna Loa was the most variable (up to 215 times as much), followed by Kipuka Nene (up to 88 times as much), Keamoku/Mauna Loa (up to 53 times as much) and Upper Ainahou (up to 41 times as much). Throughout the breeding seasons, February was the most variable month (46 - 215 times as much differences in rainfall).

Plant density

The dominant berry bush species varied between sites (Table 2). Kukaenene was most abundant at Three Trees Kipuka; Uulei and Pukiawe at Ainahou; Mamaki at Kipuka Kahalii; and Ohelo, *Buddleia*, *Ageratina* and *Dubautia* at Devastation.

Table 2: Average plant density per 100 m^2 of species studied in eight scrubland study areas. Blackberries and *Rumex* at Devastation were distributed in clumps and did not occur in the randomly chosen survey plots.

	3 Trees	Devastation	Rim	Ainahou	K. Nene	Kau	Kahalii	Pen 7
Altitude (m)	*1830*	*1130*	*1120*	*910*	*880*	*880*	*790*	*730*
Plots (100 m^2)	*(n=2)*	*(n=5)*	*(n=8)**	*(n =4)*	*(n=4)*	*(n=3)*	*(n=10)**	*(n=2)*
Food source: berries								
Kukaenene	3.5	1.0	-	-	-	-	-	-
Uulei	-	-	-	13.0	-	1.0	-	-
Mamaki	-	-	-	-	-	-	0.75	-
Pukiawe	3.0	1.0	6.2	31.3	24.0	17.7	0.25	14.0
Ohelo	-	3.0	2.4	-	-	-	-	-
Food source: leaves								
Buddleia	-	1.8	-	-	-	-	1.7	-
Rumex	-	n.a.	-	-	-	-	0.5	-
Ageratina	-	3.4	-	-	-	-	1.0	-
Dubautia	-	12.4	-	-	1.0	-	0.8	-

** because of sparse vegetation cover, 400 m^2 were surveyed and then totals divided by 4.*

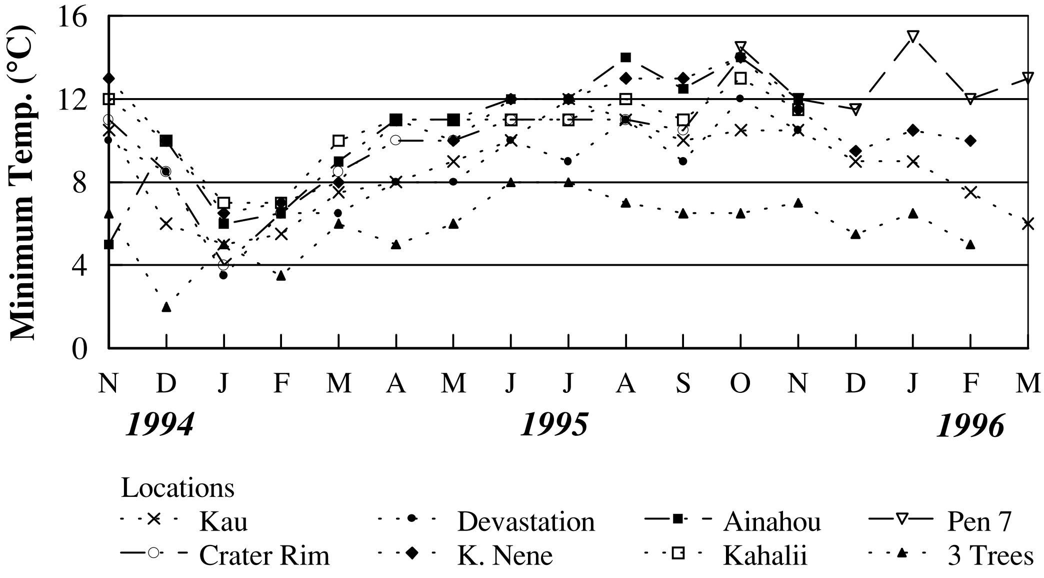


Fig. 2: Monthly minimum temperatures in eight scrubland sites within Hawaii Volcanoes National Park between November 1994 and March 1996.

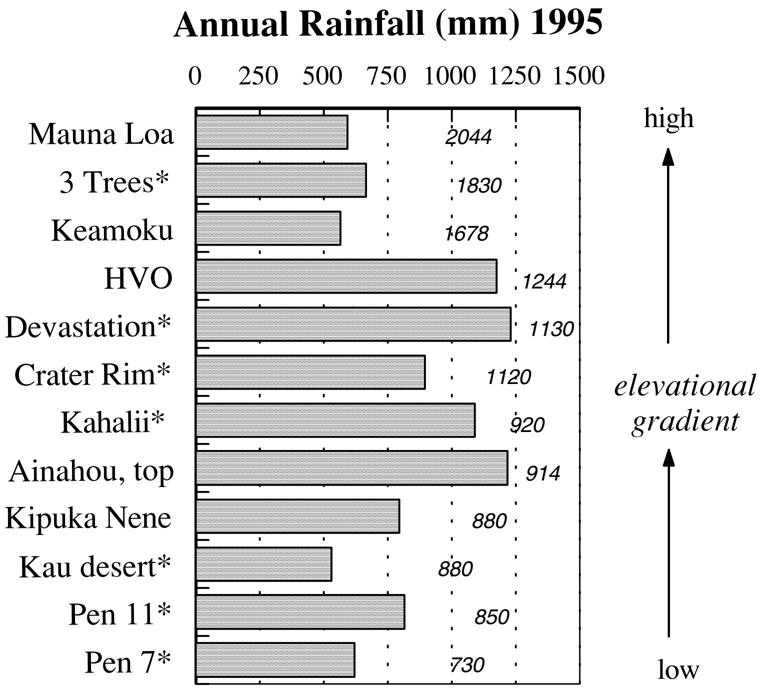


Fig. 3: Annual rainfall in 1995 at sites within Hawaii Volcanoes National Park. The asterisks indicate data measured in the scrubland study sites, the remainder is courtesy of the Hawaii Volcanoes National Park Fire Department. Numbers to the right of the bars indicate the approximate elevation of the site in meters.

Frequency of geese resighted in scrublands

The proportion of individual birds resighted in scrublands varied between months (Fig. 4). It was high at the onset of the breeding season in October 1994, during molt in March 1995 and in September 1995 during summer flocking. The variation in monthly rainfall during the breeding seasons explained a small part of the variation in resighting frequency in scrublands (F = 4.41, df = 1, P < 0.05) when fitted as the single explanatory variable. However, rainfall had no significant effect when month was included (Months October to March: F = 5.29, df = 5, P < 0.0001; controlling for year: F = 4.09, df = 1, P < 0.05), which suggests that the rainfall variation between months only explained part of the variation in goose distribution. The overall percentage of individuals resighted in open scrublands was similar between the two breeding seasons with 38% (1994/95) and 37% (1995/96). The resighting data for other habitats are not shown but the majority were from grassland habitat.

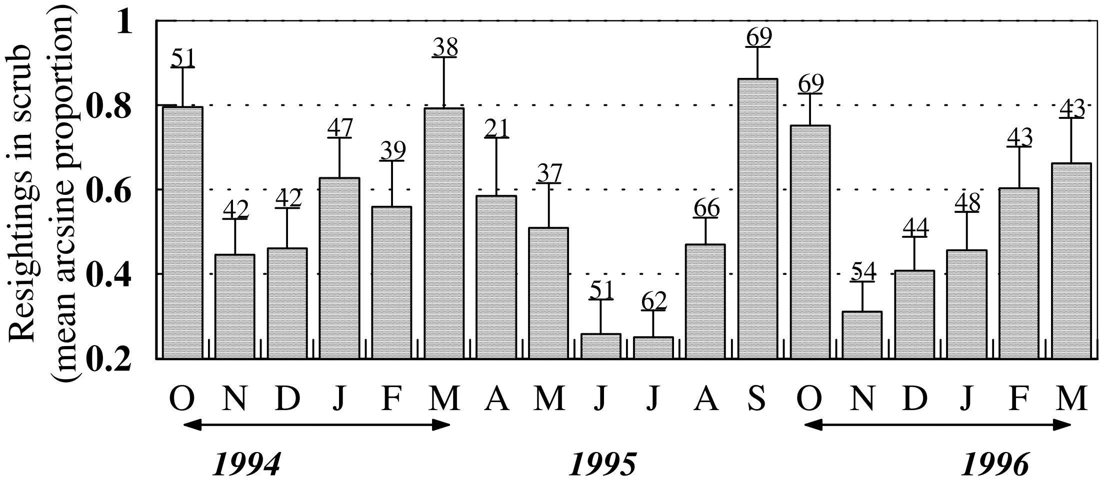


Fig. 4: The mean arcsine proportion individual birds were resighted in open scrubland habitat varied between months (F = 4.42, df = 17, P < 0.0001). Sample sizes (including pairs, single males and single females) and standard errors are indicated. When not resighted in open scrubland, birds were mostly seen in grasslands. The breeding seasons are indicated with an arrow.

Phenological patterns and rainfall

Most Mamaki, Pukiawe and Ohelo bushes fruited almost continuously, but numbers of fruits fluctuated throughout the year. Blackberry and Kukaenene fruited seasonally. The production of ripe berries was synchronized within Mamaki, Blackberry and Kukaenene, but varied among individual Ohelo and Pukiawe bushes. Plants produced new leaves almost continuously and there was no coordinated loss of leaves among bushes.

At most sites, Pukiawe fruited most heavily in the wet winter months when demand for berries by nesting geese was high (Fig. 5). Fruiting in Uulei was greatest at Ainahou in September and at the Kau desert in October, at the end of the dry summer (Fig. 5). The

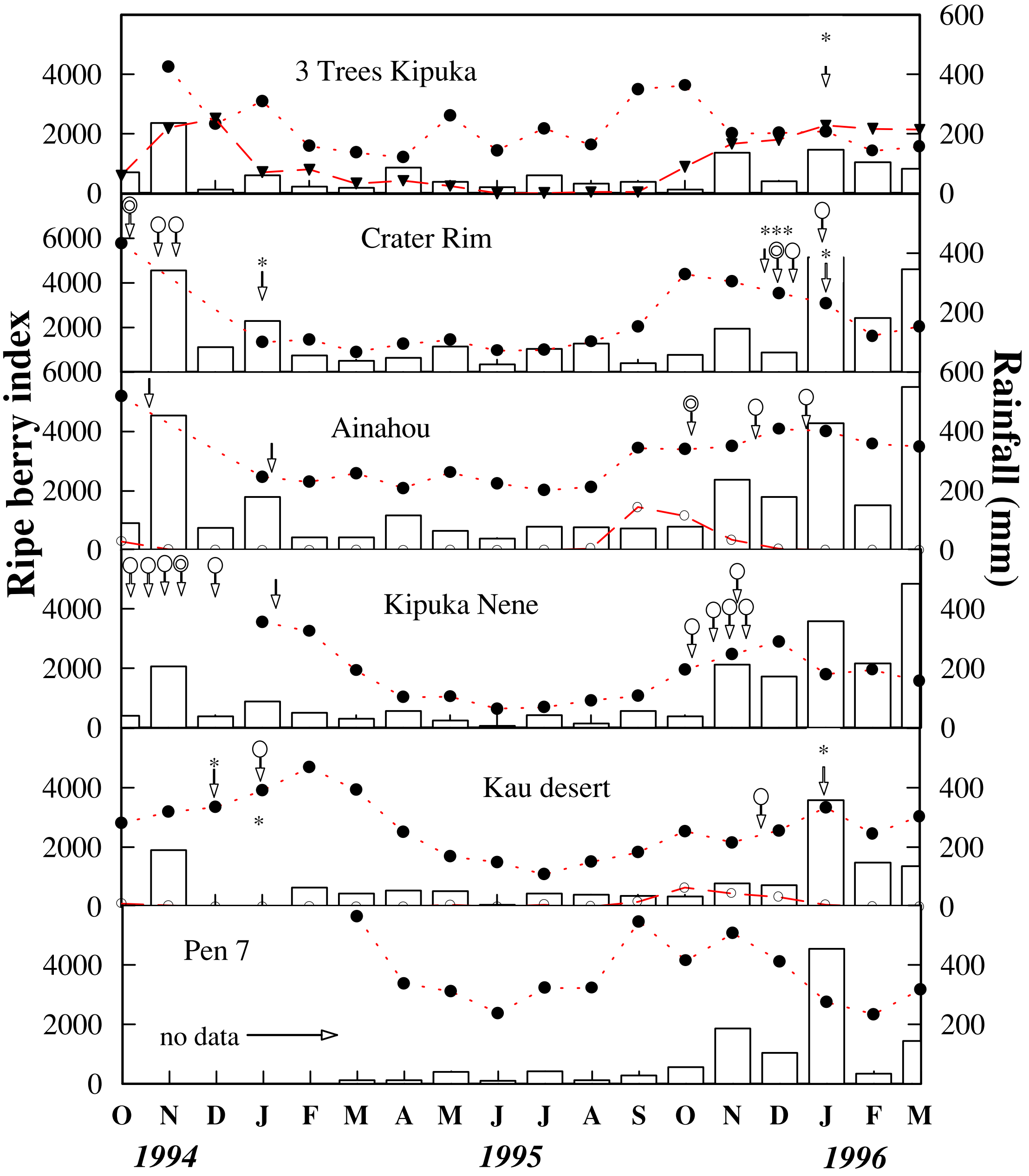


Fig. 5: Phenology of ripe Pukiawe berries (filled circles), ripe Uulei berries (open circles) and Kukaenene (closed triangles, for graphical purposes multiplied by 10) at six sites between October 1994 and March 1996 in relation to monthly rainfall (indicated by histogram bars). Arrows indicate nest initiation (single arrow = unsuccessful, arrow with circle = hatched, arrow with double circle = fledged, * indicates the estimation of nest initiation month from indirect evidence such as female brood patch or nest inspection after hatching).

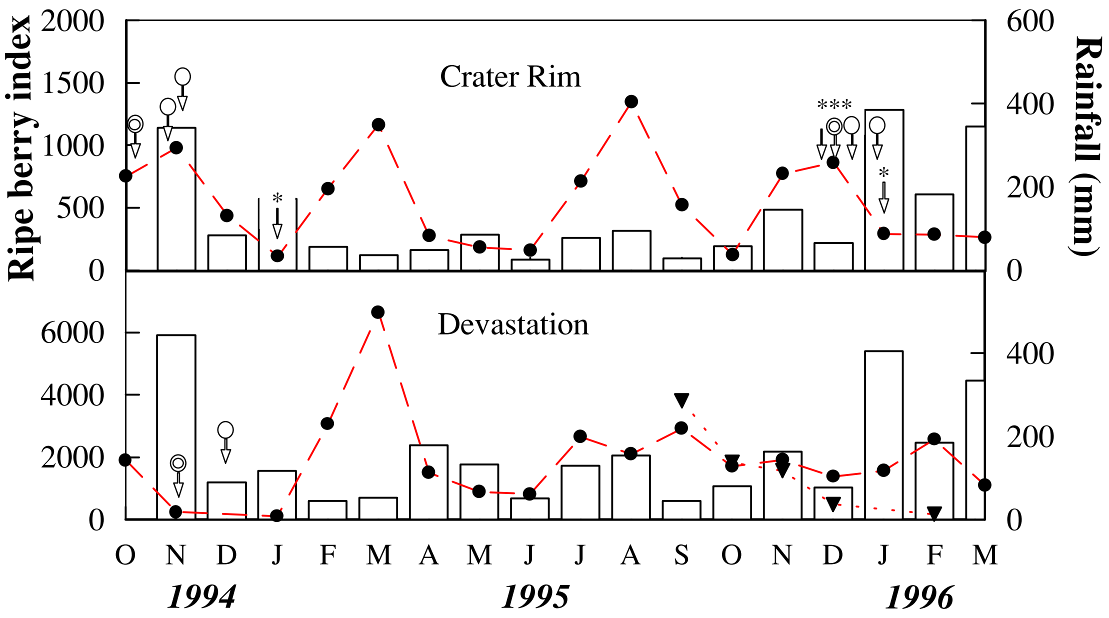


Fig. 6: Phenology of ripe Ohelo berries (filled circles) at Crater Rim and Devastation and Kukaenene (filled triangles) at Devastation in relation to monthly rainfall (bars). Arrows indicate nest initiation (for an explanation of the symbols see Figure 5).

number of Uulei berries was lower in the Kau Desert and fruiting peaked later, which coincided with lower precipitation in this area. Around Crater Rim, fruiting in Ohelo peaked three times (Fig. 6): in March, August and November/December. At Devastation, my phenological observations were probably obscured by people picking berries. The peak in March coincided with the one at Crater Rim, but there were no other distinct peaks. Rainfall did not appear to affect the Ohelo fruiting pattern at these two sites.

At Devastation, the number of ripe Kukaenene berries decreased steadily between September 1995 and February 1996 (Fig. 6). In the same time period, during the wetter winter months, Kukaenene berries at the high elevation site, Three Trees Kipuka, increased in numbers (Fig. 5). At Kipuka Kahalii, Mamaki fruiting peaked at the end of the summer (Fig. 7). Rainfall and the number of Mamaki berries correlated well in some months (e.g. between December 1994 and March 1995), but seemed unrelated in other months.

Vegetative growth activity was lowest in March and April (Fig. 8) perhaps due to a longer-term effect of a drop in rainfall following wet winter conditions. It is unclear how the monthly rainfall data related to growth at other times: in some months growth appeared to increase after a month of high rainfall, but in other months there was no obvious pattern.

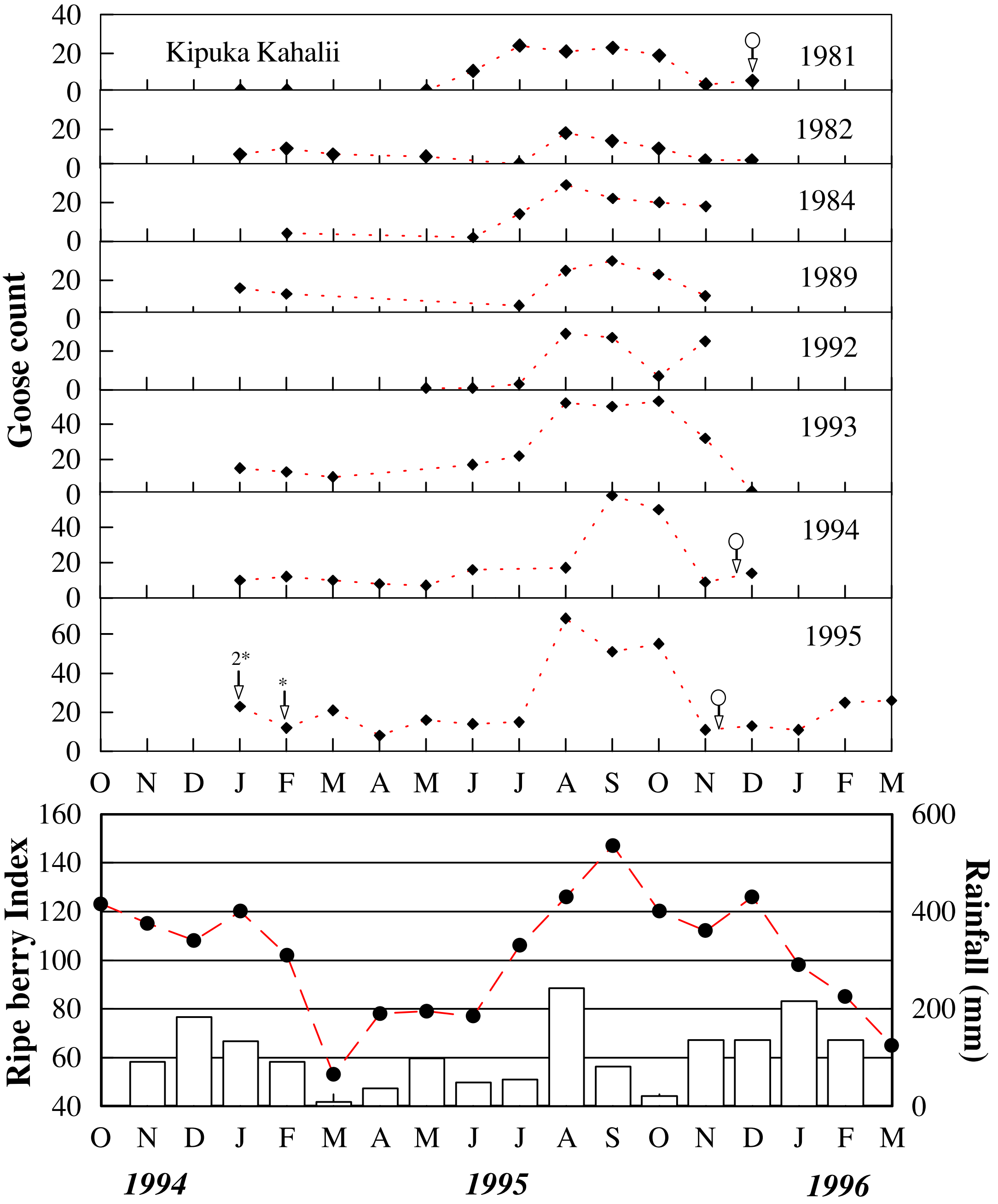


Fig. 7: Monthly maximum number of geese sighted at Kipuka Kahalii in selected years between 1981 and 1996 (upper graphs) in relation to the phenology of ripe Mamaki berries (dots) and rainfall (bars, lower graph). Years that are not presented had either a poor resighting effort or were similar to the above pattern.

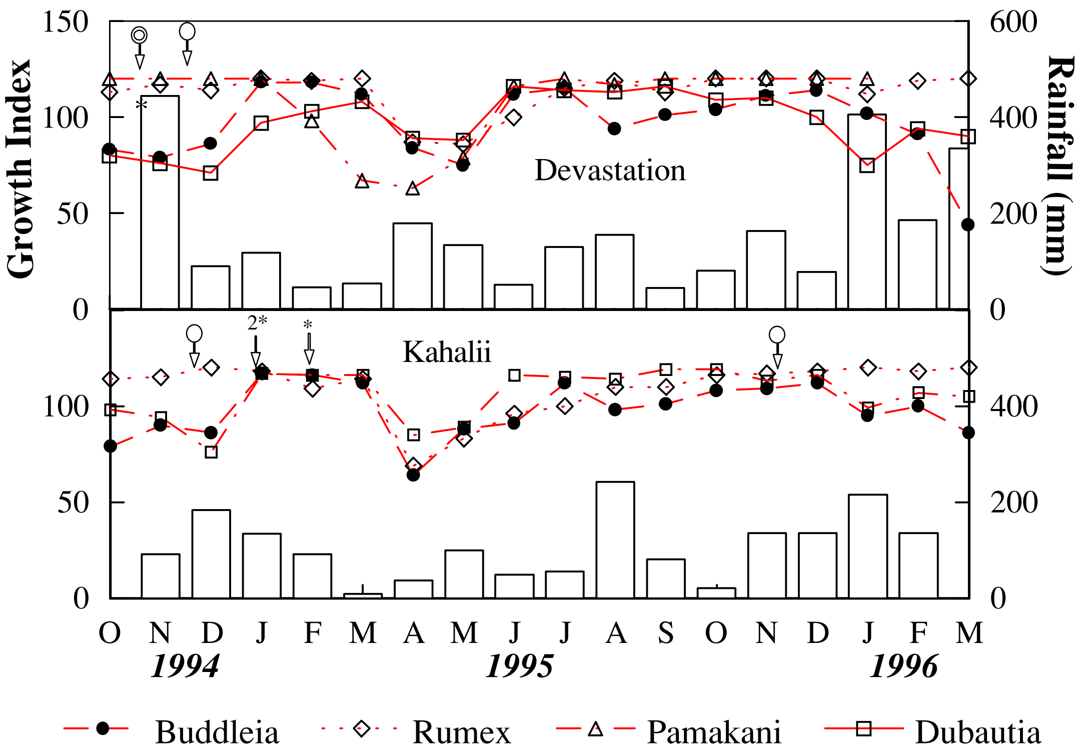


Fig. 8: Vegetative growth in four plant species at Devastation and Kipuka Kahalii in relation to monthly rainfall (bars). Arrows indicate nest initiation (for an explanation of the symbols see Fig. 5).

Goose distribution in relation to berry phenology

At Kipuka Kahalii, Geese were apparently attracted by ripe Mamaki berries from 1981 onwards, when the first geese were seen in this area (Fig. 7). Goose numbers counted at Kipuka Kahalii gradually increased to a maximum in 1995. In 1995, ripe Mamaki berries reached a peak in September, coinciding with large numbers of geese in the vicinity.

At Devastation, a peak of ripe Blackberries was expected in July towards the end of the dry season based on the number of unripe berries recorded in May and June, but the berries were depleted by an unknown source (Fig. 9). Although my data are incomplete, Blackberries at Devastation apparently attracted Hawaiian Geese in July in some years prior to my study. When Blackberries were unavailable at Devastation in July, the geese that had used the site in previous years switched to alternative feeding sites, e.g. the Volcano golf course (37 birds) and some to the grasslands at Ainahou (7) and Kipuka Nene (5). Few birds that switched habitat were seen in scrublands, although three birds were sighted at Kipuka Kahalii and two at the Crater Rim area.

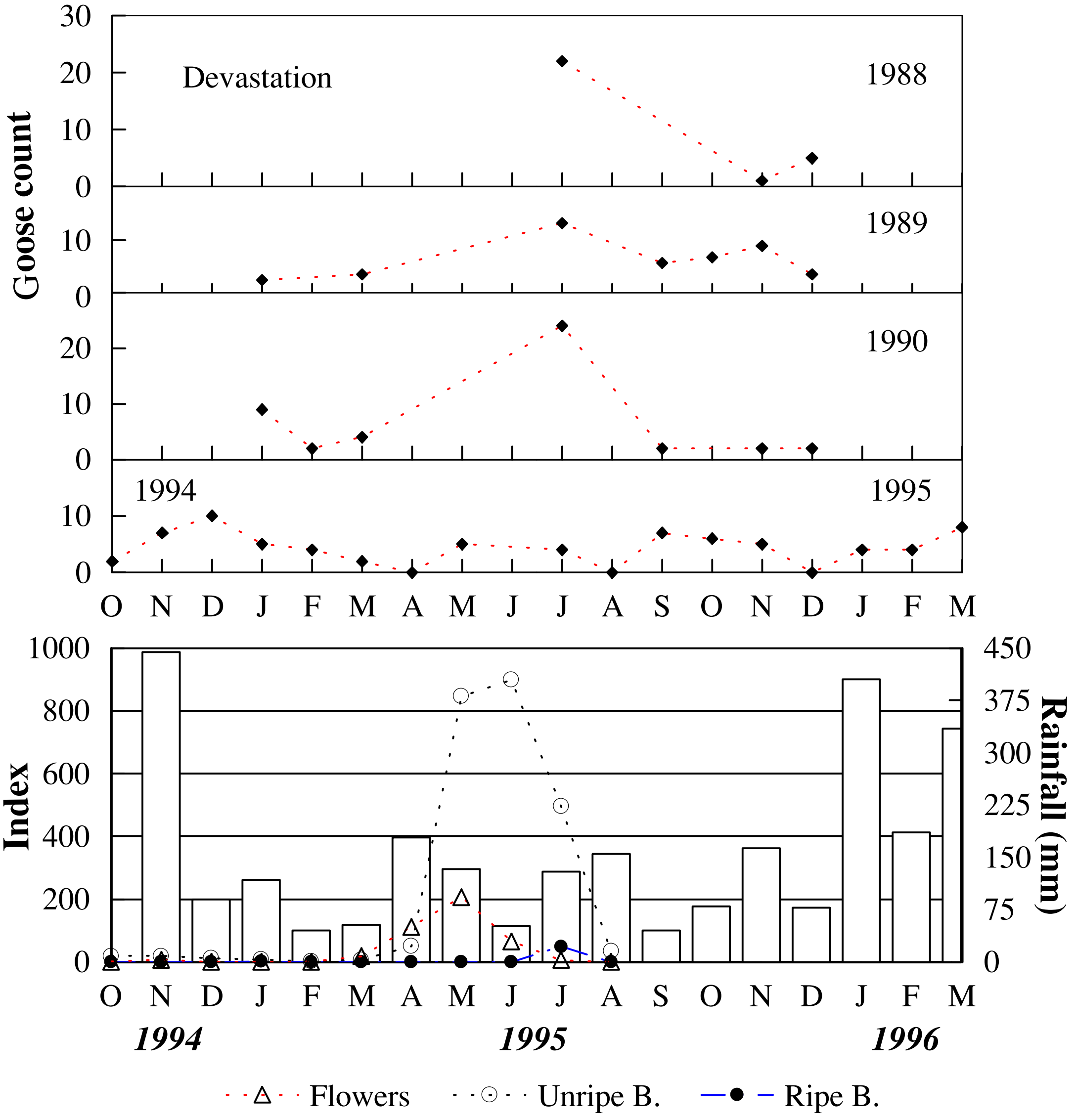


Fig. 9: Monthly maximum number of geese sighted in selected years between 1988 and 1996 in relation to Blackberry phenology at Devastation between 1994 and 1996. Data on Blackberry phenology was collected between October 1994 and August 1995, after which branches died.

Timing of nesting

Between 1975 and 1996, Hawaiian Geese initiated nests from September to March with a peak in November and December (Fig. 10). In those two months, 74% of all nests in the wild were initiated. Unlike in other geese (Cooke *et al.* 1995), there was no seasonal pattern in clutch size (months October to February: $F = 0.29$, $df = 4$, $P > 0.05$). Hatching and fledging success gradually declined throughout the breeding season (Table 3), although these trends were not statistically significant (hatching success: $G = 1.49$, $df = 4$, $P > 0.05$; fledging success: $G = 6.13$, $df = 4$, $P > 0.05$).

Table 3: Hatching and fledging success in relation to month of nest initiation at Hawaii Volcanoes National Park (1975 - 1996).

Month	**hatching**			**fledging**		
	success	fail	% success	success	fail	% success
October	11	1	92	5	7	42
November	30	3	91	9	21	30
December	20	3	87	3	15	17
January	3	1	75	0	4	0
February	3	1	75	0	2	0

Timing of nesting in consecutive years varied considerably for some individuals. For example, one female's nest initiation dates varied from 27 - 93 days between years (n = 3), whereas another initiated nests within 1 - 9 days in consecutive years (n = 4). Some females varied nest initiation dates in some years, but not in others (e.g. they laid exactly on the same day in their first and second year, but in the third year they nested 10 days later). The mean number of days between nest initiation dates in different years was 16.6 ± 2.1 days (n = 50 nest initiation date comparisons of 17 females).

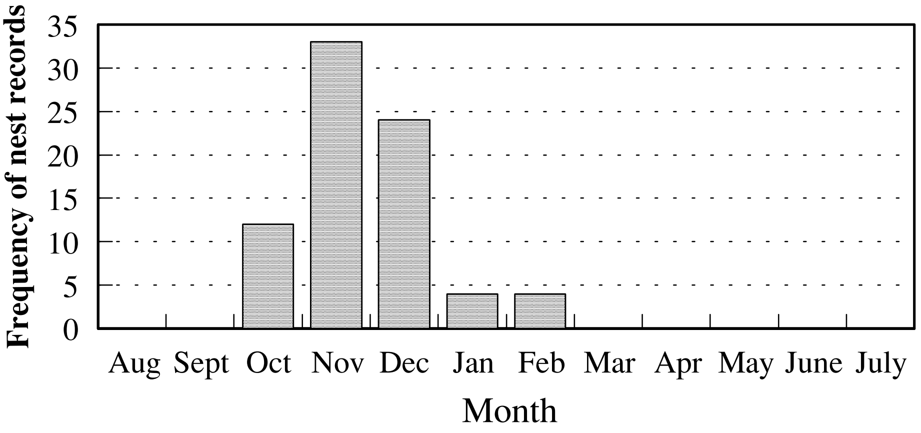


Fig. 10: The frequency of nest initiation between 1975 and 1996 (as determined by lay date) in Hawaii Volcanoes National Park in the wild (n = 77). Second clutches were excluded.

Timing of nesting in relation to rainfall and plant phenology

Most nests were initiated between November and January, which had high average rainfall (Fig. 10, Appendix 3). Not all Novembers and Decembers, however, were wet (Appendices 2 and 4). Analyzing the long-term nesting data on a monthly basis revealed that patterns of nest initiation were not related to actual monthly rainfall before, during or after incubation (Fig. 11).

During my study, most nesting occurred at Kipuka Nene, Kau Desert, Crater Rim, and Upper Ainahou (Table 4).

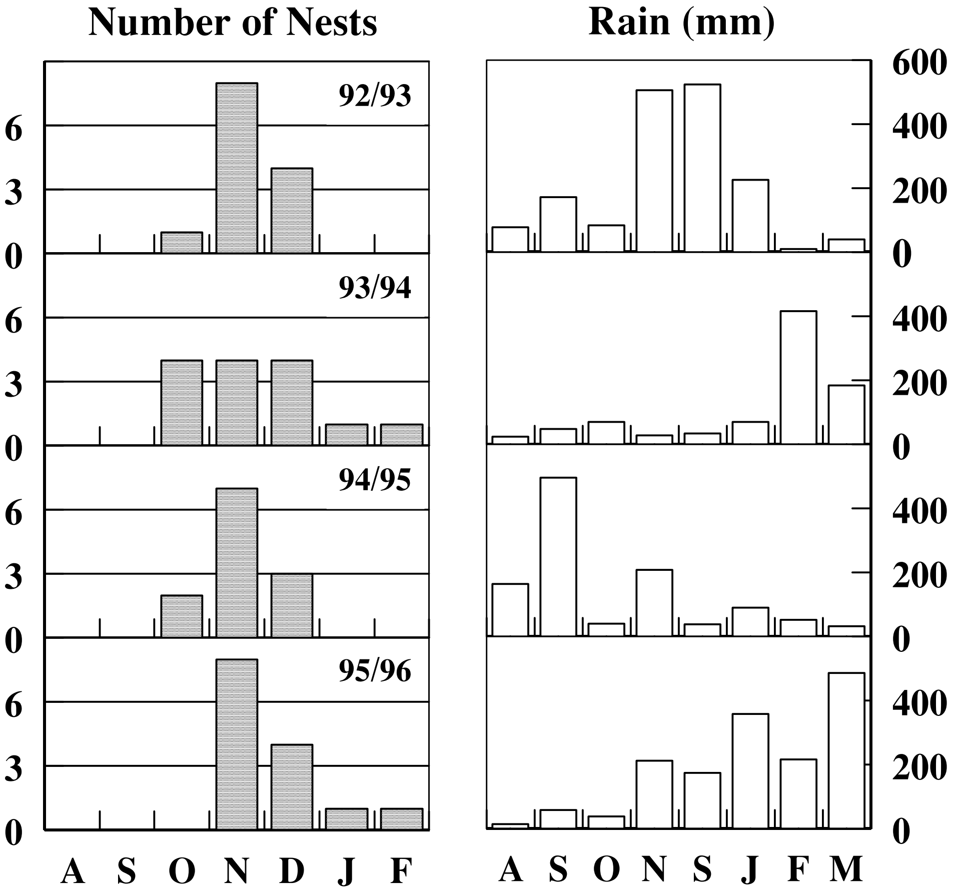


Fig. 11: Number of nests initiated between the 1992/1993 and the 1995/1996 breeding seasons and monthly rainfall from a central point in Hawaiian Goose habitat (Kipuka Nene). There was no apparent pattern between rainfall and nest initiation.

Table 4: Number of nests (or females showing evidence of breeding) found in the wild during the 1994/95 and 1995/96 breeding seasons. Only nests for which hatching date was known or could be estimated are presented.

	Number of nests	
Scrubland	1994/95	1995/96
Lower Ainahou	2	0
Upper Ainahou	2	6
Devastation	2	0
Kipuka Nene*	12	8
Kahalii	4	1
Kau	4	6
Crater Rim	4	6
Unknown**	6	3
Total	36	30

* *includes Hilina Pali*

***includes indirect evidence of nesting (e.g. brood patch)*

In 1996, nests in three nesting areas (Kipuka Nene, Crater Rim and Ainahou) were initiated when the number of ripe Pukiawe berries was at a peak (Fig. 12). The monthly number of individual birds resighted at these areas peaked in November and December, one month after the summed indices for ripe Pukiawe berries (Fig. 12).

Although nest records during the phenology study were limited, early broods tended to be more successful, reflecting the trend in the long-term data. In 1994, only the earliest brood fledged at Crater Rim. The goslings hatched when Pukiawe and Ohelo (Fig. 5 and 6) availability was high. In addition, the family used the Devastation area and might have depleted Ohelo berries there. In January, when most of the berries were depleted, the young birds were able to take advantage of increased young growth in plants (Fig. 8); young goslings were observed to forage on young *Buddleia* leaves and some *Rumex* plants showed signs of heavy browsing. I also observed that young growth in Gosmore, an important gosling food (Black *et al.* 1994), was high in January. In 1995, only the earliest brood at Ainahou fledged. The first nest was active during a period of high berry availability with both Uulei and Pukiawe abundant, whereas later only Pukiawe berries were abundant, but Uulei berries were not available. At Kipuka Kahalii, only early nests initiated during periods of relatively high Mamaki berry availability successfully hatched young (Fig. 7). Nests initiated later, in January and February, preceded the lowest availability of Mamaki berries in March and failed without exception. Some early nests failed due to external events such as predation and severe weather. In 1994, a nest initiated at Ainahou in October was predated by a dog. In 1995, a gosling hatched from a nest initiated at Kipuka Nene in October disappeared after a storm.

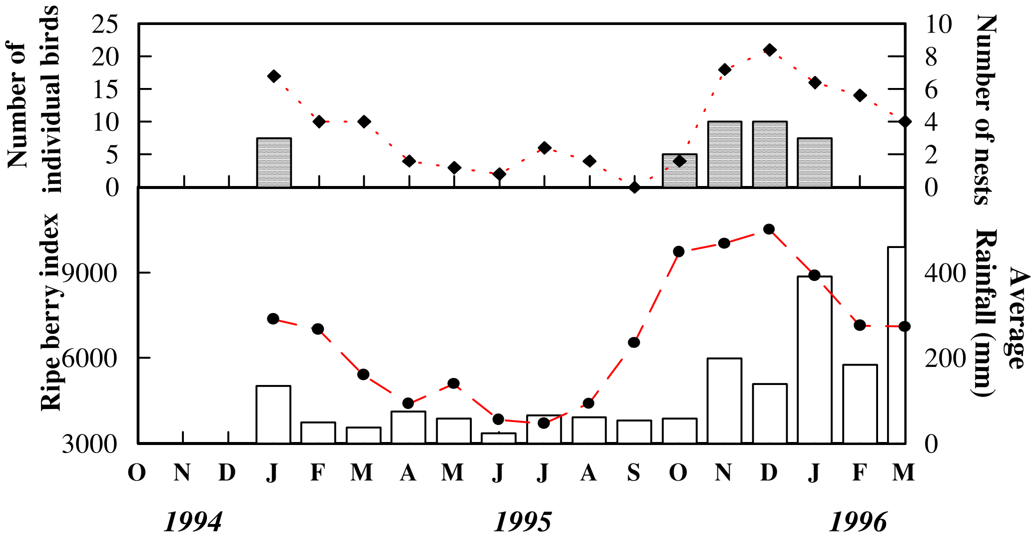


Fig. 12: The monthly number of individual birds resighted at Kipuka Nene, Crater Rim and Ainahou (dotted line with diamonds) in relation to the number of nests initiated there (gray bars), the phenology of ripe Pukiawe berries (lower line with dots; indices of all three areas combined) and average rainfall (bars, lower graph).

DISCUSSION

Plant phenology in relation to rainfall

In tropical climates, fruits generally ripen in the late dry to mid rainy season (Smythe 1970, Wolf 1970, Crome 1975). However, some tropical species fruit during other periods, some unpredictably, some continuously (Croat 1975), and this variation is often related to differences in local climate due to elevation. Although Hawaii is considered subtropical, tropical observations are helpful in understanding the phenological patterns observed. In my study, most species fruited almost continuously (e.g. Mamaki, Pukiawe and Ohelo), although some fruited seasonally (e.g. Uulei, Blackberry and Kukaenene). Fruiting in some species (e.g. Mamaki, Uulei) peaked at the end of the dry season, with others (e.g. Pukiawe) peaking in the wet season. Fruit ripening is determined by a combination of internal and environmental parameters, such as hormones and temperature, light and rainfall (Nitsch 1970, Smythe 1970, Gorchov 1985, Rathke and Lacey 1985). Phenology, especially in Pukiawe, Uulei and Ohelo, varied between sites receiving varying amounts of rainfall and differing minimum temperatures and elevations. Similar variation in phenology has been described by Bridges *et al.* (1981) for some Hawaiian tree species. Rainfall relationships are widely viewed as an important factor in determining the flowering and fruiting periods. The role of rainfall, however, is complex and not well understood (Bridges *et al.* 1981). In Hawaii, few studies have shown the climatological mechanisms involved in phenology and even fewer studies have considered the amount of variation between years. Rainfall variation in Hawaii is considerable between years and months, and little is known about the short-term effects of rainfall on the vegetation. The variation in phenologies observed in this study highlight the need for longer-term studies to investigate fully the effect of varying rainfall patterns on phenology.

Goose distribution and food availability

Goose distribution in scrublands varied throughout the year. Scrublands were used most at the onset of the breeding season in October, during molting in March and in September during summer flocking, reflecting different stages in the birds' annual cycle. Some of the observed distribution patterns were associated with variation in rainfall which, in turn, may affect phenological patterns. The forage quality in one habitat relative to another may explain part of the variation in the observed distribution patterns: if food availability and quality in the grasslands is low, birds may move to scrublands and *vice versa*.

During this study, Hawaiian geese were seen feeding on Mamaki berries at Kipuka Kahalii, especially during the peak of the Mamaki fruiting period between July and October. Kipuka Kahalii was created during the 1969 eruption of Mauna Ulu, less then 2 km away. Mamaki, Aalii and Dubautia colonized this newly created cinder field and the first Hawaiian Goose nest was found 6 years after the eruption had ceased (H. Hoshide pers. comm.). Initially, Mamaki bushes were smaller (H. Hoshide pers. comm.) and probably could only support a small number of geese. The increase in goose numbers at Kipuka Kahalii might therefore be due to two factors: firstly, bushes increasing in size were able to support more geese; secondly, the Hawaiian Goose population grew significantly between 1981 and 1995. Therefore, it is likely that more geese might have 'learned' about this important feeding site from flock members.

Fruit production was well synchronized in some species, including Mamaki and Blackberry, which may have allowed the geese to built up a tradition in exploiting these seasonally abundant food resources. In other species like Ohelo and Pukiawe, however, a large variation in fruiting patterns occurred. The temporal and spatial variability of berry abundance in Pukiawe and Ohelo might be related to variation in rainfall between months, years and sites and fruit depletion by the geese. Irregular fruiting patterns, similar to those I observed in Ohelo, are common in some tropical plants which are thought to be influenced by the removal of fruit. Experimental removal of fruits resulted in higher ripening rates (Levey 1987), a response that allows the plant to increase dispersal success. The total amount of food available for the geese appears to be affected by the interplay between the availability of various berries and young growth in perennials, herbs and grasses. In some areas, vegetative growth increased when berry availability dropped (perhaps through depletion), offering additional forage to the geese.

Geese as seed dispersers

Some studies have shown that the abundance and type of dispersers influence flowering and ripening schedules (Wolf 1970, Thompson and Willson 1979, Stiles 1980). Hawaiian Geese are probably the main seed dispersers for many plant species growing on the open lava flows of Hawaii, such as Pukiawe, Ohelo and Mamaki, a task which may, in addition, have been performed previously by now extinct bird species. It is possible that some plant species have co-evolved with Hawaiian Geese and time their fruiting peaks to coincide with Hawaiian Goose demand, to ensure seed dispersal. The ripening of Uulei berries coincided with the pre-breeding period in which geese have a high food demand. Seeds that were consumed by Hawaiian Geese had higher germination rates than unconsummated seeds (F. Duvall pers. comm.), which has also been described for introduced game birds (Cole *et al.* 1991).

In Hawaii, the dispersal of introduced, and often invasive, plant species by birds is a major conservation problem. For example, by feeding on Blackberries, Hawaiian Geese may spread seeds into undisturbed habitats. Another example is the introduced, invasive Russian Olive (*Olea europaea africana*) that is readily eaten by Hawaiian Geese at Ainahou and has recently been found 2 km away at Kipuka Kahalii, suggesting that the birds dispersed the seeds. At Kipuka Nene, Hawaiian Geese fed on berries of the non-native Firebush (*Myrica faya*), probably the most invasive plant in the summer-dry lava deserts (Cuddihy and Stone 1990). Hawaiian Geese appear to be opportunistic in their choice of food plant as long as they meet nutritional demands. In 1995, when Blackberries at Devastation were not available for the geese, birds fed elsewhere instead. Removal of exotic shrubs, especially in ecologically fragile areas, is an important goal of ecosystem management.

Timing of nesting

Most Hawaiian Geese initiated nests in November when average rainfall was highest. However, few birds nested in January which had the second highest average rainfall. Therefore, rainfall appears to explain only part of the observed nest initiation pattern.

Unlike in temperate and arctic nesting goose species (Barry 1962, Ryder 1972, Findlay and Cooke 1982), clutch size in Hawaiian Geese appeared to be independent of lay-date with no discernible trend throughout the breeding season. Clutch size in most bird species is affected by food availability. The more nutrient reserves a female can accumulate prior to laying, the larger her clutch. With extremely variable rainfall patterns throughout the breeding season, food availability may have been variable in consecutive years, which may explain the lack of a seasonal trend in clutch size.

Individual differences in the timing of nesting

Individual females varied their time of nesting between years; some had a narrow window, while others differed by more than three months. This might represent different evolutionary strategies. Several types might survive in the population because of the great annual and monthly variation between sites in environmental conditions before, during and after incubation. Similar to arctic geese (Raveling 1978), Hawaiian Geese may be able to adapt yolk formation to local environmental conditions and delay nesting when environmental conditions are unfavorable.

Timing of nesting according to food availability

Annual fluctuations in food abundance contribute to the temporal limitations of breeding seasons throughout central America (Leck 1972). In New Zealand, female Kakapo only nest in years when certain food plants are seasonally abundant (Moorhouse and Powlesland 1991). In a wide range of species early breeders tend to fledge more chicks (Daan et al. 1989, Rohwer 1992) and this observation is often associated with higher food availability earlier in the season. Timing of nesting in arctic geese is dependent on the availability of lush green growth after the spring thaw (e.g. Owen 1980, Ely and Raveling 1984, Sedinger and Raveling 1986). Eggs hatch when the nutritional value of the vegetation is high, which allows rapid growth of the goslings. On Hawaii, Black *et al.* (1994) found a seasonal decline in food quality and density between November and January. In subsequent years I found that berry abundance in some plants, e.g. Pukiawe, Mamaki and Uulei, declined in some areas, but patterns varied between sites, years and species. Ohelo berries, for example, fluctuated throughout the year without any clear seasonal trend. In many cases, birds that nested earlier in the season were more successful, but other events such as predation and severe weather caused deviation from the predicted pattern. Breeding pairs compete for a limited amount of food and not all pairs will be successful in securing a good territory (Black *et al.* 1994). Birds that nest early may be more successful because they defend better territories. Furthermore, food resources in the brood rearing areas are likely to decline throughout the season. The lack of lush, nutritious forage is especially detrimental for young goslings, which die when not gaining enough weight (Banko 1988). Young Capercaille chicks call more frequently when they are hungry, increasing the risk of being detected by a predator (D. Dugan pers. comm).

Local differences in predation pressure is likely to have an effect on distribution patterns and might also affect the timing of nesting. Egg predation is more likely to occur during times of low food availability (Prop *et al.* 1984). At such times, females take longer incubation recesses in order to feed, leaving the nest unprotected (Banko 1988).

Vegetative growth in four plant species was lowest in April and May, which coincides with the end of the Hawaiian Goose breeding season. Young growth in plants is nutritious for geese and important for gosling growth. The observed patterns of vegetative growth probably occur in other food plants in the scrubland habitat, and it is possible that the lack of vegetative growth in April limits the breeding season. Late broods rarely fledge and this may be due to the lack of nutritious food which allows growth. After breeding, geese accumulate fat reserves before they start molting in March. During molting, many birds live off their fat reserves (Owen 1980). During the flightless period, birds have been observed in sparsely vegetated desert (H. Hoshide pers. comm.), suggesting that they do not feed much during molt. For Hawaiian Geese, molting coincides with the period of low vegetative growth.

Management implications

The most frequented area at Kipuka Kahalii is at high risk of destruction from volcanic eruption of the close-by Mauna Ulu volcano, which is still active. Planting additional areas with Mamaki would lower the chances of all sites being destroyed at once and would secure additional forage for the Hawaiian Goose population. Picking of native berries by people reduces scarce natural food resources for Hawaiian Geese and should only be allowed in areas which are not utilized by geese. Predator control is most important just before, during and after peak nesting between October and February.

Future research

The decision and learning processes involved in determining where and when to feed must be complex in Hawaiian Geese. They are skilled in exploiting patchily distributed food, and they select food plants of high nutritional quality (also see Chapter 5). To better understand what they base these decisions on, long-term fluctuations of the nutritional value of their food over time and between sites should be studied.

SUMMARY

The seasonal distribution patterns of individually marked Hawaiian Geese (*Branta sandvicensis*) are described in relation to the availability of their food plants in scrubland. Phenology of the main food plants in scrublands varied between species. Most species fruited continuously. Fruiting in some species peaked at the end of the dry season, whereas others peaked in the middle of the wet season. The phenology of food plants varied between sites and with elevation. Geese appeared to time their movements and nesting according to local food availability. Between 1960 and 1996, peak nest initiation was in November and December, which had high average rainfall. Generally, geese that nested earlier in the season, when berry availability was high, tended to be more successful in rearing young but other events, such as predation, caused some early breeders to fail.

Appendix 1. Species composition in scrubland areas studied in Hawaii Volcanoes National Park (data from 100 m^2 random quadrates, some ferns and sedges remained unidentified).

Species (Common name)	Kahalii	Aina-hou	Pen 7	Kipuka Nene	Devas-tation	Cr. Rim	Kau	3 Trees
Ageratina riparia (Pamakani)	x				x			
Andropogon virginicus (Broomsedge)	x	x	x	x	x	x	x	x
Anemone hupehensis (Japanese Anemone)					x			
Anthoxanthum odoratum (Sweet vernalgrass)								x
Axonopus fissifolius (Carpetgrass)					x			
Bidens pilosa (Spanish needle)					x			
Buddleia asiatica (Butterfly bush)	x				x			
Bulbostylis capillaris		x		x	x	x	x	
Coprosma ernodeoides (Kukaenene)					x			x
Deschampsia nubigena (Hairgrass)								x
Dodonaea viscosa (Aalii)	x	x	x	x		x	x	x
Dubautia scabra	x			x	x			
Dubautia ciliolata						x		
Dryopteris spp.						x		
Olea europaea africana (Russian olive)	x							
Eragrostis brownei								x
Epilobium billardierianum (Willow herb)					x			x
Fragaria fesca (Strawberry)	x				x			
Gahnia gahniiformis		x		x			x	x
Pseudognaphalium sandwicensium (Cudweed)			x					
Holcus lanatus (Velvet grass)								x
Hypochoeris radicata (Gosmore)					x			x
Juncus spp.					x			
Lantana camara (Lantana)	x		x					
Melinis minutiflora (Molasses grass)	x	x	x	x			x	
Metrodideros polymorpha (Ohia lehua)	x	x		x	x	x	x	x
Myrica faya (Firetree)	x		x					
Nephrolepis multiflora	x				x	x		
Oenothera stricta (Evening Primrose)								x
Osteomeles anthyllidifolia (Uulei)		x					x	
Pellaea ternifolia								x
Pipturus albidus (Mamaki)	x							
Pityrogramma austroamericana						x		
Polygonum capitatum (Knotweed)					x			
Psidium guajava (Guava)	x		x					
Pteridium sp.	x							
Rubus argutus (Florida Blackberry)					x			
Rumex acetosella (Sheep sorrel)								x
Rumex giganteus (Pawale)					x			
Rumex skottsbergii (Pawale)	x				x			x
Rubus rosifolius (Thimbleberry)								
Melinus repens (Natal Redtop)	x							x
Sadleria cyatheoides	x				x	x		
Schizachyrium condensatum (Beardgrass)						x		
Silene hawaiiensis (Catchfly)						x		
Sporobulus africanus (Rattail grass)								x
Styphelia tameiameiae (Pukiawe)	x	x	x	x	x	x	x	x
Setaria gracilis (Foxtail)					x			
Verbascum thapsus (Woolly Mullein)								x
Verbena litoralis (Vervain)								x
Vaccinium reticulatum (Ohelo)					x	x	x	x
Waltheria americana (Uhaloa)			x					

Appendix 2: Monthly range of rainfall (mm) at Hawaii Volcanoes National Park between 1988 and 1995.

Month	K. Nene *(850 m)*	Ainahou *(920 m)*	Halemaumau *(1100 m)*	HVO *(1240 m)*	Keamoku *(1700 m)*	Mauna Loa *(2330 m)*
January	37 - 705	68 - 778	23 - 640	41 - 639	42 - 612	37 - 488
February	9 - 416	12 - 492	9 - 410	17 - 418	9 - 240	2 - 430
March	5 - 440	41 -574	19 - 485	20 - 441	3 - 159	4 - 473
April	20 - 199	60 - 190	28 - 180	32 - 115	21 - 252	27 - 252
May	4 - 63	54 - 168	16 - 157	23 - 125	18 - 134	26 - 160
June	0 - 39	39 - 87	7 - 64	8 - 87	6 - 87	7 - 94
July	6 -367	65 - 395	22 - 335	17 - 437	18 - 363	24 - 389
August	13 - 164	33 - 403	24 - 217	43 - 270	32 - 155	35 - 312
September	45 - 495	40 - 531	28 - 430	35 - 523	38 - 164	38 - 261
October	40 - 562	78 - 575	28 -343	46 - 301	13 - 287	15 - 355
November	27 - 826	37 - 1092	23 - 824	23 - 965	13 - 368	16 - 654
December	27 - 523	39 - 461	37 - 327	12 - 391	12 - 223	10 - 205

Appendix 3: Monthly mean rainfall (mm) at Hawaii Volcanoes National Park between 1988 and 1995.

Month	K. Nene *(850 m)*	Ainahou *(920 m)*	Halemaumau *(1100 m)*	HVO *(1240 m)*	Keamoku *(1700 m)*	Mauna Loa *(2330 m)*
January	223	275	203	257	161	167
February	157	184	154	202	94	159
March	151	183	147	140	71	114
April	65	102	62	68	71	73
May	29	74	57	64	66	68
June	17	58	24	36	30	36
July	125	162	122	136	119	162
August	79	119	83	107	69	116
September	153	185	137	159	105	132
October	158	179	117	133	107	111
November	292	399	291	305	154	260
December	213	250	164	164	110	111

Appendix 4: Monthly rainfall (mm) at Kipuka Nene between 1988 and 1995.

Month	1988	1989	1990	1991	1992	1993	1994	1995
January	58	316	705	131	37	225	69	111
February	21	284	350	62	23	9	416	28
March	107	440	39	364	5	40	184	30
April	20	199	61	66	74	24	21	57
May	35	54	4	7	63	30	13	25
June	0	39	15	9	30	10	25	7
July	6	349	57	44	75	367	63	42
August	112	81	28	133	78	24	164	13
September	45	61	161	183	171	47	495	57
Oktober	274	562	71	117	84	69	40	45
November	331	40	826	181	506	27	218	205
December	156	62	354	375	523	33	27	173
Total	1165	2487	2671	1672	1669	905	1735	793

Chapter 5: Foraging behavior and temporal use of grasslands by Hawaiian Geese: Implications for management

INTRODUCTION

In spite of major conservation efforts, the Hawaiian Goose (*Branta sandvicensis*), widely known as the Nene, is still one of the most endangered waterfowl species in the world. The breeding success in the wild remains low, and without releases of captive-bred birds, numbers may rapidly decline (Black and Banko 1994). Predation by introduced mammalian predators and the poor availability of food are thought to be the main obstacles on the Nenes' route to recovery (Baldwin 1947, Stone *et al.* 1983, Banko 1982, Black 1995). The low incidence of nesting suggests that many females cannot accumulate sufficient body reserves for egg-laying and incubation due to poor foraging conditions (Banko 1992). Recent studies on gosling mortality showed that lack of adequate nutrition is especially detrimental for young birds (P. Baker and H. Baker pers. comm.).

We do not know what habitats the Hawaiian Geese used in the times prior to Polynesian and European settlement. Today, birds nest and roost in open scrubland in lava deserts where they feed on berries and on grasslands created by humans, such as ranches, golf courses, lawns around housing areas and campgrounds, where they fatten up prior to breeding and rear their goslings (Black *et al.* 1994). This pattern follows that of many Arctic geese foraging on agricultural fields and pastures during migration and in the wintering grounds (reviewed by Black *et al.* 1994). After removal of the ungulates within Hawaii Volcanoes National Park, previously grazed pastures, mainly consisting of introduced grass species, have become overgrown (Cuddihy and Stone 1990) and thickets have formed which are not used by the geese. For the purpose of this study, two overgrown sites were mowed and I subsequently compared them with established sites which had previously been mowed or grazed by livestock. I asked whether the vegetation composition and cover, seedhead abundance, grass height, protein and water content of grass, rainfall, temperature and time of year contributed to the variation in grazing pressure.

I discuss the implications of my findings for grassland management and the role managed grasslands could play in the recovery of Hawaiian Geese.

STUDY AREA AND METHODS

I collected data at Hawaii Volcanoes National Park and the adjacent Kapapala Ranch (Fig. 1). Hawaii Volcanoes National Park comprises an area of 85,000 hectares and holds a population of about 200 Hawaiian Geese (Banko *et al.* in press). I studied grazing behavior in the breeding season from December 1994 to March 1995 and in the pre-breeding and breeding season from August 1995 to March 1996. The grasslands varied in size, boundary type, management regime, soil and other environmental factors. I measured the size of the grasslands with the Global Positioning System 'Pathfinder'. They ranged from 0.1 - 4 hectares and were mowed or livestock-grazed periodically. A boundary index was recorded ranging from open to very enclosed (1 = open, short grass, 2 = open, surrounded by tall grass and bushes, 3 = open, tall grass and bushes surrounding and within, 4 = closed, a few trees surrounding and within, 5 = closed, many trees surrounding and within) (Table 1). Most soils were porous, not holding water.

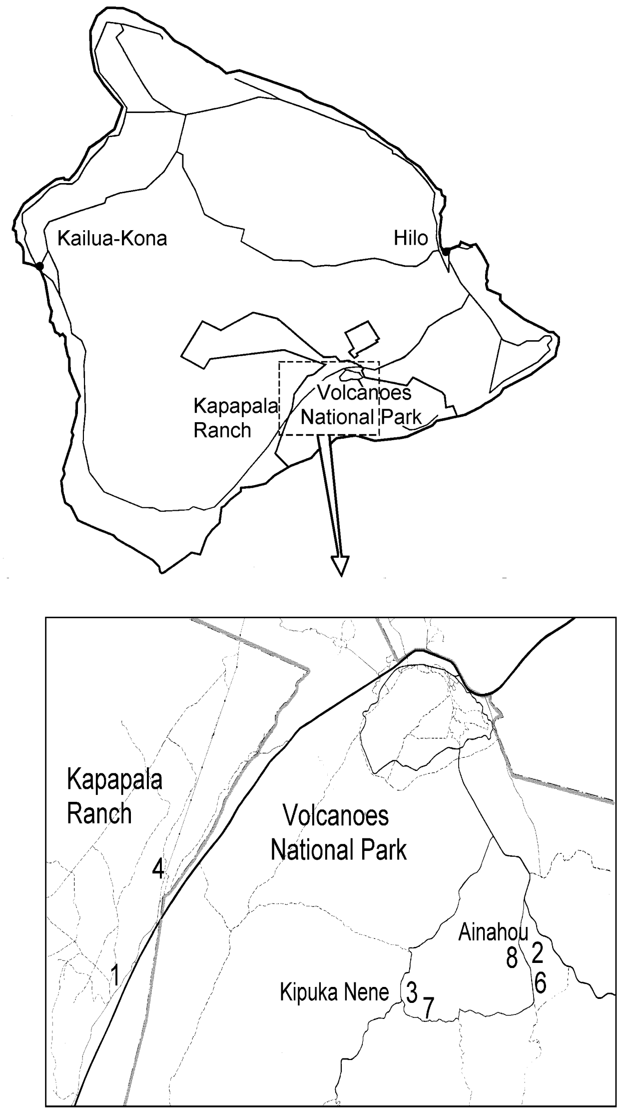


Fig. 1: Location of Hawaii Volcanoes National Park, Kapapala Ranch and study sites.

Table 1: Area size, boundary index and management regime of the study sites. Area sizes only account for managed grassland, islands of tall vegetation within the grasslands were excluded. Areas that were kept at least partially short by the geese were considered to be goose grazed.

#	Site	Area size [m^2]	Boundary	Management
1	Ainapo Corral (Kapapala Ranch)	29,110	1	overgrazed by cattle
4	Halfway House (Kapapala Ranch)	40,000 (est.)	1	overgrazed by cattle
3	Kipuka Nene Campground	1,520	5	mowed/goose grazed
7	Kipuka Nene mowed area	2,140	2	mowed
8	Ainahou, Pen 11	5,200	3	mowed/goose grazed
5	Ainahou, Pine area	1,160	4	mowed
2	Ainahou, Big Pen	5,290	4	mowed/horse grazed
6	Ainahou, Lower mowed area	5,210	5	mowed

Sites 2 and 6 were previously overgrown with mainly Kikuyu grass (*Pennisetum clandestinum*) until they were mowed in November 1994. Site 7 was initially mowed in 1992, whereas the other sites were mowed or grazed much earlier. Site 3 has been a recreational picnic area since the early 1940s, and later became a campground, and the pastures at sites 5 and 8 were periodically mowed for the geese by the National Park Service since 1992.

I made observations of the behavior of the geese at sites 2 and 8 during 13 days between November 94 - March 95 (149 hours), and during 11 days between August 95- March 1995/6 (119 hours). Observations were spread throughout the season. The majority of birds observed were non-breeders or failed breeders. The behavior of all geese present in an area was scan sampled from dawn to dusk (for a daily average of 11 hours, total of 268 hours). An audio beeper gave a signal every 10 minutes and the behavior of all individually marked birds visible at that instant was recorded (Martin and Bateson 1986). Behaviors included vigilance, feeding, loafing, preening, walking and social interactions (courtship, agressive encounters) (Inglis 1977).

I measured weekly grazing pressure by counting and removing droppings, which had accumulated in seven days prior to measurement, within a 1.12 m radius of randomly placed stakes (each plot covering an area of 4m^2) (Owen 1971, Summers and Stansfield 1991). The number of plots ranged between 9 and 25 according to area size. I estimated percentage vegetation cover visually to the species level in each dropping plot to the nearest 5%. Species covering less than 5% were estimated to the nearest percent. I subsequently classified vegetation types using TWINSPAN (two-way indicator species analysis; Hill, 1979). I distinguished two vegetation types at each site, which I refer to as patch types (Table 2). All scientific names and families (Wagner *et al.* 1990) of the prevalent plant species are listed in appendix A. Grass species growing in tufts are called bunch grasses as opposed

Table 2: Patch types and total mean vegetation cover. (Numbers) indicate number of plots.

Site	Patch	Prevalent Plants	% Vegetation cover
1	1 (10)	*Paspalum*, some *Lotus* and *Sporobulus*	102±6
	2 (5)	*Eleusine*, some *Solivia* and *Portulaca*	101 ± 9
2	1 (11)	*Pennisetum*, *Kyllinga*	106 ± 3
	2 (6)	*Pennisetum*, *Kyllinga,* some *Digitaria*	114 ± 3
3	1 (7)	*Pennisetum*, some *Sporobulus*	119 ± 7
	2 (8)	*Sporobulus,* some *Chloris* and *Vulpia*	87 ± 11
4	1 (10)	*Paspalum*, *Desmodium* and *Kyllinga*	115 ± 1
	2 (10)	*Paspalum, Desmodium, Trifolium* and *Kyllinga*	115 ± 2
5*	1 (9)	*Paspalum*, *Kyllinga, Desmodium*, some *Trifolium*	120 ± 7
6*	1 (19)	*Pennisetum*, *Kyllinga*	83 ± 2
7	1 (4)	*Pennisetum* and *Desmodium,* some *Melinis*	95 ± 9
	2 (9)	*Digitaria, Andropogon*	59 ± 10
8	1 (13)	*Pennisetum*, *Kyllinga*	116 ± 5
	2 (12)	*Pennisetum*, *Kyllinga,* some *Desmodium*	88 ± 6

to sward-forming species. All plants under study were introduced species. The study sites at Hawaii Volcanoes National Park were dominated by the sward-forming Kikuyu grass and the Kapapala Ranch was dominated by grass of the genus *Paspalum*. Most of the Kipuka Nene area contained bunch grasses. The Ainahou area had less bunch grasses and was dominated by Kikuyu grass and the sedge, *Kyllinga brevifolia*. Plant species with high average cover were also widespread and abundant, but some of the species with a low average cover occurred regularly.

In the 1994/1995 breeding season, I took ten random grass height measurements in each dropping plot every three weeks and calculated a mean for each plot. The grass height measurements were divided into three classes: short (1.6 - 5.5 cm), medium (5.6 - 11.5 cm) and tall (11.6 - 23.5 cm). I determined the production of seedheads in the 1995/1996 breeding season once a month, by counting them in a 50 cm x 50 cm area in each dropping plot. In the same time period I collected fresh Kikuyu grass monthly in each of the grasslands. Samples were sorted, weighed and dried at 70ºC overnight for subsequent analysis of crude protein (nitrogen x 6.25; Kjehldahl), expressed as percentage dry weight (Owen 1971). The water content was obtained by subtracting dry weight from fresh weight. I focused on Kikuyu grass because it is readily eaten by the geese and widespread, allowing a comparison between sites (Black *et al.* 1994).

To examine the effects of rainfall and temperature on grassland usage, I placed 'minimum-maximum' thermometers and rain gauges in each area and checked them weekly. At Kipuka Nene and Ainahou I used weather data collected by the National Park Service.

STATISTICAL METHODS

All analyses were undertaken using general linear models, with either binomial or Poisson error structure. The resultant changes in deviance are equivalent to the chi-squared statistic and were tested accordingly (NAG 1993, Crawley 1993).

Diurnal patterns of grassland usage

I used the maximum count within each hour to reflect the number of birds present in the course of a day (Black *et al.* 1991). To compare the yearly, seasonal and daily variation in the time the geese spent grazing, I used an analysis of variance using a binomial error distribution in GLIM (NAG 1993, Crawley 1993). The average number of birds feeding within an hour was the response variable, and the average number of birds within an hour, the binomial denominator. Factors were location, date, year and hour (time of day). Averages over hourly intervals (2-12 scans) were used to reduce the effect of data dependence. Small sample sizes, e.g. hours with only one scan and days with less than 25 scans, were excluded from the analysis. I tested differences between sites and categories of behavior with non-parametric chi-square tests.

Grazing pressure

I employed several analyses of variance and covariance models to determine which variables affected grazing pressure. Initial fits to the models indicated that the dropping count data were over dispersed, and consequently the constraints imposed by the declaration of Poisson error distribution were modified by adjustment of the scale parameter. This was achieved by dividing the Pearson Chi-square statistic of the final model by the residual degrees of freedom (Crawley 1993). Explanatory variables were location, date, season, protein and water content of the grass, grass height, vegetation type and cover, elevation, number of seedheads, rainfall and temperature. Not all of these were fitted to the same model. Variables that caused a significant increase in deviance were retained in the model. Insignificant terms were removed. I also tested all biologically meaningful interaction terms.

To reduce effects of data dependency, only the number of droppings accumulated over certain time periods were used for analysis (monthly, per season and over an entire year). Each season amounted to 23 weeks: the 1994/1995 breeding season (24. October 94 - 29. March 95), the 1995 summer (19. April 95 - 18. September 95) and the 1995/1996 breeding season (10. October 95 - 13. March 96). Sample sizes indicate the number of plots.

GLIM was also used to compare differences between classes. In multiple comparisons, significance levels were controlled by using sequential Bonferroni tests, otherwise, the significance level was set at $P < 0.05$. Percentage data were arcsine transformed prior to analysis.

RESULTS

Diurnal patterns of grassland usage

Birds flew from their desert roosting places to the grasslands between 6.15 and 7.30 hours in the morning, and left the grassland between 16.00 and 17.45 hours. Numbers varied throughout the day, ranging between 1 and 24 geese. The mean maximum number of geese per hour (Fig. 2), reached a peak at 14.00 hours, and then declined until the geese left the area. Figure 3 shows that the percentage of birds feeding peaked at 8.00 and 15.00 hours and was lowest at 12.00 hours.

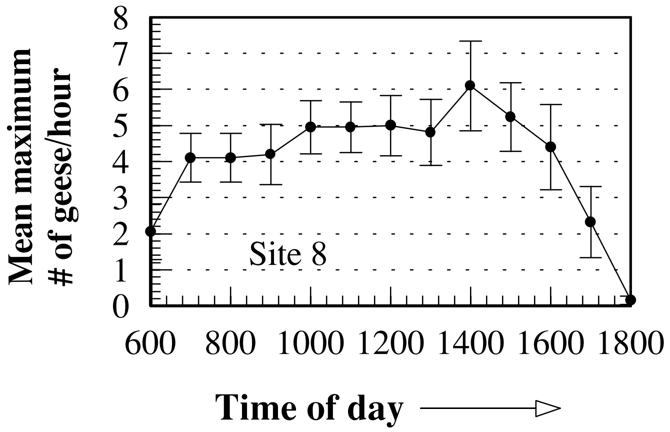


Fig. 2: Goose numbers varied throughout the day (F = 7.2, df = 12, $P < 0.01$) and with date (F = 8.56, df = 20, $P < 0.01$). There was no difference between the two breeding seasons. Presented are the mean maximum number of geese per hour counted on 24 observation days. There was no difference in the arrival and departure times of the geese between the two years (Mann-Whitney-U-tests for flying in: W = 135, N = 12 and 7, $P < 0.22$ and departing: W = 98, N = 10 and 8, $P < 0.82$).

The percentage of birds feeding varied between site 2 and 8 ($\chi^2 = 5.6$, df = 1, $P < 0.025$) and dates ($\chi^2 = 38.2$, df = 21, $P < 0.025$), but there was no significant difference between the two years. The geese spent more time feeding and less time loafing at the newly established site 2 (inside the enclosure), compared to the more established site 8 (Fig. 4). The time spent feeding at site 2 decreased from 57% in 1994/1995 to 47% in 1995/1996.

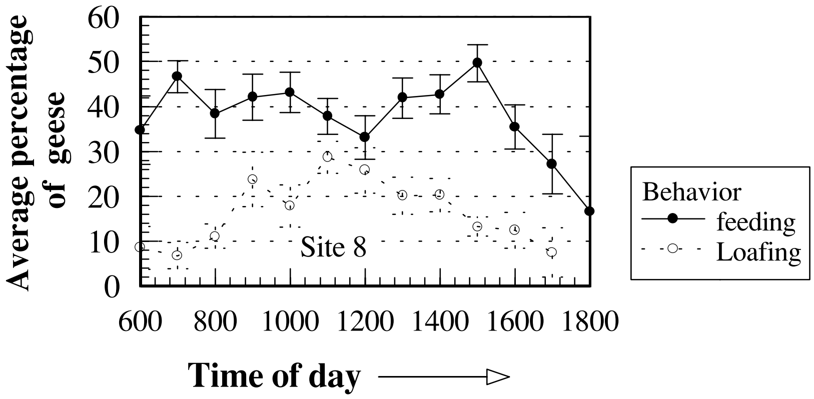


Fig. 3: The percentage of geese feeding and loafing varied through the day. The hourly pattern was significant for loafing ($\chi^2 = 24.78$, df = 12, $P < 0.025$).

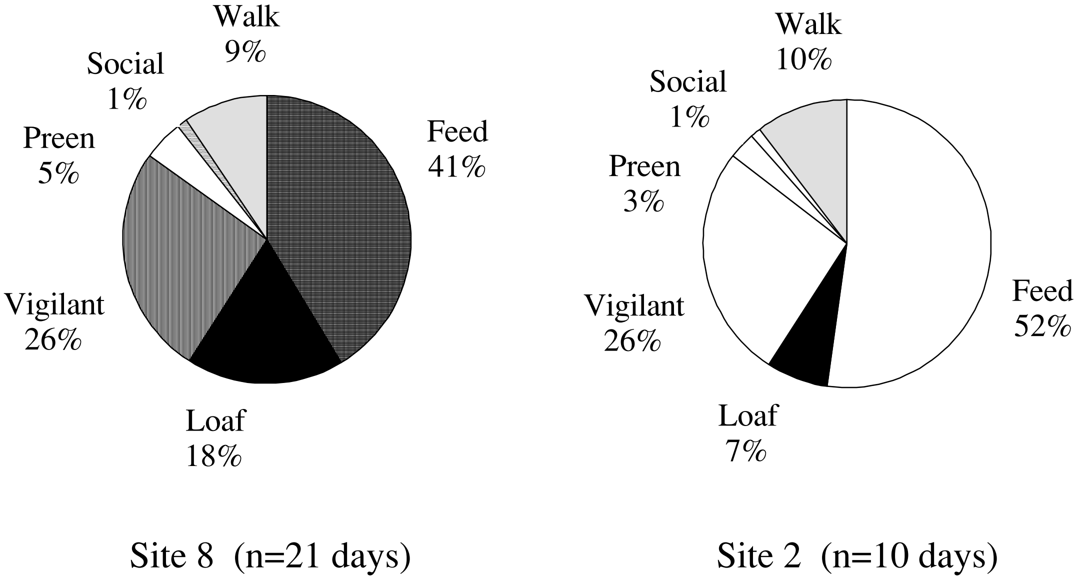


Fig. 4: Activity budgets of Hawaiian Geese in two grasslands. the geese fed more and loafed less at site 2 ($\chi^2 = 6.141$, df = 1, $P < 0.025$). There was no significant difference between the two breeding seasons.

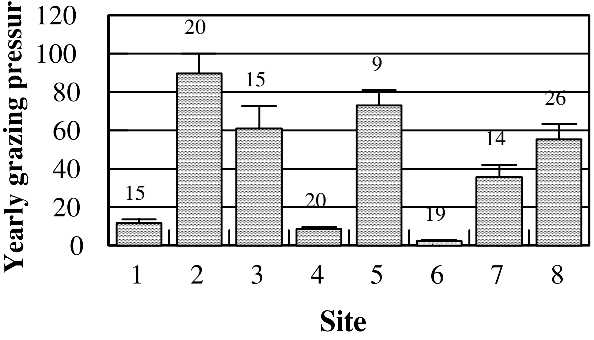


Fig. 5: Variation in grazing pressure between sites ($\chi^2 = 228.7$, df = 7, $P < 0.001$). Values indicate the yearly accumulated number of droppings/4m^2, sample sizes indicate the number of plots in each location, means are between plots.

Grazing pressure

The yearly grazing pressure varied between sites (Fig. 5). It was highest at sites 2, 3, and 8, intermediate at site 7 and low at sites 1 and 4 (Kapapala Ranch); site 6 had the lowest grazing pressure. Some of the between-site variation in grazing pressure might be explained by differences in management and boundary type. The geese apparently selected the mowed and grazed grassland sites (Fig. 6a) and used open sites less than closed ones (Fig. 6b). Sites with an extensive tree canopy were used less than sites with only a few trees ($\chi^2 = 12.49$, df = 1, $P < 0.001$). Area size did not affect grazing pressure. At some sites, goose-grazing pressure increased after mowing or horse-grazing.

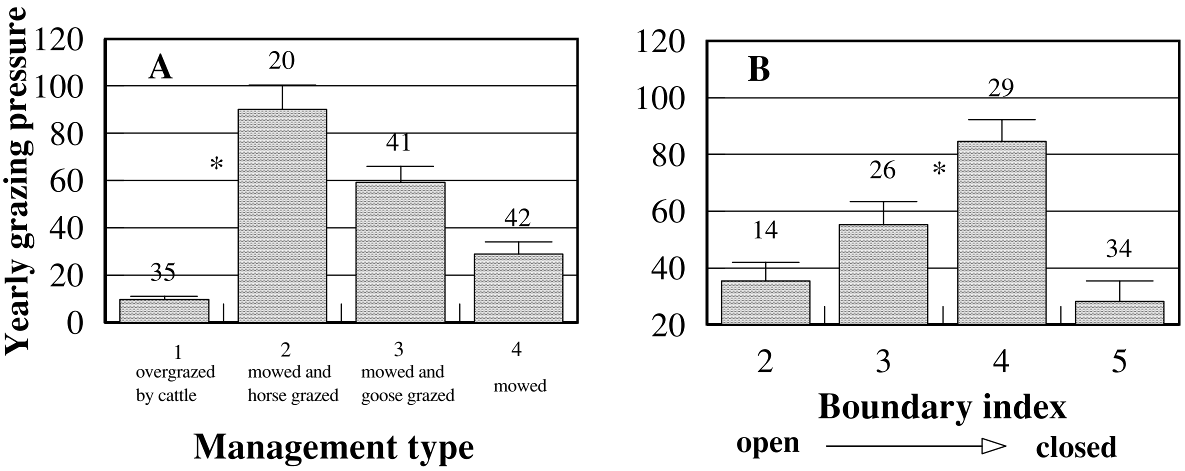


Fig. 6: Yearly grazing pressure in A. Different management types ($\chi^2 = 6.94 - 80.96$), df = 1, $P < 0.01 - 0.001$, all types are significantly different from each other) and B. Different boundary types (significant differences between 2/3, 2/4 and 4/5; $\chi^2 = 4.29 - 13.36$, $P < 0.001 - 0.05$). Sample sizes indicate the number of plots, * indicates the periodic presence of captive birds. the yearly grazing pressure is expressed as the mean number of droppings/$4m^2$ accumulated over a year. Means are between plots.

The observed preferences for a certain vegetation type were persistent through all seasons (Table 3). Grazing pressure was higher in the Kikuyu grass patch compared to the bunch grass patch (Fig. 7). When having the choice between a mixed patch type with Kikuyu and a legume (*Desmodium sandwicense*) and pure Kikuyu, the geese grazed more in the mixed type (Fig. 7).

Vegetation cover may also explain grazing pressure variation in some sites. In areas comprising short Kikuyu, the geese grazed more in dense grass cover (Fig. 8a), whereas in areas with taller grass, they grazed more in less dense cover (Fig. 8b). The association with a lower cover of *Kyllinga* (Fig. 8c) was detected at site 4, and of *Sporobulus* (Fig. 8d) at site 8. The amount of *Desmodium*, or bare ground, apparently did not influence grazing pressure. At site 4, the grazing pressure was also influenced by the topography; it varied between vegetation patch types, but the elevation of the plots explained more of the variation. The higher-elevated plots were grazed more ($\chi^2 = 13.09$, df = 1, $P < 0.001$).

Table 3: Comparison of droppings accumulated over a period of one year (24.10.94 - 24.10.95) in two different vegetation types, degrees of freedom = 1.

Site	χ^2	P <	Type with higher dropping density	Type with lower dropping density
2	9.3	0.05	*Pennisetum*, *Digitaria*	*Pennisetum*, *Kyllinga*
3	22.1	0.001	*Pennisetum*	*Sporobulus, Chloris, Vulpia*
4	6.3	0.025	*Paspalum*, *Desmodium*, *Trifolium*	*Paspalum*, *Desmodium, Kyllinga*
8	5.4	0.025	*Pennisetum*, *Desmodium*	*Pennisetum*, *Kyllinga*

Seedheads of grasses were most abundant in the winter months (October - January) (Fig. 9), however, in general, a higher number of seedheads did not attract more geese. I tested this by fitting the number of droppings accumulated in the four weeks prior to the seedhead count as a response variable, and the number of seedheads in each plot as an explanatory variable. Site 4 on Kapapala Ranch was an exception to the general finding, but only in August ($\chi^2 = 4.23$, df = 1, $P < 0.05$, N = 18), when a high number of seedheads apparently attracted more geese.

The use of different grass heights varied between sites. In the National Park, grazing pressure was greatest in grass of medium heights (5.6 - 11.5 cm) ($\chi^2 = 16.6$, df = 2, $P < 0.001$; Fig. 10). The tallest grass height class (11.6 - 23.5 cm) had by far the least goose usage. Shorter grass heights were used on the intensively cattle-grazed Kapapala ranch (2.4 - 7.9 cm).

The correlation between protein and water content was significantly correlated at site 3 (r = 0.78, df = 6, $P < 0.05$), site 8 (r = 0.83, df = 6, $P < 0.02$) and site 2 (r = 0.74, df = 6, $P < 0.05$) and for all locations combined (Fig. 11). Kikuyu grass with low water content was also low in protein. Water content in the grass and monthly precipitation were not correlated.

Protein and water content in Kikuyu grass changed over the study period and differed between sites (Fig. 12). Paired t-tests showed that the grass at the newly managed site 6 had a significantly lower protein content than the established site 8 (t = 2.6, N = 8, P = 0.04) and also a significantly lower water content (t = 2.6, N = 8, P = 0.035). Hawaiian Geese rarely used site 6. The minimum temperature ranged between 6ºC and 8ºC and did not influence grazing pressure.

To test for regular grazing cycles at the different sites, I plotted autocorrelation functions (ACF's) of the weekly grazing pressure using SYSTAT. There was no regular cyclical pattern to the observed fluctuations in grazing events.

Variation in grazing pressure might be explained by more factors than the quality of the grassland alone. Birds might be absent because they are nesting, molting or there are seasonally better resources in the neighbouring scrublands. In my final models I included these variations as an intrinsic date or season effect. At all sites, grazing pressure varied significantly between months. At many sites either year or rainfall caused a significant change in deviance, but year and rainfall were not significant in the same model. (Fig. 13; Table 4). There was an intrinsic seasonal pattern and a departure from that pattern caused by rainfall. It is, however, difficult to tease them apart, as rainfall itself followed a seasonal pattern.

Table 4: The effect of month, year, rainfall and patch type on grazing pressure (October 1994 - March 1996). Patch type was characterized by the vegetation type

	Month	*(df = 12)*	Year	*(df = 1)*	Rainfall	*(df = 1)*	Patch type	*(df = 1)*
	χ^2	*P <*	χ^2	*P <*	χ^2	*P <*	χ^2	*P <*
Site								
1	47.94	0.001	39.84	0.001	-	n.s.	5.51	0.025
1	48.16	0.001	-	n.s.	32.9	0.001	5.51	0.025
2	342.9	0.001	21.34	0.001	-	n.s.	25.06	0.001
2	303.6	0.001	-	n.s.	41.39	0.001	24.6	0.001
3	192.9	0.001	26.4	0.001	5.086	0.025	131.3	0.001
4	26.74	0.01	-	n.s.	-	n.s.	14.91 [a]	0.001
5	310.8	0.001	-	n.s.	-	n.s.	only 1 type	
6	132.2	0.001	-	n.s.	-	n.s.	only 1 type	
7	78.01	0.001	14.23	0.001	-	n.s.	18.67	0.001
7	82.37	0.001	-	n.s.	15.27	0.001	18.79	0.001
8	105.9	0.001	13.39	0.001	-	n.s.	50.35	0.001

[a] *at site 4 the elevation of the plot is used instead of the vegetation type*

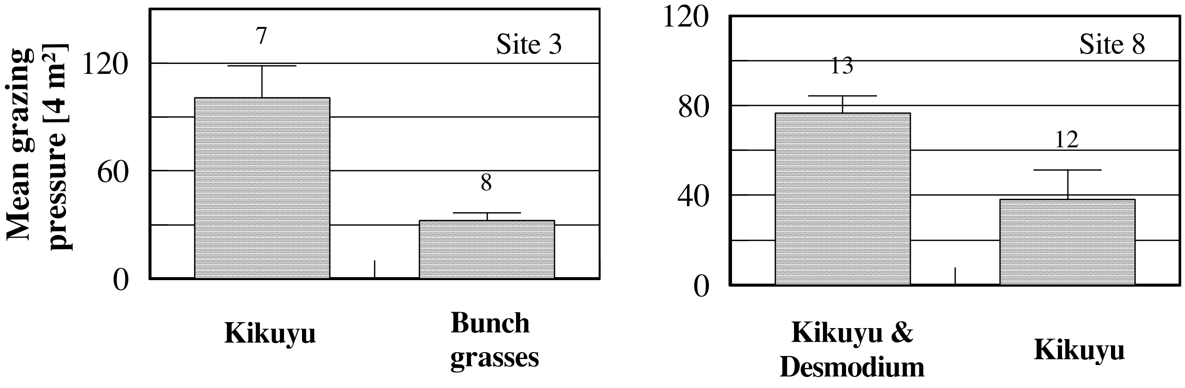


Fig. 7: Variation of yearly grazing pressure with vegetation type (droppings accumulated between October 1994 and October 1995). Species names indicate plants with the highest cover, not communities. Sample sizes indicate the number of plots. The geese grazed more in patches with Kikuyu grass than bunch grasses ($\chi^2 = 22.09$, df = 1, $P < 0.001$) and more in Kikuyu/*Desmodium* than in pure Kikuyu ($\chi^2 = 5.4$, df = 1, $P < 0.025$).

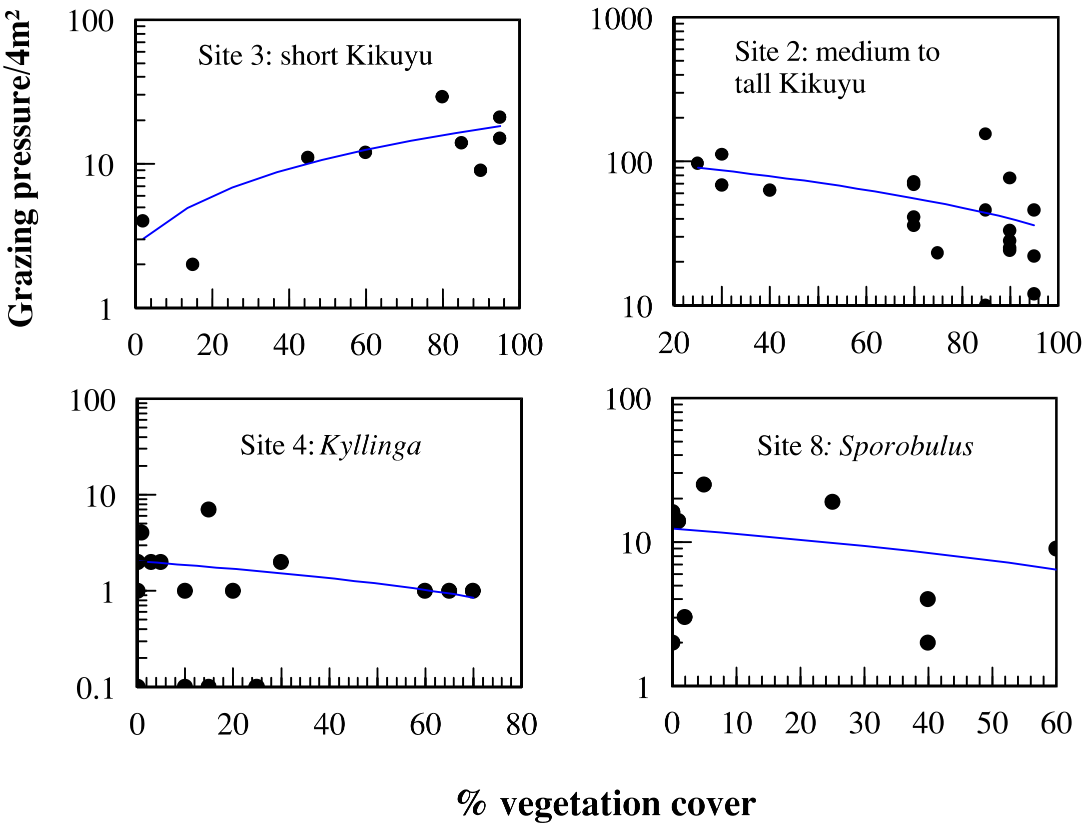


Fig. 8: Grazing pressure in Kikuyu grass, *Kyllinga* and *Sporobulus* with varying cover. At site 3 a high cover of Kikuyu grass was selected for ($\chi^2 = 14.9$, df = 1, $P < 0.001$), at the other sites the geese used plots with a higher cover less (Kikuyu at site 2: $\chi^2 = 17.8$, df = 1, $p < 0.001$, *Kyllinga* at site 4: $\chi^2 = 9.38$, df = 1, $P < 0.005$ and *Sporobulus* at site 8: $\chi^2 = 5.48$, df = 1, $P < 0.01$). The dropping density accumulated eight weeks before and after the vegetation cover assessment (between 18.01.95 and 3.05.95) was used to indicate relative grazing pressure.

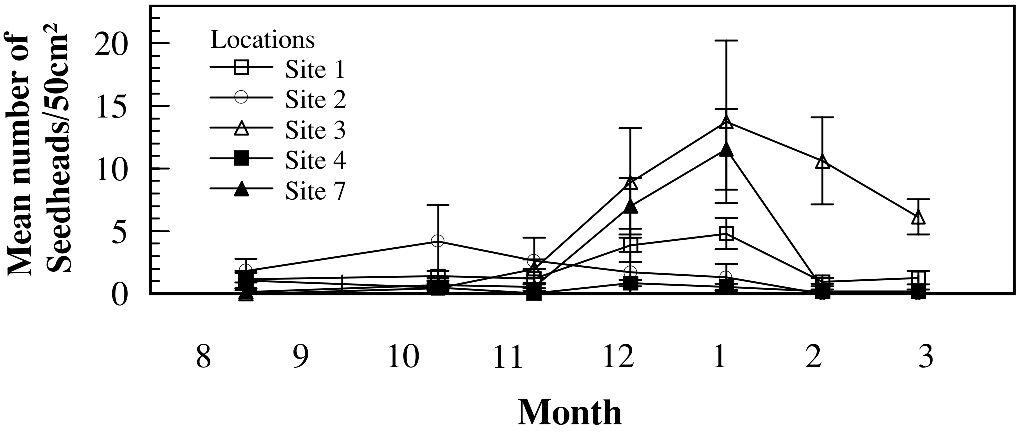


Fig. 9: The change of the mean number of seedheads over time (August 1995 - March 1996). Predominant species at site 1 and 4: *Paspalum* and *Digitaria*, at site 3 and 7: *Sporobulus* and other mixed bunch grasses and at site 2: *Digitaria*. In February site 7 was mowed, hence the sudden absence of seedheads. Sample sizes are equal to the number of plots in each site.

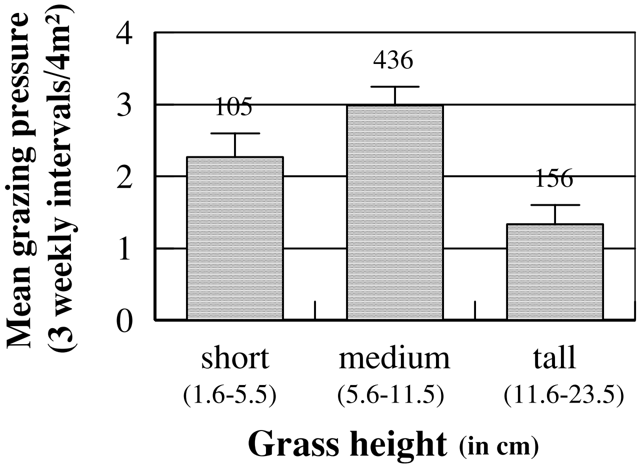


Fig. 10: Grazing pressure in different grass heights in Hawaii Volcanoes National Park. Measurements were taken every three weeks at five locations over a period of 21 weeks. The droppings accumulated in the three weeks prior to the grass height measurements indicated the relative grazing pressure. Sample sizes indicate the number of plots the grass height was measured in.

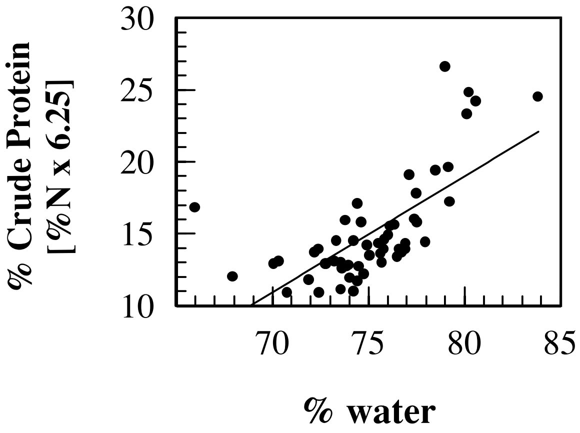


Fig. 11: Correlation of protein and water content in Kikuyu grass (all locations: r = 0.69, df = 52, P < 0.0001)

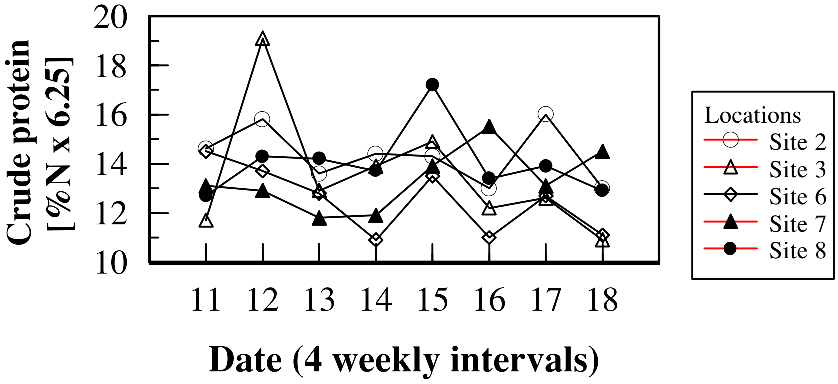


Fig. 12: The change of protein content in Kikuyu grass over time (July 1995 - March 1996). The grass at site 6 had a significant lower protein content than the grass at site 2 (n = 8, t = 4.25, P = 0.004) and site 8 (n = 8, t = 2.58, P = 0.036).

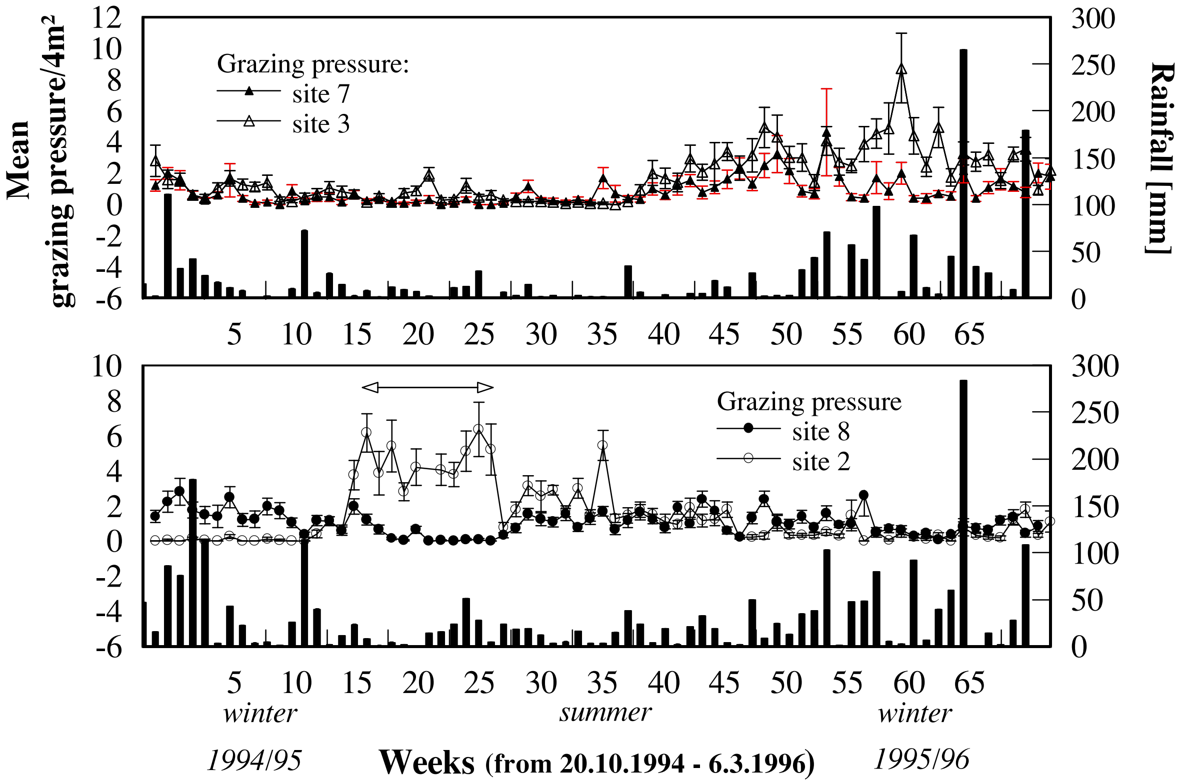


Fig. 13: The change of mean weekly grazing pressure (lines) and rainfall (bars) over time. Sample sizes correspond with the number of plots in each site (site 2: n = 20, site 3: n = 15, site 7: n = 14, site 8: n = 26). Weekly values are presented for detail, because of temporal autocorrelation between the weekly data however, only monthly accumulated values were analyzed. After controlling for location ($\chi^2 = 853$, df = 7, $P < 0.001$), the grazing pressure was different between months ($\chi^2 = 76.3$, df = 17, $P < 0.001$). At most locations grazing pressure varied also between season and/or years and/or with rainfall (see Table 4). The arrow indicates a periodic presence of semi-captive birds at site 2.

DISCUSSION

Managers once believed that Hawaiian Geese would thrive in volcanic scrubland at high elevation, where the last remaining birds were found. However, birds reintroduced into these areas had poor survival rates compared with those in mid and low elevations, where they had access to managed agricultural habitats (Black *et al.* 1997). Many healthy goose populations throughout the world are making use of man-made sites in order to meet their daily energetic requirements (reviewed by Black *et al.* 1994). Hawaiian Geese have adapted to man-made habitats and readily use introduced plant species for foraging.

Understanding variation in grazing pressure in geese is not an easy task, as it cannot be explained by a single factor. In my study, Hawaiian Geese selected habitats with food plants of a high protein content. They favored vegetation patches with Kikuyu grass sward as opposed to patches with bunch grasses, and grazed more in mixed grass-legume than in pure grass sward. Kikuyu grass sward is higher in protein than bunch grasses, and legumes have even higher levels of protein than Kikuyu grass (Black *et al.* 1994). Research on many herbivores, including other geese, has confirmed the suitability of crude protein as an indicator of forage quality (Owen 1981, Sedinger and Raveling 1984, Festa-Bianchet 1988), and geese are able to select forage of high nutritional quality when available (Owen 1971, Sedinger and Raveling 1984, Prop and Deerenberg 1991). My study indicates that Hawaiian Geese are no exception to these findings.

That the geese used most grasslands less during dry periods could have two explanations. Grass with a low water content is proportionally higher in fiber (Owen 1981) and, as shown in this study for Kikuyu grass, lower in protein, which increases the physical effort of grazing and digestion (Prop and Vulnik 1992). Especially in periodically dry areas, the amount of rainfall may explain plant quality and quantity, and the subsequent grazing behavior of geese. Further research is needed into the short-term effects of rainfall on the vegetation (daily measurements) and the effects of rainfall duration on grazing pressure.

Hawaiian Geese used newly managed sites less than other, longer established ones. The new sites may have been unfamiliar to the birds, furthermore, the protein content in Kikuyu grass was lower. In other goose species, individuals using sites with a high forage quality spend less time feeding (Bédard and Gauthier 1989, Black *et al.* 1991). In my study, Hawaiian Geese spent less time feeding in the established site, suggesting the plant quality and abundance was better than at the newly managed site. From 1994 to 1995, I found a decrease in feeding time by 10% in the newly managed site. This might be explained by an increasing forage quality after repeated mowing of this previously unmanaged site. In many grass species, repeated mowing or grazing increases the protein content (Sedinger and Raveling 1986, Gadallah and Jefferies 1995, Ydenberg and Prins 1981). Thus, given good initial forage quality and sufficient rainfall, geese may themselves be able to improve the quality of the sward to a certain extent.

Colonization of new habitats is likely to occur with a change in selection pressure. Many Arctic geese shifted to new habitats after their populations had increased and some of their traditional habitats had deteriorated (Owen and Black 1991, Black *et al.* 1991). In contrast, the Hawaiian Goose population in my study is in danger of further decrease, and although more extensive measurements are needed, I provided data that new sites were nutritionally less attractive than established, traditional ones. To attract Hawaiian Geese to new sites, those must offer a higher-quality forage, and even then they might not shift to them, especially if the established sites are not overcrowded. The size of the managed areas has to be adapted to the population size.

Hawaiian Geese are faced with a variable climate, and hence fluctuating forage quality. Droughts are a fairly common phenomenon in the normally wet winter months, but they are unpredictable. If the vegetation quality deteriorates during the critical time of incubation and brood rearing, birds might not be able to successfully rear their offspring. An adequate growth rate for goslings is only possible if accessible supplies of high quality forage are available

(Gadallah and Jefferies 1995). Black *et al.* (1994) showed that the forage plants of Hawaiian Geese are depleted throughout the season and do not regenerate quickly, especially in unmanaged areas. Reduced supplies of forage due to earlier grazing are thought to cause reduced growth rates in Black Brant (Sedinger and Flint 1991) as well as in Snow Geese (Cooch *et al.* 1991). Adult Hawaiian Geese fly to better sites when food resources are getting low (Black *et al.* 1994), when leading goslings however, they cannot travel far and must use what is available in the area. The nutritional inadequacy of the grasslands seems especially detrimental for goslings (P. Baker and H. Baker pers. comm.) and may be the key factor in limiting population growth.

Today, most endangered species are managed in an ecosystem approach with emphasis on areas with threatened status (Martin 1994). Species like the Hawaiian Goose however, have managed to utilize disturbed habitats and benefit from introduced plants as a food resource (Black *et al.* 1994). Although the restoration of disturbed habitats remains a long-term objective (Stone and Scott 1985), the adaptability of the Hawaiian Goose can be turned into an advantage on its' way to recovery. Managing pastures adjacent to nesting areas is a quick and comparatively inexpensive means of providing the birds with food. By managing grasslands overgrown by introduced grass species like Kikuyu, Molasses, Beard grass (*Schizachyrium condensatum*) and Broomsedge for the geese, some of the disturbed ecosystems may benefit. Corridors of short grass serve as effective firebreaks in areas with high fire risk. Most native plant species are not adapted to fire (Mueller-Dombois 1981) and fire also facilitates invasion by alien species (National Park Service 1989). From a conservation point of view, a reduction in the seed production of introduced grass species is favorable as it reduces the spread of these species into non-invaded areas.

In 1997, the State of Hawaii Government passed the 'Hawaii Endangered Species Recovery Act', that allows incidental take of an endangered species on private land. The Act opens new possibilities for the reintroduction of endangered species on private land. Some ranches for example provide excellent feeding opportunities for Hawaiian Geese. Prior to future reintroductions however, the pasture vegetation and seasonal local rainfall patterns should be assessed and only adequate pastures with adjacent scrubland nesting habitat should be considered. Dry habitats should be avoided. Adequate predator control in these areas remains vital to ensure breeding success.

Golfcourses meet my criteria of grasslands with short, nutritious grass perfectly, and many Hawaiian Geese use them. However, various problems are associated. Geese get killed or crippled by golfballs, the adjacent nesting sites are usually cut-off by roads which causes roadkills, pesticides are freely used and parent geese leading goslings are vulnerable to disturbance. A possible solution would be to create set-aside areas on golfcourses that are nutritionally more attractive and concentrate geese away from human activity.

The population of the Hawaiian Goose on Kauai is increasing steadily for two apparent reasons: (1) They use lush, cattle grazed and irrigated pasture vegetation in the lowlands, and, (2) the number of introduced predators is low. Providing high quality pastures enables more birds to accumulate sufficient body reserves for breeding and results in higher fledgling success, furthermore, strong and healthy birds may be more likely to escape predation.

Increased breeding success in the wild is the main goal for recovery. To achieve that goal, I emphasize the importance of large-scale sanctuaries in the wild, including both intensively managed grasslands and natural scrubland nesting habitats coupled with predator control. To determine the required size of sanctuaries, I recommend detailed studies on the carrying capacity of Hawaiian Goose habitat. Good management can result in doubling the carrying capacity of grasslands (Owen 1977). Furthermore, a study on different management regimes including mowing, livestock grazing, irrigation, fertilization and burning treatments could reveal which treatments yield the highest carrying capacity.

Immediate management implications

My immediate conclusions and implications for pasture management include the following. (1) Hawaiian Geese grazed most heavily on an intermediate grass height (approx. 5 - 11 cm). Mowing or grazing grass higher than 11 cm will optimize pastures for the geese. (2) The geese used grasslands less during drought periods. Irrigation could be useful as a management tool, especially during the breeding season. (3) The geese grazed more in grass sward than in areas with bunch grasses. Although seedheads of bunch grasses are eaten by the geese, they are only seasonally plentiful, whereas short grass sward is scarce but with adequate management could be available year round. Repeated mowing favors grass sward growth and reduces bunch grasses. (4) Geese grazed more in areas with grass high in protein. Fertilizer application is likely to improve pasture quality. (5) Management activities in grasslands should be carried out when bird numbers using the pastures are low (e.g. during molting), or after 16.00 hours, when most birds leave the pastures and fly to the roosting sites.

SUMMARY

Foraging behavior of Hawaiian Geese (*Branta sandvicensis*) visiting a variety of grasslands was studied in Hawaii Volcanoes National Park. For the purpose of this study, two overgrown sites were mowed and subsequently compared with established sites which had previously been mowed or grazed by livestock.

Relative grazing pressure varied between sites and at different times of the year. Sites differed in plant species composition and quality, seedhead production, grass height and rainfall. Plants were largely introduced species.

Hawaiian Geese grazed more in areas with the sward-forming Kikuyu grass (*Pennisetum clandestinum*) than in areas with bunch grasses, selecting sites that had grass with a high water content. The water content in the grass was correlated with the protein content. Grazing pressure decreased in grass taller than eleven centimeters. Over time, the variation in rainfall explained a large part of the differing grazing pressure, suggesting that geese used grasslands less during dry periods. The plant quality in the newly-mown sites was relatively low and did not attract birds.

I discuss why Hawaiian Geese remained in established sites and did not move to newly managed sites. To encourage feeding opportunities for this endangered species, my results suggest that grasslands could be managed at a height below twelve centimeters, irrigated in drought periods and fertilized.

Appendix: Scientific and common names of prevalent plant species (Wagner *et al.* 1990).

Family	Latin name	Common name
Poaceae	*Pennisetum clandestinum*	Kikuyu grass
	Melinis minutiflora	Molasses grass
	Andropogon virginicus	Broomsedge
	Eleusine indica	Wiregrass
	Paspalum conjugatum	Hilo grass
	Sporobulus africanus	Rattail grass
	Digitaria violascens	Violet crabgrass
	Vulpia bromoides	Brome fescue
	Chloris virgata	Finger grass
Cyperaceae	*Kyllinga brevifolia*	Kaluha
Fabaceae	*Lotus subiflorus*	
	Desmodium sandwicense	Spanish clover
	Trifolium repens	White clover

Chapter 6: Breeding biology of released Hawaiian Geese: An assessment of the reintroduction program

INTRODUCTION

In the middle of this century fewer than 30 Hawaiian Geese remained in the wild (Smith 1952). To save the species from extinction, recovery efforts concentrated on captive rearing and subsequent release. Since 1960, over 2200 captive-reared Hawaiian Geese have been released into the wild. Today, Hawaiian Geese are found on three islands (Fig. 1). Survival of most of the released birds was low (Black *et al.* 1997), and reproduction was limited because many pairs bred infrequently and few goslings survived to fledge (Banko 1992). Many Hawaiian Geese could not accumulate sufficient body reserves for breeding. When releases were reduced from 1978 onwards, wild populations declined dramatically both on Hawaii and Maui (Devick 1981a, b, Morin and Walker 1986, Black *et al.* 1991, Black 1995). Releasing birds kept populations artificially high (Banko and Elder 1990, Black and Banko 1994) but did not remove the causes of the decline. Some of the released birds, however, managed to reproduce and in this chapter I will outline why some birds were more successful than others.

Following a bird's success throughout the reproductive cycle can indicate stages where problems may occur. Problems may be caused by harsh environmental conditions or by low individual reproductive ability. The body reserves a female can accumulate prior to egg laying determines the number of eggs she can produce and are important for maintenance during incubation (Thompson and Raveling 1987). A large proportion of infertile eggs is sometimes a sign of a genetic problem or inbreeding depression, which may be especially evident in small and/or reintroduced populations (Rave *et al.* 1999). Egg fertility may be affected by fine-tuning of male and female behavior during copulation. The likelihood of egg predation will increase with predator densities or if cues lead predators to a nest. The number of eggs hatched is indicative of both female and male performance during incubation. Female success during egg laying and incubation may partly depend upon the male's protective abilities (Black and Owen 1989, Black *et al.* 1996). When food availability is low, females are forced to take longer incubation recesses increasing the risk of egg predation and chilling (Banko 1988). How many goslings survive to fledging depends on food resources during rearing and the protective abilities of the parents.

Various authors have previously described aspects of Hawaiian Goose breeding biology (Devick 1981a, b, Kear and Berger 1980, Banko and Manuwal 1982, Banko 1988, 1992, Black and Banko 1992, Black *et al.* 1994), covering shorter time periods within the reintroduction project. Recently, the Nene Recovery Initiative collated all data collected

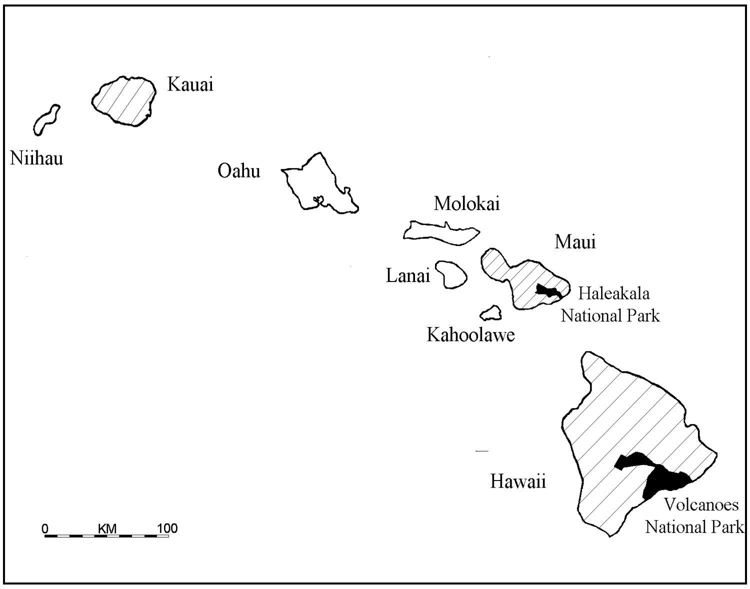


Fig. 1: The main Hawaiian islands with Hawaii Volcanoes and Haleakala National Park; shaded are islands with wild Nene populations.

throughout the program into a comprehensive database (Hunter and Black 1995), making an analysis of the long-term data possible.

In this chapter I will summarize the long-term breeding records that have been collected between 1960 and 1995 in relation to various reintroduction parameters. This includes a comparison between three reintroduction regions which differ in elevation, climate and/or habitat characteristics. Throughout the Hawaiian Goose reintroduction program, supplemental feeders in predator exclosures were used that can be viewed as an experiment to test if food and predation are limiting factors in the wild habitat. A comparison of reproductive parameters included two types of birds: Wild controls that did not use the supplemental feed and exclosures and captive birds that lived inside the exclosures at all times. Determining the variation in reproductive components between different rearing and release styles enabled me to test the significance of social learning to future performance of individuals. With some reintroduction methods parents were removed from an otherwise extended parent-offspring relationship, as is documented for geese (Black and Owen 1989a). A comparison of reproductive parameters between different management periods gave an indication how success changed over time. Early management concentrated on captive breeding and release, later management included predator control in wild nesting areas, provisioning of supplemental food and grassland management. Finally, I put my results in context of some previous authors' findings and discuss changes that may have occurred throughout the reintroduction program. The analysis of the breeding performance of released birds allows an assessment of the success of the reintroduction program and the formulation of suggestions for future initiatives.

BACKGROUND AND METHODS

Rearing and release methods

Hawaiian Geese were reared at three principal sites: the Pohakuloa breeding facility on Hawaii run by the Hawaii State Division of Forestry and Wildlife (DOFAW), Hawaii Volcanoes National Park on Hawaii, and Haleakala National Park on Maui (Fig. 1 and 2). Birds at Pohakuloa were reared in comparatively small pens, many of them without their parents (Kear and Berger 1980). First clutches were often removed to induce parent geese to lay additional clutches. Electric incubators, domestic hens and muscovy ducks were used to incubate eggs. After hatching, young were reared in large sibling groups or fostered with vocal and visual contact of adults; a few were directly fostered by adults (Kear and Berger 1980). Birds were fed on a daily basis. Most of the Pohakuloa birds were released in specially constructed release pens on State sanctuaries at between 2 and 4 months of age. Birds were made temporarily flightless by using 4 methods (Banko and Elder 1990): 1) feather clipping - clipping the outermost primaries on one wing, 2) feather pulling - removing the outermost

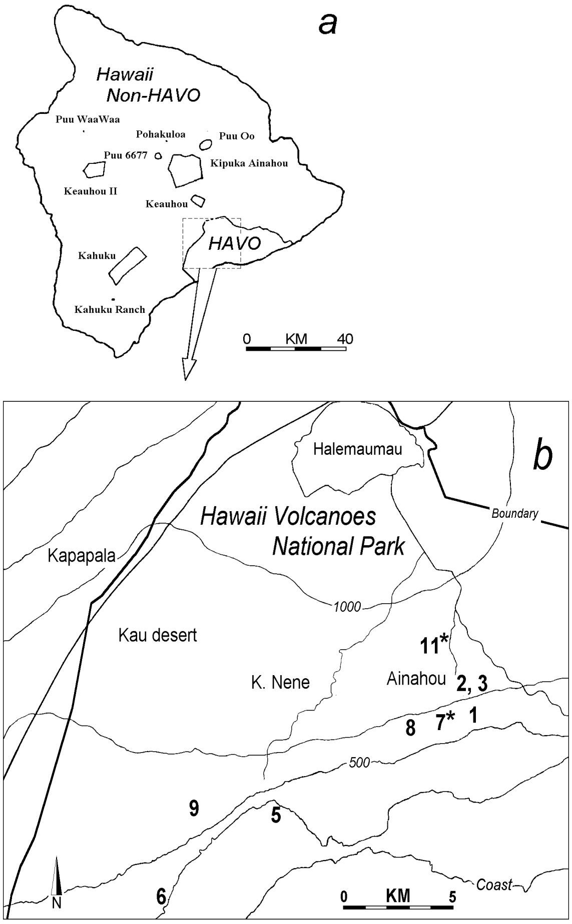


Fig. 2a: Island of Hawaii with release regions HAVO and Non-HAVO (some of the State Sanctuaries and associated areas are indicated) and b: Part of Hawaii Volcanoes National Park with numbers indicating rearing and release pens (* = pens used in management period 2; contours in 250 m intervals)

primaries from one wing, which would grow back in 6 - 8 weeks, 3) feather binding - tying the outermost primaries on one wing for a period of 1 - 3 weeks and 4) pre-fledging - releases were made 1 - 3 weeks prior to fledging (i.e., at about 8 - 10 weeks of age). In the National Parks, all young were reared in large open-top pens (Fig. 2b) with their parents and often remained in contact with them long after fledging (Hoshide *et al.* 1990). Wild birds were allowed to fly into the pens and to mingle with captive ones, enhancing social experience for the young (Banko 1982). Captive breeders were provided with commercial chicken food and water; human contact during weekly maintenance was kept to a minimum. In addition, birds foraged on the vegetation within the pens. Fledged young eventually flew from the pens, but typically returned to their captive parents at regular intervals. To supplement the low production of the captive flock at Hawaii Volcanoes National Park, a cooperative agreement with the State Division of Forestry and Wildlife (DOFAW) was implemented in 1984. Young goslings from the Pohakuloa breeding facility were fostered to captive pairs in the National Park breeding pens. All wild caught and unbanded birds were considered to be parent-reared in the wild.

Many of the pens were remote and access difficult, hence they were phased out from 1984 onwards. A feeder and water in the former release Pen 7 (Fig. 2b) kept attracting wild breeding pairs from 1983 onwards and another complex of 8 smaller, closed-top breeding pens held the first captive breeders in 1987 (Pen 11). Predators were controlled at all pens.

Release sites

Hawaiian Geese reared at the Pohakuloa breeding facility were released in six specially established sanctuaries (Fig. 2a; Kear and Berger 1980). These included four upland sites run by the State: Keauhou, Keauhou II, Kipuka Ainahou and Kahuku on Hawaii and two sites run by the National Park Service: An upland site at Haleakala National Park on Maui and a low to mid-elevation site at Hawaii Volcanoes National Park (hereafter 'HAVO'). The main objective of the HAVO release program was to restore populations at low and mid elevations in environments which simulate natural conditions and produce a high quality rather than high quantity of birds (Banko 1988). The release sites at HAVO were dominated by exotic *Andropogon virginicus* grasslands with patches of introduced *Melinis minutiflora* and *Pennisetum* spp. and scattered native and exotic shrubs. Birds dispersed from the release sites to breed in a variety of habitats including lava deserts with dry scrubland of different succession stages (Chapter 2) and used grassland to rear their goslings. Vegetation in the lava deserts was predominantly native, whereas grasslands consisted mostly of naturalized grasses and herbs, that were readily eaten by the geese. The upland sites consisted of sub-alpine dry scrubland, often with low vegetation cover (Gagné and Cuddihy in Wagner 1990). The site on Maui included a large, horse-grazed pasture, which was dominated by introduced grasses, while the State sanctuaries were managed by providing either self-feeders containing commercial chicken crumble and permanent water sources and/or fertilizing the scrub vegetation and planting small lawns of introduced Kikuyu grass *Pennisetum clandestinum*

(Banko and Elder 1990). On average, Haleakala received more rainfall than the sites on Hawaii (Banko and Elder 1990).

Banding

Most birds were banded with individual aluminum or plastic leg bands. The loss of color bands used in the early stages of the program is considered to be mainly a problem for individual identification; total band loss was minimal between 1960 and 1975 (Devick 1975) and highly unlikely with the introduction of U.S. Fish and Wildlife Service sequentially numbered metal rings in the early 1970s. Thus it was possible to group the birds into an either 'released' (banded) or 'wild' (unbanded or wild caught and subsequently banded) category. For individual identification, every bird was attributed a unique bird number to account for partial band loss and rebanding efforts. I was able to identify most birds with partial band loss by checking the band combination of their mates and the location and date of resightings.

At HAVO, banding effort was excellent with most wild broods captured and banded before fledging. Broods that were missed accounted for the relatively small number of unbanded birds (annual range estimated at 8 - 26 % of the total population). Population size was estimated from the number of banded individuals identified to be alive in the year preceding each breeding season by adding unbanded mates of banded birds and a small proportion of unbanded pairs and unbanded singles (as determined from resightings during the summer flocking period, when large numbers of birds aggregate).

On the remainder of Hawaii island ('Non-HAVO'), many wild fledglings remained unbanded. Unbanded birds may represent truly wild birds, offspring from mixed pairs (a wild bird paired with a released bird) or offspring from pairs where both male and female were released.

Nest searches and visits

Nests were found within 10 study areas (Fig. 1 and 2) that were divided into three regions: Hawaii Volcanoes National Park (HAVO), all other sites on Hawaii (Hawaii Non-HAVO) and Haleakala on Maui. The methodology and frequency of nest searches varied between sites and years. At HAVO, nest searches were carried out throughout the breeding season between October and March for most years from 1976 onwards. Depending on vegetation density, field workers spread out between 20 - 30 meters apart searching the desert nesting habitat on parallel transects. Droppings and tracks in the sand were used as clues for nests, and ganders guarding the nest from a high vantage point were a give-away. Banko (1988) used a trained dog to find nests. Taking advantage of a high nest site fidelity, known nest sites were checked at regular intervals in subsequent years. The long breeding season makes a constant search effort difficult, and there are no records of how many hours field workers spend searching over the years or what areas they covered. I was therefore not able to control for observer effort. To minimize disturbance and to avoid leading potential predators to nests, visits were kept to a minimum. At each nest visit the clutch size, number of fertile and infertile eggs, number of eggs predated or broken and number of eggs hatched was noted. Egg fertility was determined by candling eggs, but in some cases unhatched eggs were assigned as infertile and hatched eggs as fertile. Death of small embryos before conspicuous development may have been interpreted as infertile in some cases, biasing my evaluation of fertility. Often the nest was only checked again after the eggs had hatched and their fate determined. A nest was considered successful if eggshells in the nest had the inner membrane intact but separated from the shell, which indicates hatching. In addition, nesting attempts were recorded when resighting a female with a brood patch or a pair with goslings or fledglings.

Young often stay with their parents until the next breeding season, allowing fledging success to be determined by locating families after the breeding season in summer flocking areas. From the resighting database, I was able to fill in some additional fledgling information (e.g. if a pair was recorded without goslings up to three months after a breeding attempt, I assumed they did not rear any goslings to the fledgling stage in that season).

Data analysis

Data were analysed using GLIM software (NAG 1993). Data on clutch size and the number of fertile eggs per nest were normally distributed, all other classifications (number of eggs infertile, predated, hatched and fledged) had a Poisson error structure. Changes in deviance for normally distributed data were tested for significance by using the F-statistic, Poisson distributed data were tested with the χ^2-statistic (Crawley 1993). Some of the Poisson distributed data were overdispersed and consequently the constraints imposed by the declaration of a Poisson error distribution were modified by adjustment of the scale parameter. This was achieved by dividing the Pearson Chi-square statistic by the residual degrees of freedom (Crawley 1993). Analyses of variance were carried out to compare reproductive parameters between regions, rearing and release method and between birds reared inside breeding pens with those reared in the wild. Variation of observer effort between regions prompted me to carry out most analyses only within region. When a bird bred in more than one region it was only included in the region that had the higher number of breeding records. Reproductive parameters between years varied not only between but within individuals. Therefore it seemed justified to include reproductive records from individuals in consecutive years. Random sampling of only one reproductive record per individual of a certain classification (e.g. release technique) was attempted, but sample sizes were too small for statistical analyses. The trend in the random data, however, matched that in the whole data in most cases. Similarly, in most analyses, sample sizes were too small to control for year effects. Most of the data analyzed were from Hawaii. Data from Haleakala were sparse and are only included in a comparison between regions.

Hatching and fledging success was defined as one or more young hatched or fledged per clutch. When more than one variable was tested, hatching and fledging success was regarded as a binary response variable following the Bernoulli distribution, an abbreviated form of the binomial distribution with the binomial denominator being declared to equal one (Crawley

1993). When testing only one variable at the time, frequencies were compared using G-tests in GLIM (Crawley 1993). These are similar to non-parametric Chi-square tests and can be used for small samples (equivalent to the Fischer's exact test). To test the significance of single parameters, t-tests were carried out on parameter estimates (Crawley 1993).

Clutches with only one egg were excluded from most analyses for three reasons: They might refer to dumped eggs of inexperienced birds, the remainder of a predated nest or might have been incomplete clutches where the female was still laying.

According to their origin, birds at HAVO were grouped into three categories: HAVO, State (Pohakuloa birds) or wild. I tested if reproductive parameters in males and females varied between the three categories. To test if partner combinations affected reproductive parameters, I coded pairs according to their rearing status: 1) both wild, 2) one wild, one captive-reared, and 3) both captive-reared. Nest records concerning pairs where the band status or age of one or both partners was not known were removed.

The reproductive parameters of birds reared and released with the techniques described above were compared within region for both sexes. Only reproductive parameters of wild birds older than 2 years of age were included. The age of unbanded birds was unknown and hence not controlled for.

A comparison of reproductive parameters between wild birds and birds nesting in pens was only meaningful for HAVO. Small sample sizes in the remainder of release sites did not allow a between-region comparison. Pairs that nested just outside a pen were excluded from the analysis as they could not be classified as truly wild or pen birds. Birds in pens included captive birds and free-flying wild birds that chose to nest inside a pen. Some wild birds might have used pens to feed or drink, or might have had access to supplementary feed elsewhere. Similarly, some wild birds might have indirectly benefited from predator control measures around pens or might have nested in an area that was controlled for predators, but these data are unknown.

Throughout the HAVO reintroduction program three management periods can be defined: Between the 1973/74 and 1983/84 breeding seasons, management of Hawaiian Geese was mainly by captive breeding in lowland breeding pens (period 1, Banko 1988). In the second period, the maintenance of pens with difficult access was discontinued and breeding continued only at two, more accessible pens (Pen 7 and 11, Fig. 2b; H. Hoshide pers. comm.). In addition, from the 1992/93 breeding season onwards, predators were controlled in some of the wild nesting and brooding areas (Stone *et al.* 1995) and small patches of grass were mowed to provide the birds with extra forage (H. Hoshide pers. comm., period 3). I tested if reproductive parameters changed between these three management periods. Breeding habitats were classified as grassland (predominantly grass cover, managed), grassy scrub (tall grasses, high vegetation cover, unmanaged) and open scrubland (low vegetation cover with scattered bushes on volcanic soil).

At Kipuka Nene, one of the main breeding sites at HAVO (Fig. 2b), predators were controlled during the breeding season from October 1992 onwards, and at Ainahou and some other areas predators were controlled from October 1994 onwards. I compared the effect of predator control on hatching and fledging success at Kipuka Nene, comparing 5 years (1987/88 - 1991/92) with no substantial predator control with 5 years with increased predator control (1992/93 - 1996/97). Data on predator control within the State sanctuaries were too limited for analysis.

Rainfall data

By increasing vegetation growth, rainfall may be indicative of the food resources a female can accumulate prior to laying and affect reproductive parameters such as clutch size and egg fertility. Rainfall during incubation may affect incubation performance and rainfall after hatching is thought to affect the availability of lush food for goslings (Chapter 5). From 1988 onwards, rainfall records were available for some nesting areas within Hawaii Volcanoes National Park. I assigned rainfall data to nests closest to weather stations at Kipuka Nene (853 m), Ainahou (914 m) and Halemaumau (1097 m). I took monthly sums of rainfall (mm) before, in and after the month of nest initiation, classified them as either dry (< 100 mm monthly rainfall) or as wet (≥ 100 mm) and then tested if reproductive parameters varied between wet and dry months.

RESULTS

Comparison between release regions

A comparison of reproductive parameters of Hawaiian Geese released in the three regions revealed that Haleakala had the highest values in most categories. Clutch size of wild Hawaiian Geese was larger at Haleakala than at either HAVO or Non-HAVO (Fig. 3a) (for statistics see Table 1). Clutch size generally ranged between 2 and 6 eggs, although one clutch with 8 and two clutches with 7 eggs were recorded, but excluded from analyses. In the wild, brood size ranged between one and four, fledgling group size between one and three. One brood of five and one fledgling group of four was recorded at Non-HAVO.

Table 1: Comparison of various reproductive parameters between the three regions HAVO, Non-HAVO and Haleakala (n.s. indicates a non-significant result).

	Region (df=2)	P <
Clutch size	F = 10.48	0.0001
# fertile	F = 6.78	0.01
# infertile	$\chi^2 = 16.19$	0.001
# predated	$\chi^2 = 3.847$	n.s.
# hatched	$\chi^2 = 2.715$	n.s.
# fledged	$\chi^2 = 12.75$	0.005
hatching success	$\chi^2 = 2.833$	n.s.
fledging success	$\chi^2 = 6.46$	0.05

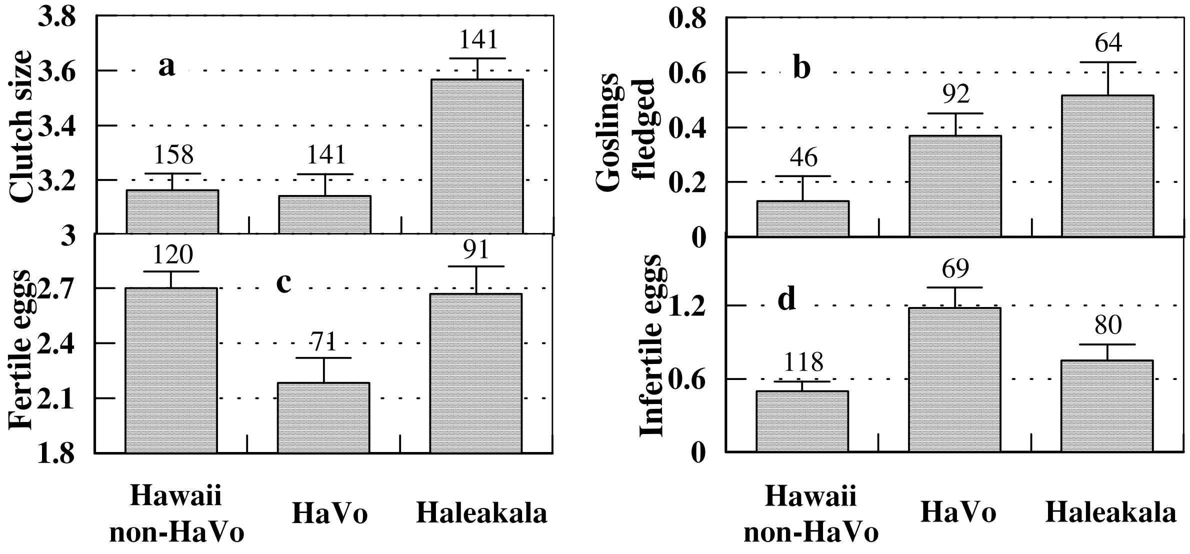


Fig. 3a: Mean clutch size, b. mean number of goslings fledged, c. mean number of fertile eggs and d. mean number of infertile eggs in the three main release areas since 1960 in the wild. Birds on Maui (Haleakala National Park) had a larger mean clutch size than birds from Hawaii, including Hawaii Volcanoes National Park (HAVO). Hawaii non-HaVo had a lower mean number of fledglings than HAVO and Haleakala. Birds at HAVO had a lower mean number of fertile eggs and a higher mean number of infertile eggs than Hawaii non-HAVO and Haleakala. Standard errors and sample sizes are indicated, for statistical results see Table 5.

The mean number of fledglings was highest at Haleakala (Fig. 3b), however the difference was only significant compared with Hawaii non-HAVO ($t = 3.16$, $df = 1$, $P < 0.01$). Furthermore, Hawaii Non-HAVO had a lower mean number of fledglings than HAVO ($t = 2.39$, $df = 1$, $P < 0.05$). HAVO had the lowest mean number of fertile eggs and the largest mean number of infertile eggs (Fig. 3c and d).

The mean number of eggs predated in the wild was lowest at Haleakala, however this difference was not significant (Table 1 and 2). The mean number of eggs hatched was similar between regions (Table 1 and 2). Furthermore, hatching success was similar, with Hawaii non-HAVO having a slightly larger rate of success, followed by Haleakala and HAVO (Table 2). Fledging success was highest at Haleakala (22.9 %), followed by HAVO (17.67 %) and lowest at Hawaii non-HAVO (7.7 %; Table 1).

A total of 366 goslings are known to have fledged in the three release regions, including 196 in the wild, 161 in or around pens and 9 of unknown origin. Most goslings fledged at HAVO with 65 reported in the wild and 141 from inside or around pens. At Haleakala, 68 wild goslings are known to have fledged and 20 from in and around pens. At Hawaii non-HAVO, 63 goslings were recorded to have fledged in the wild. Large numbers of unbanded geese at Haleakala and Hawaii Non-HAVO suggest that recruitment in these areas may have been higher than recorded in the database.

Table 2: Summary of nest records in the wild since 1960 by region. Nests that contained less than two eggs were excluded in all means except for hatching success. Data on mean clutch size, number of goslings fledged and fertility are presented in Figure 3, for statistics see Table 1.

Region	Total clutches	Clutch size	Predated eggs			Hatched eggs			Hatching success		
									total		Success
	n	range	n	mean	S.E.	n	mean	S.E.	Fail	Succ	(%)
Non-HAVO	232	2-5	117	0.43	0.10	142	1.85	0.12	71	138	66.0
HAVO	295	2-5	37	0.57	0.19	103	1.61	0.13	104	144	58.1
Haleakala	160	2-6	85	0.22	0.08	112	1.91	0.15	47	78	62.4

Comparison of reproductive parameters of pairs of wild versus captive-reared origin

At HAVO, nest records were available from 21 wild birds (10 females, 11 males), 86 birds that originated from the HAVO breeding pens (41 females and 45 males) and 47 birds that originated from the State breeding facility at Pohakuloa (25 females, 22 males).

Birds reared in the wild may have advantages over birds reared in captivity, e.g. the knowledge of feeding sites may improve their reproductive success. Wild males had a higher hatching success than captive-reared males (G = 29.8, df = 1, $P < 0.0001$), but wild females had a lower hatching and fledging success than captive-reared females (hatching success: G = 4.28, df = 1, $P < 0.05$, fledging success: G = 7.5, df = 1, $P < 0.01$). Effects appeared to be gender specific. Captive-reared females had higher hatching and fledging success than captive-reared males (hatching success: G = 61, df = 1, $P < 0.0001$, fledging success: G = 14.7, df = 1, $P < 0.001$). Fledging success was higher in wild males when compared with wild females (G = 11.56, df = 1, $P < 0.001$). For hatching and fledging success of males and females of different origins see Table 3.

Table 3: Hatching and fledging success in relation to male and female origin in Hawaii Volcanoes National Park. All banded birds less than 3 years old were excluded.

	Hatching			Fledging		
Female origin	Success	Fail	*% Succ.*	Success	Fail	*% Succ.*
Wild	9	14	*39.1*	4	16	*20*
Released (State origin)	40	10	*80*	37	7	*84.1*
Released (HAVO origin)	35	35	*50*	56	13	*81.1*
Male origin						
Wild	11	21	*34.4*	25	13	*65.8*
Released (State origin)	5	29	*14.7*	23	12	*51.11*
Released (HAVO origin)	6	53	*10.16*	33	28	*54.1*

Partner combinations

To test whether the origin of partners influenced reproductive parameters, I compared nest records of pairs with the following combinations: 1) both released, 2) one wild, one released and 3) both wild. Table 4 gives an overview of hatching and fledging success in the different pair groups. Fledging success was highest in pairs with at least one wild partner as opposed to pairs with no wild partner ($G = 10.22$, df = 1, $P < 0.005$). Hatching success, however, was similar between the two groups ($G = 0.42$, df = 1, $P > 0.05$). Pairs with two wild birds were rare and the small sample sizes do not allow a direct comparison. In mixed pairs, hatching and fledging success was similar between pairs with wild males and pairs with wild females (hatching: $G = 1.0$, df = 1, $P > 0.05$ and fledging: $G = 0.2$, df = 1, $P > 0.05$). The origin of partners did not influence any other reproductive parameters such as clutch size, number of fertile/infertile eggs, eggs hatched or number of fledglings.

Table 4: Hatching and fledging success in relation to partner origin from HAVO pairs nesting in the wild. All banded birds less than 3 years old were excluded.

	Hatching			**Fledging**		
Pair origin	Success	Fail	*% Succ.*	Success	Fail	*% Succ.*
Released-released	49	35	*58.3*	8	60	*11.8*
Released - wild	30	13	*69.8*	13	23	*36.1*
Wild-Wild	2	5	-	1	5	-

Rearing and release methods

Black *et al.* (1997) demonstrated that rearing and release methods had an effect on subsequent survival. In this analysis I tested if it affected a bird's subsequent reproductive parameters.

At Non-HAVO, the mean number of eggs predated in clutches laid by females released with the feather-pulling method was higher (mean ± SE: 0.7 ± 0.3 eggs per clutch, n = 22 clutches) than for birds released a few weeks prior to fledging (no predation, n = 16; $\chi^2 = 9.9$, df = 1, $P < 0.005$). There were no records of offspring from females released with the feather-pulling method.

Differences in hatching and fledging success with regard to rearing and release method are described in Table 5. Females reared in sibling groups and released with the feather-pulling method had a lower hatching and fledging success than females reared and released with other methods (hatching success: $\chi^2 = 8.6$, df = 1, $P < 0.005$ and fledging success: $\chi^2 = 3.9$, df = 1, $P < 0.05$). Males reared in sibling groups failed more often to hatch young than did parent-reared birds (captive parents; $\chi^2 = 5.8$, df = 1, $P < 0.025$). At HAVO, females fostered with captive parents at 3 - 6 weeks of age (late foster-reared, without prior parental contact) had a higher hatching success than all the other parent-reared categories ($\chi^2 = 14.9$, df = 1, $P < 0.001$), but did not have a significantly higher fledging success. Males reared in the wild had a higher hatching and fledging success than released parent-reared males (excluding late foster-reared birds; hatching: $\chi^2 = 4.4$, df = 1, $P < 0.05$, fledging: $\chi^2 = 6.5$, df = 1, $P < 0.025$). In both sexes, clutch size, number of fertile or infertile eggs and number of young hatched did not vary with rearing and release techniques in either region. Interactions between rearing and release techniques were not significant.

To test whether the differences in reproductive performance between release regions that I described earlier were a result of the differences in rearing and release techniques employed, I fitted a model containing region, rearing and release technique. Region was not significant in models containing rearing or release method. This suggests that differences between regions might be at least partially caused by different rearing and release methods.

Table 5: Female and male known subsequent hatching and fledging success (and failure) in relation to rearing and release history (groups with small samples are not presented)

Females			**Hatching success**			**Fledging success**		
Region	Rearing	Release	Fail	Suc.	%	Fail	Suc.	%
Non-HAVO	Sibling group, no adult contact	Feather-pulled	13	22	*63*	15	1	-
		Pre-fledging	2	13	-	2	2	-
		Total:	**15**	**37**	***71***	**17**	**3**	***15***
HAVO	Fostered w/ captive parents	Full-winged	11	40	*78*	40	6	*13*
	Open pen, parents can't fly		22	23	*51*	38	7	*16*
	Wild		4	3	-	5	2	-
	Open pen, wild parents		14	14	*50*	23	4	*15*
	Closed pen, captive parents		12	3	-	12	2	-
		Total:	**63**	**83**	***57***	**118**	**21**	***15***
Males			Fail	Suc.	%	Fail	Suc.	%
Non-HAVO	Sibling group, no adult contact	Feather-pulled	13	46	*78*	13	2	-
		Pre-fledging	4	8	-	4	1	-
		Total:	**17**	**54**	***76***	**17**	**3**	***15***
HAVO	Fostered w/ captive parents	Full winged	8	19	*70*	25	3	*11*
	Open Pen, parents can't fly	Full winged	15	22	*59*	29	4	*12*
	Wild		4	17	*81*	10	7	-
	Closed pen, captive parents		13	13	*50*	23	3	-
		Total:	**40**	**71**	***64***	**87**	**17**	***16***

Comparison of wild birds with those nesting in pens

Hawaiian Geese at HAVO nested either in the wild or in breeding pens. Birds in pens were provided with supplemental feed and were protected against predators. Breeding pairs in pens had a larger clutch size, more fertile eggs per clutch, less infertile eggs per clutch, a lower number of eggs predated, a larger number of goslings hatched and a larger number of goslings fledged (Fig. 4: a - d). Furthermore, their mean hatching and fledging success was larger (Fig. 4e).

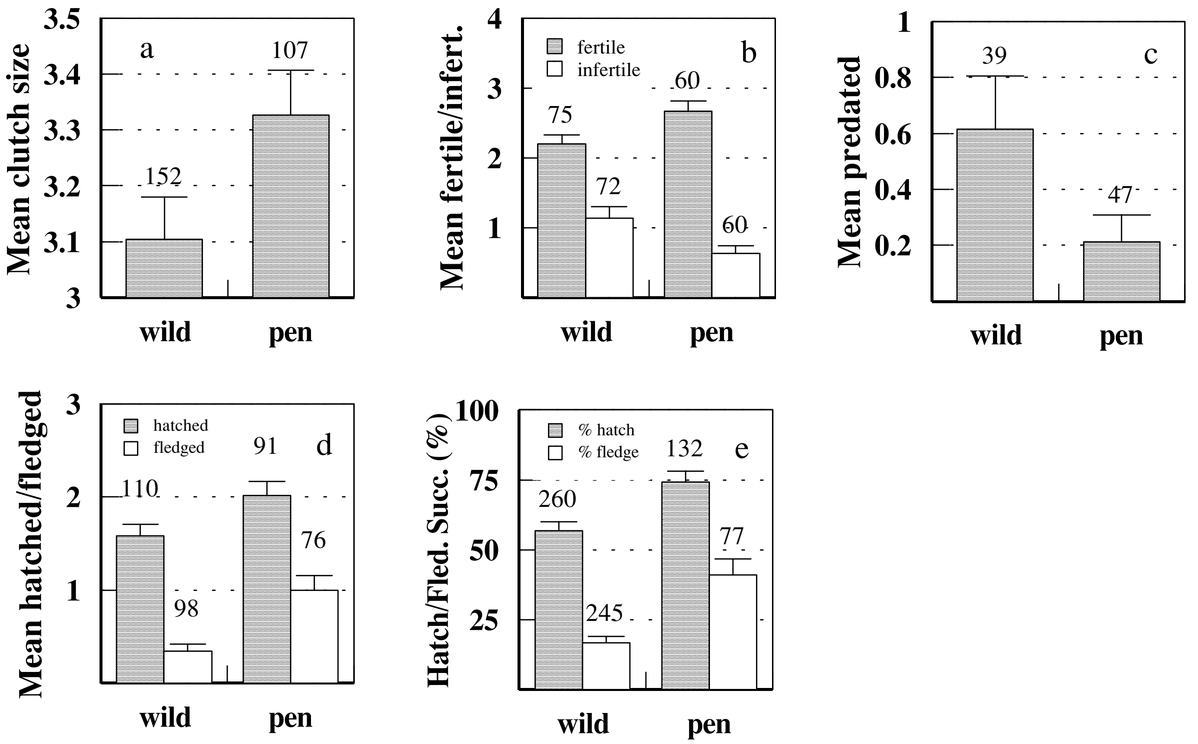


Fig. 4: Reproductive parameters in the wild and in pens. Breeding pairs in pens had a larger clutch size (a; F = 3.91, $P < 0.05$), more fertile eggs per clutch (b; F = 4.47, $P < 0.05$), less infertile eggs (c; $\chi^2 = 6.47$, $P < 0.025$), a lower number of eggs predated (d; $\chi^2 = 16.35$, $P < 0.0001$), larger hatching (e; $\chi^2 = 11.52$, $P < 0.001$) and fledgling success (e; $\chi^2 = 20.52$, $P < 0.0001$). Degrees of freedom equal one in all comparisons. Data from Hawaii Volcanoes National Park only. Standard errors and sample sizes are indicated.

Hatching and fledging success during three management periods

Splitting the HAVO data into three management periods revealed differences of reproductive parameters (as described in the methods: period 1 between 1973/74 and 1983/84 with management mainly by captive breeding in low to mid-elevation breeding pens; period 2 between 1985/86 and 1991/92 with captive and semi-captive breeding mainly at Pen 11 and Pen 7; period 3 from 1992/93 onwards with predator control in wild nesting and brooding areas and grassland management).

In the last five years of the reintroduction program at HAVO, 36 fledglings were produced in the wild, as opposed to 29 fledglings in the 19 previous years. This coincided with an increasing population size (Fig. 5) but also with increased predator control efforts in some nesting and brooding areas and the provisioning of mowed grasslands. Compared to the fledglings produced in captivity, the percentage of wild fledglings increased from 20% in the first period to 29% in the second period to 51% in the last period (G = 17.2, df = 2, $P < 0.001$). Brood size and fledgling group size did not vary between management periods. Hatching success decreased from 66% in the second period to 54 % in the third period of the reintroduction program (Fig. 5), which coincided with an increasing population size. There was no significant change in fledging success over time. From 1973 onwards, 68% of the wild

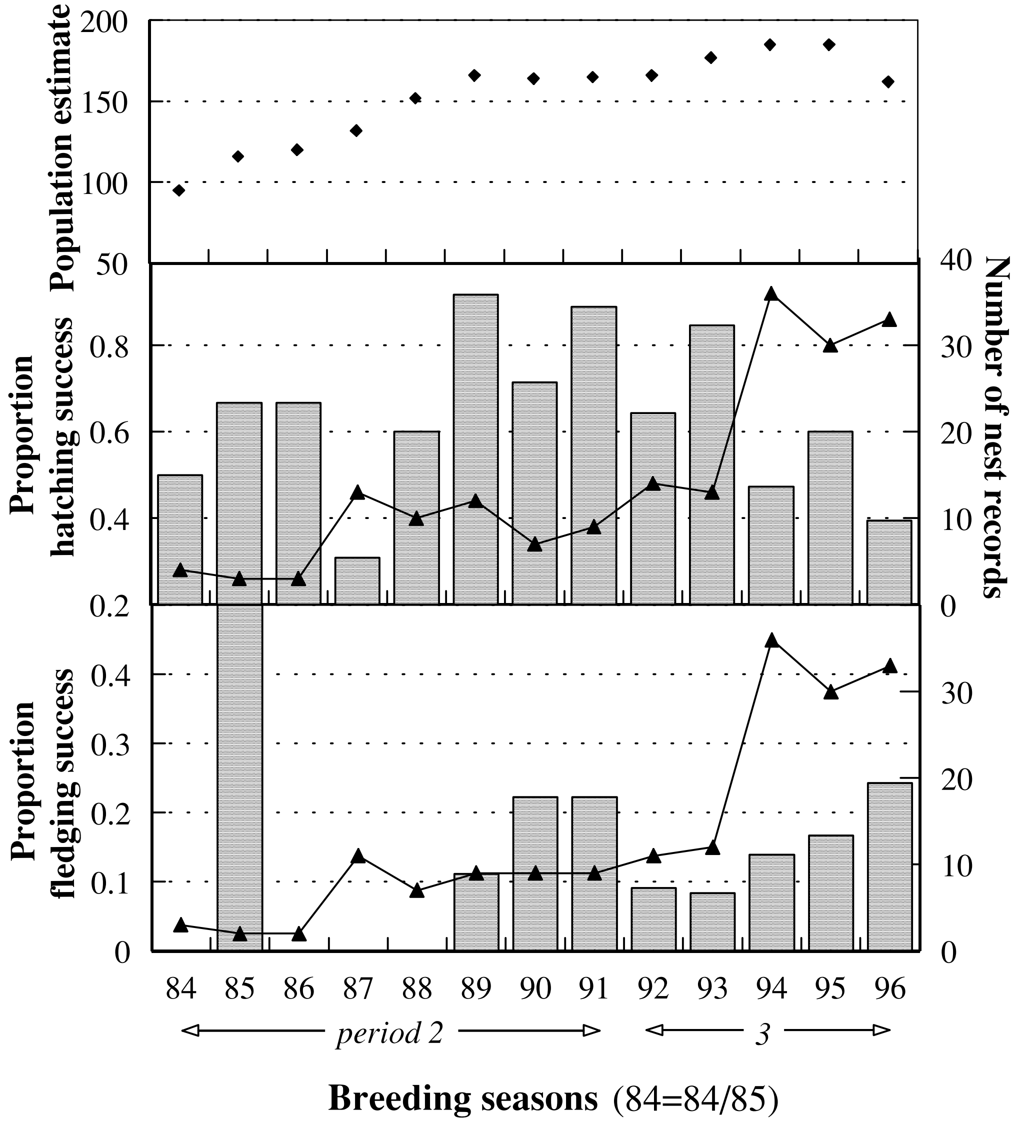


Fig. 5: HAVO population size and proportion of hatching and fledging success in relation to the number of nest records. Records from birds with unknown hatching and fledging success were excluded. The proportion of hatching success varied between years ($\chi^2 = 26.7$, df = 12, $P < 0.01$). Population size and time period dropped out of the model containing year. When not fitting year, hatch success was affected by population size ($\chi^2 = 7.2$, df = 1, $P < 0.01$) and time period ($\chi^2 = 5.0$, df = 1, $P < 0.05$). Fledging success increased from 1992 onwards, but was not affected by year, population size or/and time period.

fledglings were produced at mid-elevation between 500 - 1000 m, 26% above 1000 m and only 6% below 500 m.

As the population increased, the percentage of nests recorded in open scrubland as opposed to other habitats increased from 68% (period 1 and 2) to 91% (period 3; G = 22.5, df = 1, P < 0.0001, Table 6), but hatching success in open scrubland decreased from 78% to 57% (G = 6.5, df = 1, P < 0.025). Fledging success stayed the same, both in open scrubland and in grassy scrub; hatching success in the latter did not change over time. Regardless of management period, hatching success was higher in open scrublands (65%) as opposed to grassy scrub (47%; G = 5.1, df = 1, P < 0.025). Birds nesting in open scrubland had a higher fledging success (18.6%) than birds nesting in grassy scrub (10.5%), but the difference was not statistically significant.

Table 6: Number of nests recorded in the wild from different habitats throughout three management periods at HAVO, number in brackets indicate percentages within management period.

	Management period					
	1		***2***		***3***	
Habitat	*(1974-1984)*		*(1985-1993)*		*(1994-1997)*	
Grass pasture	1	*(2)*	7	*(10)*	3	*(2)*
Grassy scrub	9	*(22)*	20	*(27)*	9	*(7)*
Open scrubland	31	*(76)*	46	*(63)*	124	*(91)*
Total:	41		73		136	

Effect of rainfall on reproductive parameters

Rainfall affects vegetation growth. In dry periods forage is less nutritious and the lack of adequate food resources may largely be responsible for low breeding success. The mean number of fertile eggs per clutch was higher when nests were initiated in wet months (Fig. 6). All the other reproductive parameters (clutch size, number of eggs hatched and fledged, hatching and fledging success) did not change significantly between dry and wet months.

Effect of predator control on reproductive parameters

When combining data from Hawaii and Maui, nest failure was due to predation in 33 of 75 documented cases (31%). To test if the initiation of predator control improved reproductive success, I compared 5 years prior to control with 5 years with control in Kipuka Nene nesting areas. Hatching success was lower in the later years with predator control (59.5%, n = 37 clutches) than in the earlier years, when not controlling for predators (92.3%, n = 13 clutches; $\chi^2 = 5.7$, df = 1, P < 0.025). Fledging success, however, was higher in the years with predator control (16.2%); no goslings fledged prior to control efforts ($\chi^2 = 3.63$, df = 1, P > 0.1; Tab. 7). Wet years without predator control did not yield any goslings at either Kipuka Nene or Ainahou (Tab. 7). A total of 12 goslings has been produced at Kipuka Nene and 3 goslings at Ainahou since predator control as well as supplemental feeding and the provision of managed grasslands started (Tab. 7).

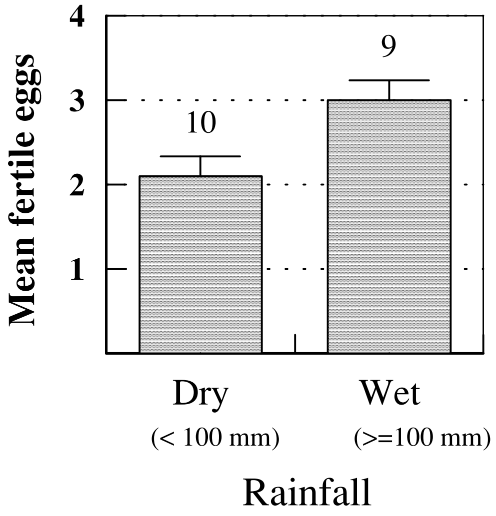


Fig. 6: The mean number of fertile eggs was higher when nests were initiated in wet months (F = 7.33, df = 1, P < 0.02). Data from wild birds at HAVO, all ages included.

Table 7: Rainfall in the breeding season (October to March), predator control and number of fledglings produced in two different areas from 1988 onwards (int. = intermediate).

Season	Rainfall (mm) *Ainahou*	Predator control	*# fled.*	Rainfall (mm) *K. Nene*	Predator control	*# fled.*
88/89	2079, wet	-	*0*	1801, wet	-	*0*
89/90	1937, wet	-	*0*	1757, wet	-	*0*
90/91	2546, wet	-	*0*	1808, wet	-	*0*
91/92	920, dry	-	*0*	739, dry	-	*0*
92/93	1363, int.	-	*0*	1387, int.	+	*0*
93/94	1339, int.	-	*0*	798, dry	+	*1*
94/95	888, dry	+	*0*	455, dry	+	*4*
95/96	1077, dry	+	*3*	997, dry	+	*0*
96/97	n.a., wet	+	*0*	n.a., wet	+	*7*

DISCUSSION

Comparison between release regions

Haleakala had the highest reproductive values in most categories. A higher mean number of goslings fledged per nest compared to HAVO and Hawaii non-HAVO might have been a result of larger initial clutch size caused by more favorable foraging conditions. Clutch size is thought to be affected by food availability in the breeding areas (Lack 1968). Rainfall in Haleakala is higher than in the other release sites and is likely to increase the availability and quality of forage there, which is beneficial to parents and young alike. Individual birds laying smaller clutches may be laying the clutch that maximizes their fitness given their breeding circumstances (Rohwer 1992). Relatively smaller clutches on Hawaii may be adaptive when food resources are low. Due to reduced competition among siblings, goslings from smaller clutches may have a higher probability of survival in times of low forage availability (but see Lessels 1986).

The low fledging success at Hawaii Non-HAVO may be a result of the comparatively lower food availability in these upland sites. Additional factors such as predation rates may also be influencing gosling survival (Banko 1992).

Birds nesting in the wild versus birds nesting in pens

Birds in pens reproduced better than those in the wild, reflecting reduced predation and/or enhanced feeding opportunities. As in Banko's study (1992), hatching success was higher in pens, but the difference was less pronounced, e.g. hatching success in pens decreased from 83% (during Banko's study) to 74% and increased from 44% (during Banko's study) to 57% in the wild. Higher hatching success in pens might be attributed to the higher nest attentiveness of captive females (Banko 1992). Food reserves enable female geese to spend more time on the nest (Ryder 1970). In Banko's study, wild females spent 3 times more time off the nest to forage compared to captive females. Some wild females had to fly to distant pastures after they had depleted food resources around nests (Black *et al.* 1994), whereas food was readily available for captive birds. Banko (1988) showed that females whose nests were closer to grass pasture (< 1 km) had better success in hatching eggs than those whose nests were further away (up to 5 km). Long absence from the nest might increase risk of egg chilling or predation and result in lower hatching success. Similar to Banko's and Manuwal's study (1982), fertility in the HAVO breeding pens was around 81%, however, it increased in wild birds from 84% to over 90% between 1984/85 and 1996/97.

Egg predation did occur inside the breeding pens which indicates that predator control measures need to be improved. During my study, I observed a mongoose climb into a pen where it searched for mice in the bird food. At the time, the goslings in this pen were almost fully grown and the mongoose did not pursue them. All geese inside and outside the pen exhibited mobbing behavior, trying to drive the predator away. This experience might have taught goslings predator recognition skills, but young goslings and eggs may need better protection to enable this goose population to recover.

Supplemental feeding in nesting areas has been shown to increase the clutch size in some birds (e.g., raptors: Dijkstra *et al.* 1982, Newton and Marquiss 1981; corvids: Högstedt 1981, Dhindsa and Boag 1990) and in some studies fledging success (corvids: Högstedt 1981, Korpimäki 1989). Hawaiian Geese in pens with food *ad libitum* had larger clutches and a higher fledging success. In a VORTEX model Black and Banko (1994) showed, that when given the amount of predator protection and food that birds received in pens, the wild population would thrive on all three islands. These computer models and my empirical data show clearly that supplemental feeding coupled with predator control is likely to increase reproductive success in the wild.

Who performs better: Wild or released birds?

Wild-type male Hawaiian Geese hatched and fledged more offspring than those reared in captivity, whereas wild-type females hatched and fledged less young than those reared in captivity. Captive-reared males had poorer hatching and fledging success than captive-reared females. These gender-specific differences may be indicative that early-learning experiences in fighting ability, for example, may be more crucial to males than females. More aggressive males have access to better feeding areas where their mates and offspring can obtain better food (Teunissen *et al.* 1985, Black and Owen 1989b, Black *et al.* 1996).

Pairs with at least one wild bird were more successful than when both partners were released. Wild birds appeared to add to the quality of a pair in terms of reproductive success. This may indicate that skills learned from parents after release are critical. For example, young birds might learn the location of feeding sites and how to defend food resources more proficiently. They may encounter a potential predator after release and learn the adequate response from their parents, which, later in life, will enable them to defend their own goslings against predators (also see Black and Owen 1987, Marshall and Black 1992).

Rear and release methods

My results indicate that the rearing and release methods employed have had an effect on subsequent breeding success. Birds reared with the feather-pulling method produced no fledglings and egg predation rates were higher than those in other rearing categories. Kear and Berger (1980) reported problems early in the reintroduction program with both the feather-pulling and feather-binding release methods, which impaired subsequent flight through damaging feather follicles or twisting the tips of the primary feathers in some birds. Subsequent mortality in birds released with the feather-pulling method was higher than when birds were released prior to fledging (Black *et al.* 1997).

Males and females reared in sibling groups had lower reproductive success than parent-reared birds. Males reared in the wild had a higher hatching and fledging success than in captivity parent-reared males.

Parent-reared birds are thought to behave more 'naturally' (Kear 1978) and socially integrated better into a flock than hand-reared or sibling-reared goslings (Marshall and Black 1992). Social skills are useful for geese when competing for food (Teunissen *et al.* 1985, Black and Owen 1989b), mates and nesting territories (Collias and Jahn 1959, Owen and Wells 1979). Parent-reared birds exhibited more vigilance behavior, which is thought to increase detection of predators in a wild environment (Marshall and Black 1992).

Parent-rearing in the wild yielded the most successful birds. This is probably due to the enhanced behavioral experience goslings gain from growing up in the wild. In addition, young stay with their parents after fledging and learn the location of traditional feeding areas.

Rearing technique has been shown to influence reproductive success in other species. In Cockatiels, effects were gender-specific. Hand-reared males were less likely to produce fertile eggs, fledging occurred only in pairs that contained parent-reared males, suggesting hand-reared males lost parental quality (Myers *et al.* 1988). Parent-reared partridges showed longer bouts of vigilance (Dowell 1988, 1989). Early learning experience appeared to be important for cockatiels to learn characteristics of nest sites and for partridges to choose roost sites. Early experience in the form of habitat imprinting is thought to influence habitat and nest site selection (e.g., in captive waterfowl: Kear 1978 or Lesser Snow Geese: Cooke and Abraham 1978).

As a result of daily contact with humans during pen maintenance and the lack of foster or real parents, taming has been observed in Hawaiian Geese bred at Pohakuloa (H. Hoshide pers. comm.). After release, some of these birds approached humans and cars without fear and as a result were often killed. Goslings from Pohakuloa that were placed with foster parents in the National Park prior to release, were less tame and behaved more like the rest of the flock (H. Hoshide pers. comm.). In New Zealand, allowing Black Stilt to breed under 'semi-natural' conditions has reduced the risks of mal-imprinting, improved the chicks' foraging efficiency and social behavior and furthermore reinforced anti-predator behavior, through the parents vocal and display behavior (Reed and Merton 1991).

Choice of nesting habitat - active predator avoidance?

Birds nesting in the open desert scrubland were more successful than in grassy scrub. Predator densities in the open scrubland habitat are thought to be lower than in grassy scrub (Stone *et al.* 1983), so that even without predator control in these areas predation rates would be expected to be lower. The improved reproductive success in open scrubland may be why birds colonized this area. Predation as a cause for nest failure has decreased since Banko's study (1988), from 62% to 31%. This might reflect increased predator control efforts and the adaptability of the geese to use nesting areas with lower predator densities (Stone *et al.* 1983).

At Kipuka Nene, surprisingly, hatching success was lower in years with predator control and higher when not controlling for predators. This could be attributed to the effects of increasing population size I described above, or to the fact that the majority of years with predator control were dryer than years without predator control. In dryer periods the digestibility and nutritious value of grass and herbs is lower than when it is wetter (see Chapter

5). As a consequence, parents have to spend more time finding food and can spend less time at the nest, increasing predation risk and chilling of the eggs, which might explain a lower rate of hatching success. In contrast, the most productive year (1996/1997) in terms of fledging production was a wet year coupled with established predator control, grassland management and supplemental feeding. In that year, the first wild recruitment in the lowlands of the National Park was accounted for by three fledglings at the end of the chain of craters road, when rainfall in this area was exceptionally high and lush forage available (D. Hu, pers. comm.). More detailed rainfall data are needed to elucidate the effect of rain on the different stages of the reproductive cycle.

Management - an assessment

At Kipuka Nene and Ainahou, management efforts appear to have resulted in more wild recruitment. The maintenance of predator trap-lines in recent years accounted for the first fledglings produced in these areas, while management of grasslands provided higher quality food for the birds.

Hatching success of wild birds, however, decreased in the last five years of the reintroduction project, which may be a density dependence effect with overall increased population size. More birds attempted to breed, but proportionally fewer succeeded. Carrying capacity of the current habitat might be reached. The scenario might be as follows: A few competitive birds defended the best habitat patches for nesting and brood rearing, whereas unsuccessful pairs were restricted to the less favorable habitat. Whereas availability of nest sites was not thought to be a problem in the early stages of the reintroduction program (Banko and Manuwal 1982), the availability, especially of good nest sites, might be limiting today (Black *et al.* 1994). Nesting geese depleted the majority of the food around their nests during incubation, leaving insufficient food resources for a second pair to nest in the same location (Black *et al.* 1994). Providing additional forage by managing grasslands could increase carrying capacity (see Chapter 5). Before drawing final conclusions, studies on carrying capacity of the current habitat need to be carried out (see Black *et al.* 1994). It is crucial to distinguish between causal factors of low productivity (predation and poor feeding opportunities) and carrying capacity effects. Releasing birds into habitat that does not allow them to successfully breed may be less than prudent (Black 1991).

Conclusion

Fluctuating productivity in Hawaiian Geese appears to be a natural phenomenon, but with the currently low population levels a series of years without recruitment might be detrimental to the species' survival. Low breeding success of reintroduced birds is often the reason why reintroduction programs struggle or fail. The importance of removing the factors that caused the decline of the species in the first place cannot be stressed enough. Captive breeding and subsequent release have undoubtedly prolonged the extinction process of the Hawaiian Goose (Black 1995, 1998a), but for the reintroduction project to be successful more birds need to reproduce in the wild. This will be achieved when introduced predators are removed and adequate forage is provided.

The wild breeding population numbering 900 birds in 1998 (Banko *et al.* in press) may be large enough to concentrate efforts on habitat management. This should include the continuation of large-scale predator control and intensive grassland management. Management needs to continue until the population will have increased to a size which allows it to escape the problems of demographic and environmental uncertainty.

Recommendations

The optimal rearing strategy for Hawaiian Geese, in terms of producing behaviorally and physically fit breeders, appears to be parent-rearing under as natural conditions as possible, as demonstrated in the National Parks. Parental contact after release appears to be important and could be increased by enabling more birds to nest in the wild. Fledgling production in wild Hawaiian Goose populations has increased recently, but is still poor. Improved reproductive success could be achieved by (1) raising the carrying capacity of the current habitat by further improving foraging opportunities through grassland management and farming of native food plants, (2) continued predator control in important nesting and brooding areas, and (3) providing sanctuaries where birds can feed and nest in a predator-free environment. Data collection within the National Parks should be continued to allow future assessment of management efforts. Studies outside the National Parks, although logistically difficult, should be encouraged to fill gaps in knowledge for those populations. Banding and resighting effort outside the National Parks should be increased to allow proper assessment of wild recruitment and movements. For future assessments of the reintroduction program, standardized data collection should be continued and improved on all islands.

SUMMARY

Since 1960, 366 goslings are known to have fledged in the three release regions, including 196 in the wild and 161 in or around pens. Numbers of goslings fledged in the wild were similar between the three regions with 68 reported from Haleakala National Park, 65 from Hawaii Volcanoes National Park and 63 from the remainder of Hawaii island.

Initial clutch size at Haleakala was greater than on Hawaii, which might have been due to better foraging conditions. Fledging success, however, was similar between Haleakala and Hawaii Volcanoes National Park, suggesting that other factors such as predation were operating.

Birds in pens reproduced better than those in the wild, reflecting reduced predation and enhanced feeding opportunities. When paired to a wild bird, released birds were more successful than when paired to a released bird. Parent-reared birds in large open top pens, which eventually flew from the pens after fledging, reproduced most successfully. Males reared in the wild had a higher fledging success than captive-reared males.

Most birds nested in open scrubland where they were more successful than in grassy scrub. In Hawaii Volcanoes National Park, a declining hatching and fledging success in the wild population suggests that the carrying capacity of the habitat may be reached. Carrying capacity could be further increased through grassland management, which, coupled with predator control, has increased gosling survival in the last five years of the reintroduction program at Hawaii Volcanoes National Park.

Chapter 7: Reproductive success and assortative pairing in Hawaiian Geese in relation to age and body size

INTRODUCTION

Throughout life, individuals become more experienced and reproductive success generally increases with age (Clutton-Brock 1988, Black and Owen 1995). First-time breeders often have limited success, but as they become older their ability to rear young appears to improve. Older geese are often more dominant than young ones and defend better patches of food, enabling them to accumulate more reserves for breeding and to provide better food resources for their goslings (Lamprecht 1986a, b).

Size also may affect reproductive success. Large individuals are often the most dominant, defend the best food resources and as a result rear more young (Scott 1980). In Lesser Snow Geese (*Anser c. caerulescens*) large females lay larger clutches (Ankney and MacInnes 1978). Large female Barnacle Geese (*Branta leucopsis*) lay larger eggs than small females (Larsson and Forslund 1992). In geese, large eggs contain more nutrients (Lack 1968, Owen and West 1988), and produce larger chicks, which are more likely to survive (Ankney 1980).

Many studies explain reproductive performance by traits of only one individual of the breeding pair (Clutton-Brock 1988, Newton 1989). In monogamous relationships, however, this would be presenting only half the picture. Geese typically pair for life and both parents rear the young. Staying together throughout life allows individuals to optimize resource procurement and maximize "reproductive fitness" (Black 1996). Over time, partners become more familiar with each other. Reproductive success has been shown to increase with pair bond duration in a variety of wildfowl (e.g. Blue Ducks: Williams and McKinney 1996; Barnacle Geese: Black *et al.* 1996; Swans: Rees *et al.* 1996). Geese that maintain a permanent bond have a higher reproductive success than geese that frequently change mates (Cooke *et al.* 1981, Owen *et al.* 1988).

In a monogamous relationship, successful breeding might be better explained by the particular combination of male and female characteristics (Choudhury *et al.* 1996) and the degree to which they result in a successful partnership. Choudhury *et al.* (1996) pointed out that Barnacle Geese maximized their breeding performance by mating with relatively similar sized partners; the greater the size disparity of mates, the lower was their breeding performance.

I use two reproductive parameters in this study, which indicate performance at different stages of the reproductive cycle. Clutch size is indicative of the fat reserves a female accumulates prior to laying (Teunissen 1985). Females with protective males can spend more time feeding and are able to accumulate more body reserves for egg-laying than females with less proficient partners (Black and Owen 1989, Black *et al.* 1996). A female with good body reserves needs shorter incubation recesses in order to feed, reducing the risk of predation and chilling of eggs (Banko 1988), thus increasing the number of eggs hatched.

In this chapter I describe how these reproductive parameters varied with the age and size of individual Hawaiian Geese, and how this was influenced by the age and size of the partner.

METHODS

My study population was a flock of about 200 captive (pinioned), individually marked Hawaiian Geese of known age with known reproductive history and body measurements. The birds roamed freely within the wildfowl collection at Slimbridge and were able to choose their mate independently. The grounds were controlled for predators and food was provided *ad libitum*. During annual health checks at Slimbridge, birds were banded with letter-coded Darvic rings, sexed through cloacal examination and measured (skull and tarsus). Clutch size was recorded for each nest from 1986 onwards. Data on the number of young hatched from each clutch from 1992 onwards was used, when Hawaiian Goose pairs were allowed to nest in the grounds under semi-natural conditions. Prior to 1992, eggs were removed and incubated artificially. Only first clutches and pairs with more than two years of reproductive success information were used for analysis. Data on fledgling success was biased by avicultural efforts and was therefore not used for analysis. Pair bond duration was calculated as the number of years since first nesting with a particular partner.

Data analysis

GLIM software (NAG 1993) was used for regression analysis and analysis of variance. Initial fits indicated that data on the number of eggs hatched were over dispersed. The constraints imposed by specifying a Poisson error distribution therefore were modified by adjustment of the scale parameter. This was achieved by dividing the Pearson Chi-square statistic by the residual degrees of freedom (Crawley 1993). A significant term caused a significant change in deviance when removed from the model, only significant terms were retained. I tested all biological meaningful interactions; they were removed from the model before testing significance levels of single terms. Year was fitted as a categorical variable. To test the significance of single parameters, t-tests were carried out on parameter estimates (Crawley 1993).

Regression analyses were performed using age as a predictor for clutch size and number of eggs hatched. After analyzing age as a continuous variable, it was classified as 1) young (1- 5 years), 2) middle-aged (6 - 9 years) and 3) old (> 9 years; adapted from Black and Owen 1995). Age disparity between partners was classified according to nine categories (young male and young female, young male and middle-aged female, young male and old female etc.). The combined age was a sum of both partners' age classes. I explored the data in three ways: Firstly I analyzed clutch size (1986-1996) and number of goslings hatched (1992 - 1996) in relation to male and female age in a GLIM model, whilst controlling for year. When attempting random sampling of only one reproductive record per individual, sample sizes became too small. The trend in the random data, however, matched that of the complete data set in most cases. To avoid pseudo replication, I analyzed the 1996 data separately (one reproductive record per individual). The 1996 data was chosen to provide background information for Chapter 8.

Male Hawaiian Geese were larger (mean ± standard deviation: skull = 95.8 ± 2.3 mm, tarsus = 85.1 ± 2.8, n = 150) than females (mean ± standard deviation: skull = 91.3 ± 2.1, tarsus = 79.4 ± 2.4, n = 125; skull: F = 275, df = 1, $P < 0.00001$, tarsus: F = 147, df = 1, $P < 0.00001$). A combination of skull and tarsus measurements in a single derived variable, the first principal component (PC1), was used as an index of overall body size (Rising and Somers 1989). In the Slimbridge population, PC1 accounted for 86.7 % of the total variance of both measures. Each sex was assigned to one of three size categories. Medium-sized birds were those within half a standard deviation of the mean PC1 score, small birds below and large birds above this level. Size differences between partners were classified as 1) same size, 2) a small with a medium or a medium with a large bird and 3) a small with a large bird. Disparity in partners' body sizes was further classified into nine categories (small male - small female, small male - medium female, small male - large female, etc.).

RESULTS

Age patterns of reproductive success in males and females

For birds whose reproductive success was monitored between 1986 and 1996, clutch size initially increased with age, levelled off and then decreased (Fig. 1a). Females produced increasingly more eggs from the ages of 1 to 10 years (F = 7.8, df = 1, $P < 0.01$) and males between 1 and 7 years (F = 5.61, df = 1, $P < 0.02$). Although clutch size generally decreased in older birds, some old females had large clutches. The number of eggs hatched was affected only by male age, with most of the variation explained by a quadratic fit (Fig. 1b). In females, there was no significant age effect on the number of eggs hatched, however there was a noticeable increase up to the age of 8 years. A few older females hatched exceptionally many young, but for the majority of females the number of young hatched decreased after the age of eight. Breeding year or interactions between breeding year and age did not have a significant effect on the number of eggs hatched by females. In 1996, a significant relationship was found between age and the numbers of eggs hatched, in both males and females (squared fit for males: $\chi^2 = 10.25$, df = 1, $P < 0.001$ and females $\chi^2 = 11.58$, df = 1, $P < 0.001$). The number of eggs hatched increased in the early years, levelled off and declined for birds older than nine years. Males and females older than nine years hatched fewer eggs (Fig. 2).

Pair bond duration

In 1996, the number of eggs hatched initially increased with pair bond duration, but later decreased (Fig. 3). Neither male or female age remained in models containing pair bond duration. The combined age classes of partners did affect the number of eggs hatched in 1996, but not clutch size (Fig. 4). The number of eggs hatched increased in the early years, peaked for birds with one young and one middle-aged partner but declined for older combined age classes.

Relative age of partners

The age combination of partners influenced reproductive success (Fig. 5). Although sample sizes were small in some of the categories, there was a trend that young and old females hatched most young with middle-aged males, but middle-aged females performed best with young males.

Bird size and pair size combinations

Neither male or female size affected reproductive performance. Large females laid more eggs than small females (large: 3.7 ± 0.14, n = 21; small: 3.3 ± 0.21, n = 9), but this was statistically not significant. Size disparity between partners did not have any effect on clutch size or the number of eggs hatched.

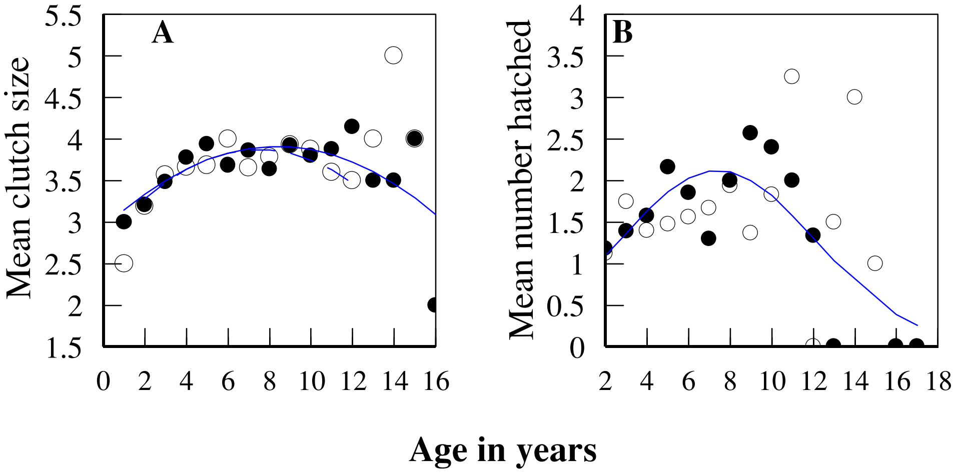


Fig. 1: The distribution of reproductive performance with respect to male (dots and solid line) and female (circles and dashed line) age in years. The lines represent fitted values. A. Mean clutch size at Slimbridge (range 2 - 5) between 1984 and 1996, for males (squared fit, F = 8.19, df = 1, P < 0.01) and females (squared fit between 2 - 12 years of age, F = 4.38, df = 1, P < 0.05). B. Mean number of eggs hatched at Slimbridge (range 0 - 5) between 1992 and 1996; for males (dots and solid line: squared fit, χ^2 = 8.5, df = 1, P < 0.005) and females (circles, no significant fit). For sample sizes and standard errors see Appendix.

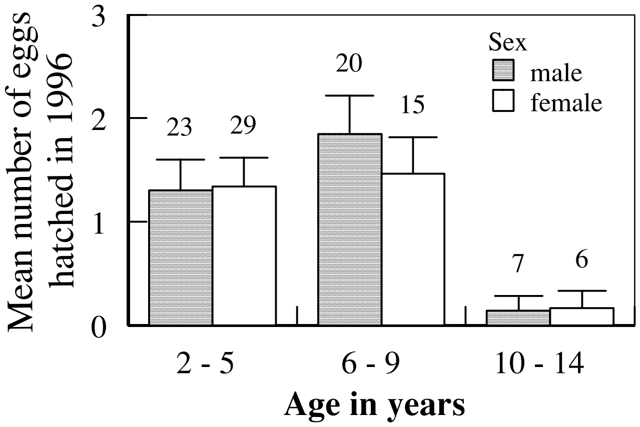


Fig. 2: The distribution of the number of eggs hatched with respect to male (grey) and female (white) age class. Sample sizes indicate number of birds. Males and females above 9 years of age hatched less eggs (for males: $\chi^2 = 10.8$, df = 2, $P < 0.005$; and females: $\chi^2 = 6.6$, df = 2, $P < 0.05$).

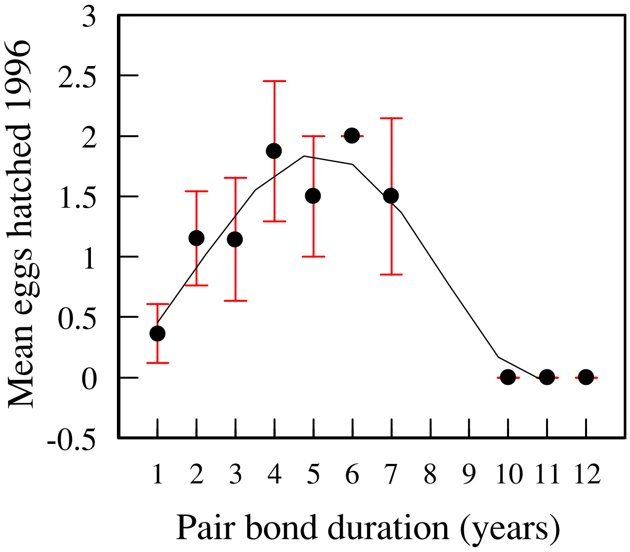


Fig. 3: The mean number of eggs hatched initially increased, but decreased for longer pair bond durations (squared fit: $\chi^2 = 13.6$, df = 1, $P < 0.001$). Standard errors are indicated. Sample sizes for pair bond durations 1 - 12: 11, 13, 7, 8, 2, 1, 4, 0, 0, 1, 2,1.

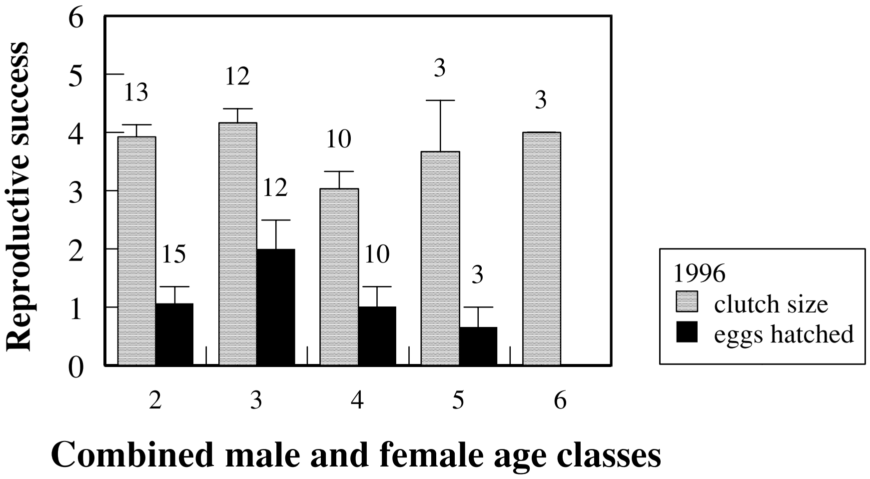


Fig. 4: Mean clutch size and number of eggs hatched with respect to the combined age classes of partners, e.g. two young birds would be a combined age class of 2 (1996 data only). Clutch size did not change significantly with age class, only class 4 was significantly lower from class 3 (t = 2.4, df = 20, $P < 0.05$). The number of eggs hatched changed significantly with age class ($\chi^2 = 12.1$, df = 4, $P < 0.025$). Standard errors and sample sizes are indicated.

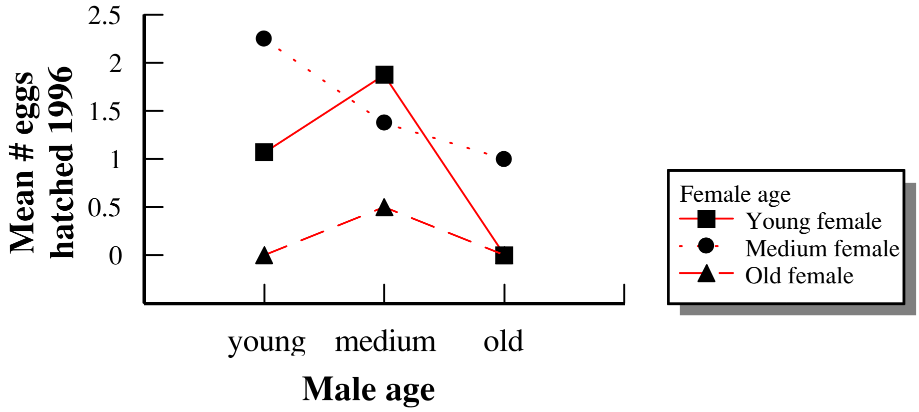


Fig. 5: The pattern of eggs hatched in relation to the mates' ages (1996 only: $\chi^2 = 16.8$, df = 8, $P < 0.05$). Sample sizes and standard errors (SE) of the pooled male-female age class comparisons: young-young 15 (0.3), young-medium 4 (1.03), young-old 1 (0), medium-young 8 (0.58), medium-medium 8 (0.38), medium-old 2 (0.5), old-young 1 (0), old-medium 1(0), old-old 3 (0).

DISCUSSION

In this study, reproductive performance in Hawaiian Geese increased with age. This has been described for several other goose species (Cooper 1978, Finney and Cooke 1978, Raveling 1981, Cooke *et al.* 1995, Aldrich and Raveling 1983, Rockwell *et al.* 1993, Black and Owen 1995) and has been attributed to increased breeding experience.

In my study, young females had smaller clutches presumably because they were less proficient foragers and did not accumulate sufficient body reserves for larger clutches (Black and Owen 1995). Young males also had smaller clutches, and hatched fewer eggs, maybe because they were less proficient in defending good patches of food for their females. Foraging and behavioral efficiency during incubation appears to be lower in young, less experienced birds, which spend more time off the nest feeding than those that have nested before (Banko 1988). Lower reproductive success in first-time breeders may also be due to a lack of experience in nest defense (Cooke *et al.* 1995). In my study, both clutch size and the number of eggs hatched decreased in older males. They may no longer be able to defend high quality food patches and nesting territories (Black and Owen 1995). In contrast, some old females hatched large clutches. The number of eggs hatched increased in the early years of the pair bond duration, but later decreased. Because some old females hatched a large number of eggs, this decline is probably attributable mainly to a decrease in male quality due to senescence, e.g. a decrease in protective abilities.

As in Barnacle Geese (Black and Owen 1995), young and old females performed best with middle-aged males. Breeding success was lower in young and old males as opposed to middle-aged males. Young males may be less experienced and old males may become senescent. Surprisingly, both, middle-aged males and females performed best with young partners. Maybe the experience of at least one of the partners was sufficient to ensure good breeding success.

In most geese, reproductive success increases with body size (Choudhury *et al.* 1996). In contrast, body size in this study had no effect on reproductive success. This might be explained by the fact that I studied captive birds, that were supplied with food and were used to people. In the wild, different selection mechanisms are likely to be operating.

SUMMARY

The effect of age and size on reproductive success was examined, and how partner age and size combinations affected it. Clutch size and the number of eggs hatched initially increased with age in males and females, then levelled off and declined for older birds. Some older females, however, had large clutches and hatched a high proportion of young. The number of eggs hatched initially increased with pair duration, but decreased later which may be attributed to old age of at least one of the partners.

Young and old females performed best with middle-aged partners maybe because middle-aged males had a higher reproductive success than younger or older males. Young males may be less experienced and old males may become senescent. Body size did not affect reproductive success.

APPENDIX: Mean clutch size at Slimbridge (between 1984 - 1996) and mean number of eggs hatched at Slimbridge (between 1992 and 1996) in relation to age with standard error and sample sizes.

	clutch size						**eggs hatched**					
	male			female			male			female		
age	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE	n
1	3	0.22	7	2.5	0.5	2	-	-	-	-	-	-
2	3.21	0.21	29	3.19	0.15	42	1.18	0.4	11	1.12	0.24	17
3	3.48	0.15	54	3.57	0.13	51	1.39	0.28	28	1.74	0.32	27
4	3.77	0.15	57	3.66	0.17	53	1.57	0.29	28	1.4	0.31	20
5	3.94	0.14	50	3.69	0.18	48	2.16	0.36	19	1.48	0.34	21
6	3.69	0.18	48	4	0.18	39	1.85	0.34	20	1.56	0.38	18
7	3.86	0.2	28	3.66	0.21	29	1.3	0.45	10	1.67	0.45	15
8	3.64	0.29	22	3.78	0.28	23	2	0.73	9	1.94	0.5	17
9	3.92	0.33	13	3.93	0.32	14	2.57	0.61	7	1.36	0.51	11
10	3.8	0.36	10	3.88	0.35	8	2.4	0.87	5	1.83	0.83	6
11	3.88	0.23	8	3.6	0.68	5	2	0.76	7	3.25	0.48	4
12	4.14	0.46	7	3.5	0.5	4	1.33	0.84	6	0	0	4
13	3.5	0.5	2	4	0	2	0	0	2	1.5	1.5	2
14	3.5	0.5	2	5	0	1	-	-	-	3	0	1
15	4	0	1	4	0	1	-	-	-	1	0	1
16	2	1	2	-	-	-	0	0	1	-	-	-
17	-	-	-	-	-	-	0	0	1	-	-	-

Chapter 8: Partner compatibility in Hawaiian Goose pair bonds: social display, proximity and reproduction

INTRODUCTION

Pair bond members of socially monogamous species spend variable amounts of time together, ranging from limited contact, only for the breeding season, to constant contact throughout the annual cycle, for the entire lifetime of partners (Black 1996). When explaining reproductive performance for individuals involved in persistent, long-term partnerships, we must consider how the combinations of pair member's qualities interact. Considering only one member of the pair would be presenting only half of the picture. For example, in Barnacle Geese *Branta leucopsis* middle-aged birds of both sexes, considered separately, reproduce at the highest level, but if a male (of any age) is paired to a young female, or a female (of any age) is paired to an old male their success is much reduced (Black and Owen 1995). Therefore, preferred mate options may depend on the interplay between the partner's qualities (Bateson 1983, Black 1996).

Coulson (1972) pointed out that the compatibility of partners may affect the fitness of both individuals. In seabirds and penguins, for example, one bird must incubate, or brood the chick, while the other is at sea collecting food. If the partners do not alternate their behaviors in a synchronous manner, the eggs or chicks are at an increased risk from chilling, starving, or depredation during periods that both partners are off at sea (Williams 1996). Compatible partners may enhance each others' survival probabilities, incompatible ones may reduce them (Marzluff *et al.* 1996).

In order to test the compatibility hypothesis, it is necessary to demonstrate that an individual will do better when paired to another partner who is not intrinsically of better quality (Ens *et al.* 1996). This has been shown in Barnacle Geese where large birds usually have the highest reproductive success on average, but small individuals of either sex do better when mated to a small individual of the opposite sex (Black *et al.* 1996; Choudhury *et al.* 1996). Since males are larger than females, and also more aggressive and dominant (Raveling 1970, Black and Owen 1989), increasing size disparity of mates could increase risk of injury to females during social display and copulation (Choudhury et al. 1996). Some females may be overly stressed by social interactions with very large mates, thus inhibiting the flow of reproductive hormones (Greenberg and Wingfield 1987). In similar sized pairings, males may harass females less, thus enhancing the potential for coordination of duties, like vigilance and foraging routines (Black *et al.* 1996, Choudhury *et al.* 1996). Male harassment of females may therefore influence female's mate choice and reproductive decisions (Gowaty 1996).

In several species with long-term partnerships reproductive success improves with the duration of the pair bond, suggesting that pair members fine-tune behaviors to achieve higher success; referred to as the mate familiarity effect (Black 1996). In seabirds with elaborate displays, it has been argued that familiarity with a mate influences the pairs' social display quality and ultimately the timing of nesting (Nelson 1965, 1972). Numerous other behaviors may require fine-tuning between pair members before optimal reproductive rates can be achieved. Besides synchrony in social display, such behaviors may include incubation and chick feeding routines, assistance in conflicts with neighbors or defense against predators. However, due to the difficulties in measuring these behaviors in wild animals few have been adequately measured, so claims that they are a prerequisite to enhanced reproductive success may be premature (Ens *et al.* 1996).

In this chapter I describe a set of behavioral attributes potentially associated with compatibility among pairs in a flock of tame Hawaiian Geese *Branta sandvicensis* that allowed close observation, thus enabling detection of behaviors that may otherwise go unnoticed. I measured pair members' participation in the triumph ceremony, a ritualized display thought to strengthen attachment and, through signaling intent, facilitating access to resources in potential competitive situations (Fischer 1965, Raveling 1970, Lorenz 1970, Radesäter 1974, 1975; Black and Owen 1988). Hausberger and Black (1990) showed that the more overt male behavior in these displays is influenced by the female's response, such that it may be encouraged or inhibited. Male display is quickly reduced when a female responds with soft calls, whereas male behavior becomes exaggerated when a female responds with loud calls and orients her head and neck toward the male. The females' supportive responses are thought to be essential for maintaining and strengthening the pair bond and to ensure reproductive success (Akesson and Raveling 1982).

I describe the degree of dissimilar and matched behavior among partners during these social displays and test whether it is related to the relative age, size and pair duration of partners, as well as to the distance with which partners associate over the course of the previous non-breeding season. Finally I compare reproductive success of pairs in relation to these attributes. I predict that partners similar in age and size, and those that have been together for some time, will show more matched behaviors, and will produce more eggs and hatch more young. I predict that females will maintain greater distances from partners they are least able to cope with; i.e. those with disproportionate overt behavior, and large body size. I discuss possible explanations for a varying degree of behavioral compatibility between partners that might be caused by differences in age (the lack of experience in a younger partner), size and dominance (inter and intra-pair aggression).

METHODS

I studied a flock of 200 captive (pinioned) Hawaiian Geese on the grounds of the Slimbridge Wildfowl and Wetlands Trust Center. The grounds hold numerous types of waterfowl, extend to about 40 ha and are enclosed with a fox-proof fence. Habitat includes grass lawns for grazing, numerous bushes and other cover for nesting and ample water for bathing. Additional grain and waterfowl feed is supplied daily by aviculturalists. Hawaiian Geese roam the grounds and are free to choose mates, nesting sites and feeding areas.

Hatch date was recorded and a web tag attached when goslings were a few days old, allowing individual identification. When the geese were caught for annual health checks, they were banded with letter-coded Darvic rings, their sex assessed through cloacal examination and their body size measured (skull and tarsus). During the breeding season between February and April, clutch size and hatching success was recorded for each pair. A number of behavioral cues were used to determine pairs, including synchronized behaviors in vigilance, feeding, defense of foraging space, as well as maintenance of proximity and social display (Black *et al.* 1996). The date of pair formation with a particular partner was taken as the first of multiple sightings when the pair was recorded together. To reduce the possibility of accepting trial partners (Choudhury and Black 1993) as true partners, I excluded associations that lasted less than six months.

Social display

Triumph ceremonies are social displays (Fig. 1) frequently observed at the onset of the breeding season, often following aggressive encounters (Fischer 1965, Lorenz 1965, Raveling 1970, Radesäter 1974, 1975). The display consists of ritualized aggressive-type elements: (1) a horizontal waving, with the head held low and outstretched; (2) an up and down vertical waving; and (3) a thrusting forward or bent neck posture (as described for Canada Geese by Blurton Jones 1960, Klopman 1968). All three combined produce a rolling movement that is displayed by one or both partners and is usually combined with a cackling vocalization (Fischer 1965, Raveling 1970).

546 triumph ceremony bouts were recorded in 53 pairs from mid-January to mid-February 1997 during 118 observation hours. Data were collected whenever geese were seen to perform the display. The following social display components were recorded: (1) initiator of social display (male or female partner), (2) distance between partners at initiation, (3) direction of display (at partner or away from it), (4) locomotion (standing, walking or running), (5) angle of displayers (angled or parallel), (6) which bird walked in the lead and which followed, (7) context (food related or social; aggressive or non-aggressive), (8) intensity of males' behavior in three classes (moderate, intermediate and exaggerated ranging from a few calls and a short to intermediate duration to many calls, exaggerated head movements, and prolonged duration), and (9) intensity of females' behavior in five classes

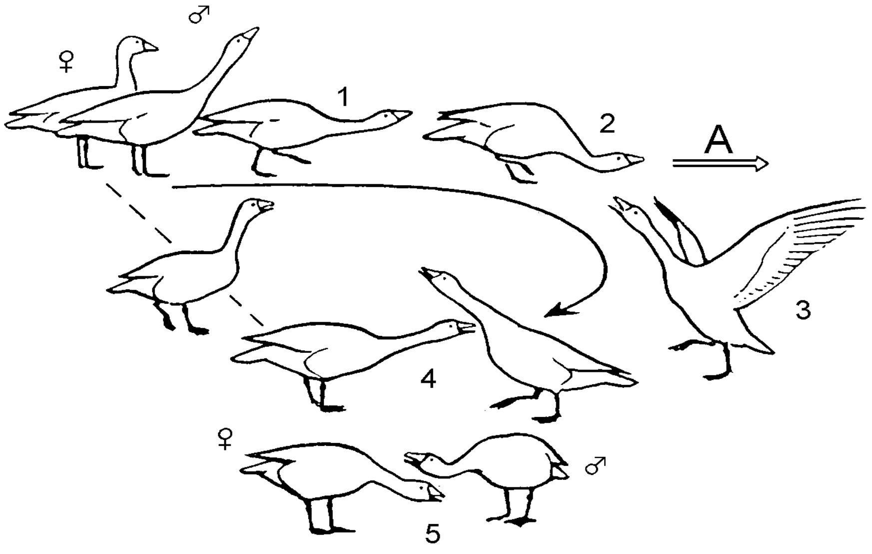


Fig. 1: Triumph ceremony involving an aggressive encounter or threat (A) with birds standing at an angle (modified for Hawaiian Geese from Fischer 1965). Postures 1 and 2 contain aggressive-type elements.

(including fleeing from displaying male, stoic (= non-responsive) behavior, moderate, intermediate and exaggerated behavior as described for the male). Males never fled from females nor did they show stoic behavior. Hawaiian Geese being perhaps the most tame of waterfowl allowed observations within a few meters of the displaying birds. I used only data from pairs that I had observed displaying at least five times during the study period, resulting in 37 pairs being included in the analysis.

To identify the diurnal pattern and likely context of triumph ceremony events, 37 groups of varying flock size with 2 - 9 focal pairs each, were watched for 105 five-minute intervals over 4 days. The occurrence and intensity of each triumph ceremony was noted with information on the displaying pair, the context (food or social), total number of birds the focal pairs were associated with (flock size), location and presence or absence of people on the grounds.

Distance between partners

In the 1996 non-breeding season (May - October), the distance between goose partners was assessed each week (instantaneous point sampling method, Martin and Bateson 1986). Distances were estimated in goose-lengths (1 GL = ca. 50 cm). This resulted in 573 observations on 43 pairs; not all pairs were seen each week. I noted presence or absence of people and supplemental food. Since birds were closer to each other when food was present

($F = 6.4$, df = 1, $P < 0.02$), I only included distance data collected when no food was present ($n = 534$). Since the presence of people did not have an affect on the distance between partners ($F = 0.06$, df = 1, $P > 0.01$), and did not change over the season ($F = 1.35$, df = 24, $P > 0.2$), I took a distance mean of the raw data for each pair. I only included pairs that I had observed at least 5 times ($n = 34$). I then arranged the mean distance values into three classes; 1) 0 - 2.9 goose-lengths, 2) 3 - 4.5 goose-lengths, 3) 4.6 - 8 goose-lengths. I excluded distances greater than eight goose lengths ($n = 7$) because they biased the data.

Statistical approach

GLIM software (NAG 1993) was used for regression analysis and analysis of variance. A significant term caused a significant change in deviance when removed from the model; only significant terms were retained in the model. Interaction terms were removed from the model before testing significance levels of single terms. When single terms appeared in a significant interaction, they were retained in the model, regardless of significance. To test the significance of single parameters, t-tests were carried out on parameter estimates (Crawley 1993).

Triumph ceremony data was analyzed using a binomial error structure in GLIM, with the number of occurrences of a particular behavior defined as the y-variable and the total number of observations as the binomial denominator. Some of the data were overdispersed and because the denominators were unequal, this was controlled for by using William's procedure (Crawley 1993). After adjusting for overdispersion, F-values were used instead of χ^2-values. For plotting purposes data on proportions were arcsine transformed before calculating means. The number of observations between categories was compared by using G-tests (Crawley 1993). Data on proximity of partners was skewed to the left, therefore subsequent analyses of variance of the log transformed data were carried out in GLIM with a normal error structure.

Most comparisons of display behavior refer to the following classifications 1) the proportion of displays where females followed males when the display was performed on the move, 2) the proportion of displays where the male's display was more intense than the female's (a comparison, hereafter referred to as "overt male behavior"), 3) the proportion of female displays that matched the intensity of their mates' displays, and 4) the proportion of female responses that were stoic responses.

Bird age was classified as 1) young (1 - 5 years), 2) middle-aged (6 - 9 years) and 3) older (> 9 years) (adapted from Black and Owen 1995, also see Chapter 7). The combined age was a sum of both partner's age classes. Age difference was classified as 1) same age, 2) one year difference, and 3) more than one year difference.

Male Hawaiian Geese were larger (mean ± standard deviation: skull = 95.8 ± 2.3 mm, tarsus = 85.1 ± 2.8, $n = 150$) than females (mean ± standard deviation: skull = 91.3 ± 2.1, tarsus = 79.4 ± 2.4, $n = 125$; skull: $F = 275$, df = 1, $P < 0.00001$, tarsus: $F = 147$, df = 1, $P < 0.00001$). Since body weight varies with season and breeding status (U. Zillich pers.

comm.), I only used structural measures of size (skull and tarsus). Only measurements from fully grown birds were used. I calculated the first principal component (PC1) from these measures after Rising and Somers (1989). In the study population, PC1 accounted for 86.7% of the total variance of both measures. Each sex was assigned to one of three size categories. Mid-sized birds were those within half a standard deviation of the mean PC1 score, small birds below and large birds above this.

RESULTS

Diurnal pattern and context of social display

Frequency of social display varied throughout the day and decreased with flock size (Fig. 2a and b). In 38 % of the 5 minute behavioral samples at least one pair displayed. Of these, 18% displayed once, 10 % twice and 10 % more than twice. After controlling for time of day, none of the other potentially confounding variables affected the frequency of triumph ceremonies; i.e. presence or absence of people ($\chi^2 = 0.01$, df = 1, $P > 0.1$), presence or absence of food ($\chi^2 = 0.13$, df = 1, $P > 0.1$), weather (sunny, overcast or rainy: $\chi^2 = 1.3$, df = 2, $P > 0.1$). Behavioral intensities probably varied with context and time of day, but our data was too limited to control for this variation. The relative behavioral responses of the partners towards each other were considered to be relatively consistent.

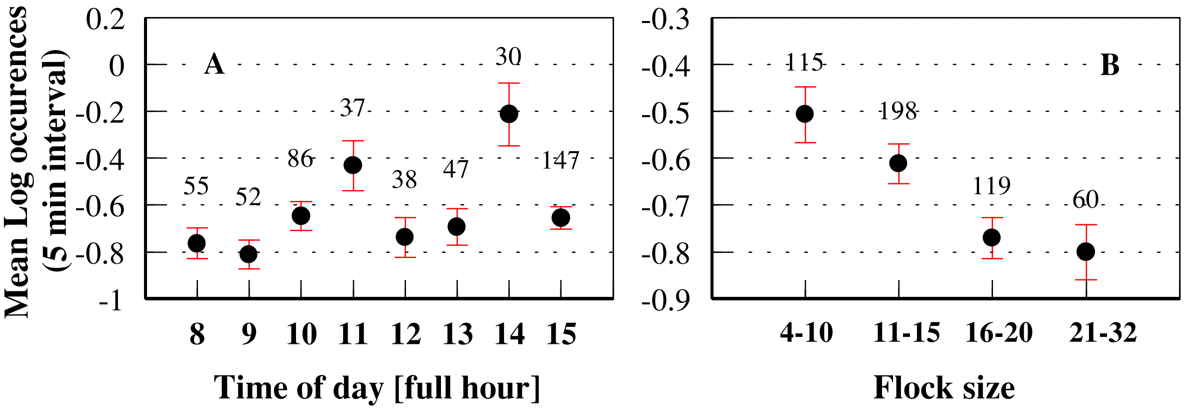


Fig. 2: Mean occurrences of triumph ceremonies in pairs observed in 5 minute sample intervals in relation to A. time of day and B. flock size. The frequency of triumph ceremonies displayed varied significantly with both flock size and time of day (flock size: $\chi^2 = 11.54$, df = 3, $P < 0.01$ and time of day: $\chi^2 = 25.78$, df = 7, $P < 0.001$). Standard errors and sample sizes (number of pairs observed in an interval) are indicated.

Displays were initiated by both sexes (males 42 %, females 56 %, 2 % simultaneous in 503 cases). When stationary, partners usually stood at an angle (96% angle, 4% parallel of 336 cases). Females were more likely to walk in front of males when displays were performed on the move (66% of 187 cases). Females fled from overt males on 11 occasions; four males bit females, 21 called in the females' ear (on 36 occasions) and 11 males slightly pecked females (on 16 occasions). Most displays were associated with a social (65%) rather than a food context (35%). Of the 352 displays with social context, 65 % were displayed after initiating an aggressive encounter, including 33 % after a threat without an actual attack.

Partner responses

Partners responded to each other's display in a variety of ways depending on the intensity of the display and the initiating sex. Males were more likely to escalate to higher intensity displays, whereas females often responded with less intense displays. For example, when males initiated a display bout with moderate displays, females usually responded with moderate displays (Fig 3a). When females initiated with moderate displays, however, males usually responded with moderate or intermediate displays (Fig. 3b). Similarly, when males initiated with exaggerated displays, most females responded with less intensive displays (Fig. 3a), but when females initiated with an exaggerated display, males always responded with exaggerated displays (Fig. 3b). Overall, the males' display was more intense than the females' (93 % males more intense, 7 % females more intense, in 264 cases).

Older males invested more in social display than younger males; older males initiated more displays and displayed more disproportionate, overt behavior than younger males (Fig. 4a, b). Older males, however, were not the most intense performers; the male display intensity did not increase with age. Females initiated triumph ceremonies more often with young and middle-aged males than with old males (Fig. 4a).

Female age was not correlated with female display intensity. Irrespective of their own age, females adjusted their effort in social display according to their partner's age, by initiating fewer displays and matching the intensity of male display less often with older males than with younger males (Fig. 4 a, b). Females in pairs with older males were also more likely to show stoic responses than females in pairs with younger males (Fig. 4c).

Females paired to large males showed more stoic behavior than females paired to smaller males (Fig. 5). Females in pairs with mid-sized males were most likely to follow males when social displays were performed on the move (Fig. 5).

The proportion of pairs with disproportionate, overt male behavior and those with female stoic responses increased with pair duration (Fig. 6) and combined age of partners (Fig. 7). Disproportionate, overt male behavior was more likely in pairs whose age differed by two or more years (Fig. 8).

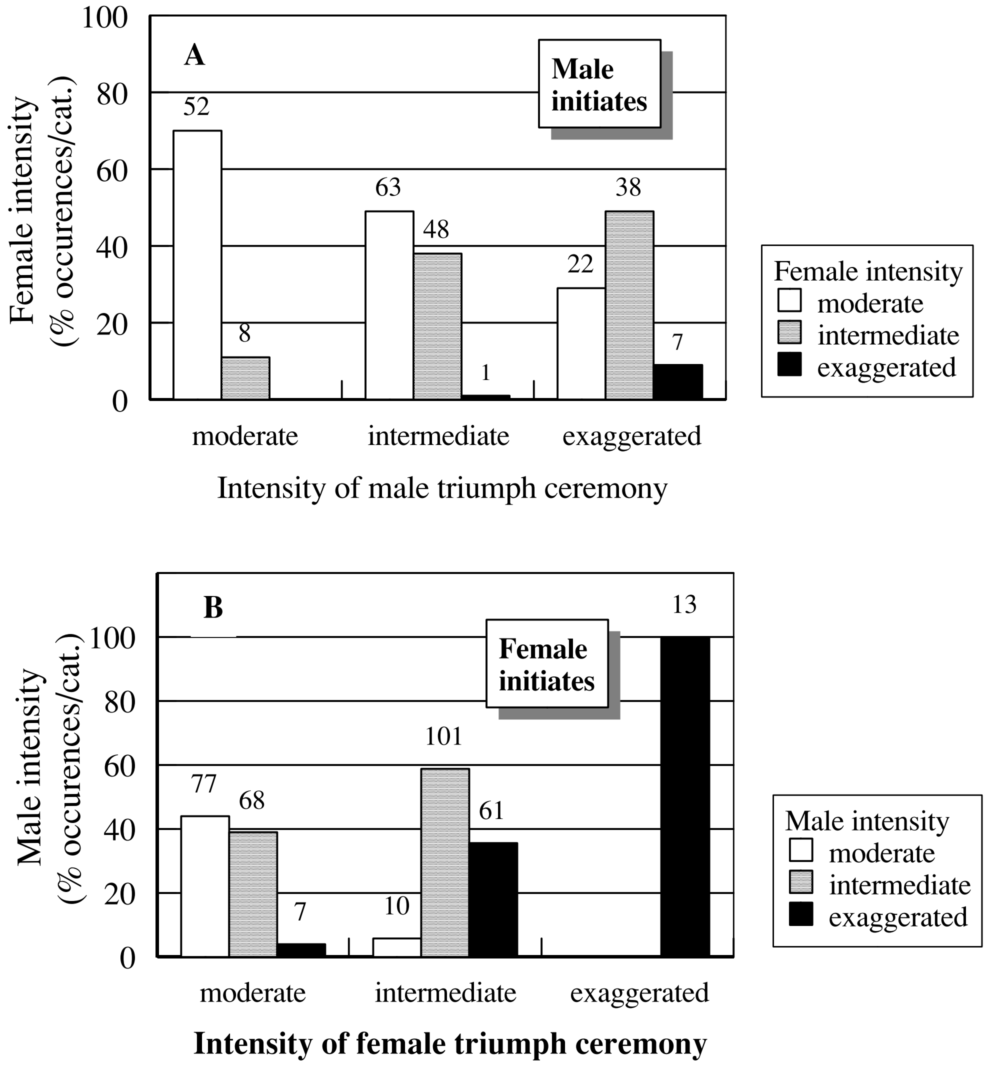


Fig. 3: Intensity of female behavior in relation to the intensity of the males' behavior A: when the male initiated and B: when the female initiated the triumph ceremony. Presented is the percentage of occurrences for each category of intensity, the number of occurrences is indicated. The intensity of the females and males triumph ceremony depended on each other (when the male initiates $G = 61.75$, $df = 4$, $P < 0.0001$ and when the female initiates: $G = 151.74$, $df = 4$, $P < 0.0001$). Female fleeing and female overt behavior were not included because they did not occur in males and account for the missing percentages.

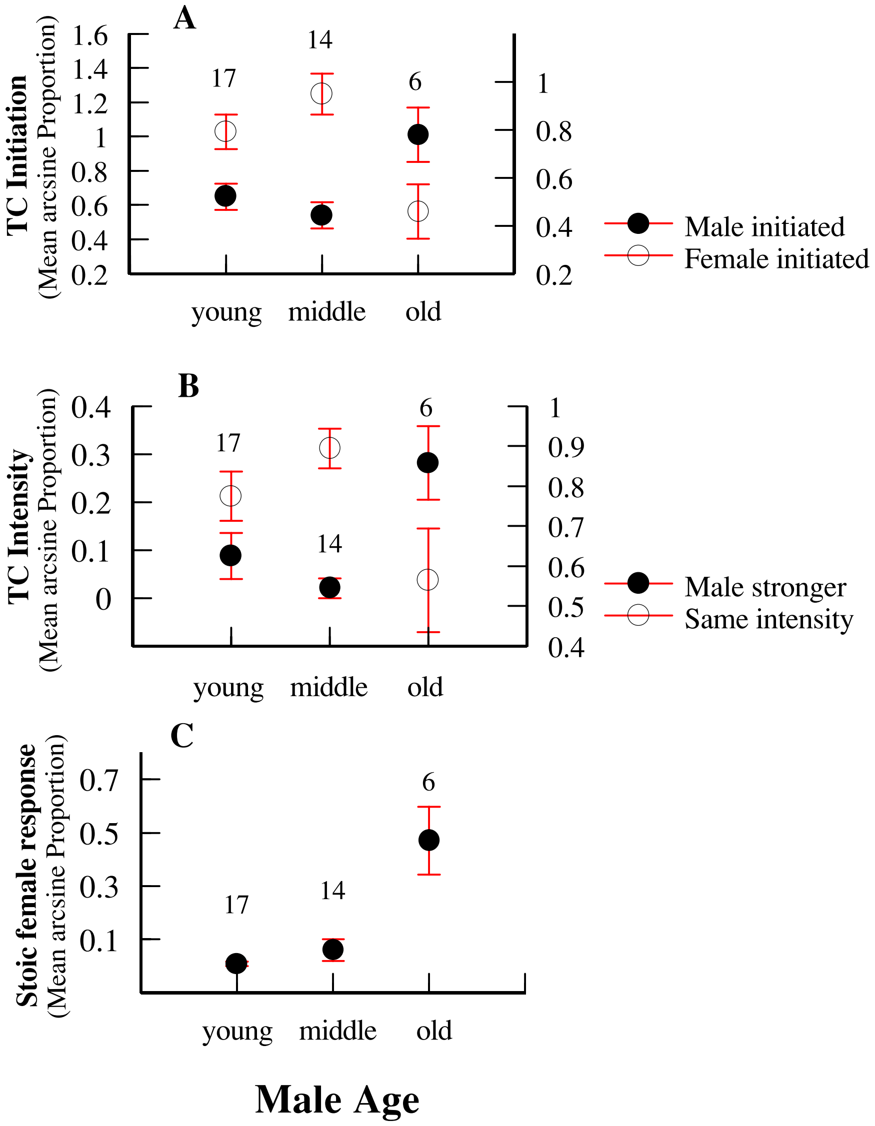


Fig. 4: The mean (arcsine) proportion of display behaviors in relation to male age. A. Old males initiated displays more often than young or middle aged males (F = 4.48, P < 0.02) and females with old males initiated less often (F = 4.88, P < 0.02). B. Old males were more likely to display a more intense triumph ceremony than their partner ($\chi^2 = 11.0$, $P < 0.005$) and pairs with old males had the lowest proportion of triumph ceremonies of same intensity ($\chi^2 = 24.67$, $P < 0.0001$). C. The proportion of stoic female response was highest with old males ($\chi^2 = 62.8$, $P < 0.0001$). Female age did not influence any of the behavioral categories. Df = 2 for all data presented. Standard errors and sample sizes are indicated.

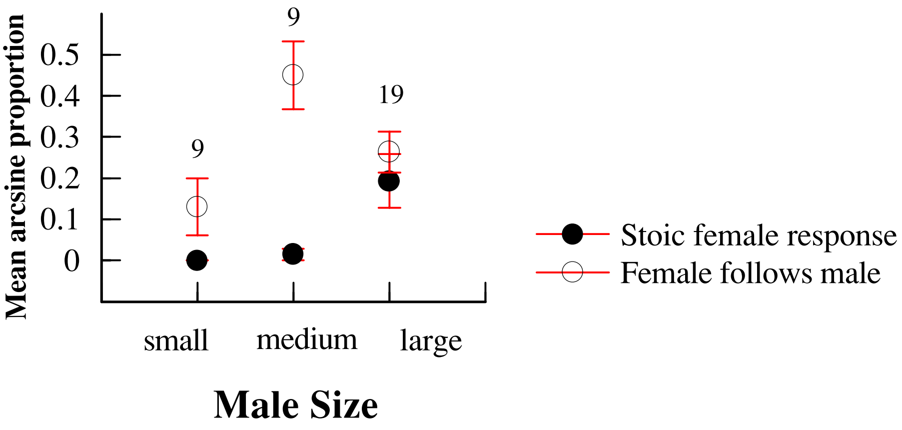


Fig. 5: The mean (arcsine) proportion of two behaviors in relation to male size. The males triumph ceremony was stronger than the females when the male was large (F = 5.6, df = 2, P < 0.01) and females followed medium sized males more often than small or large males ($\chi^2 = 6.25$, df = 2, P < 0.05). The size of the female did not influence the behavior of the pair. Standard errors and sample sizes are indicated.

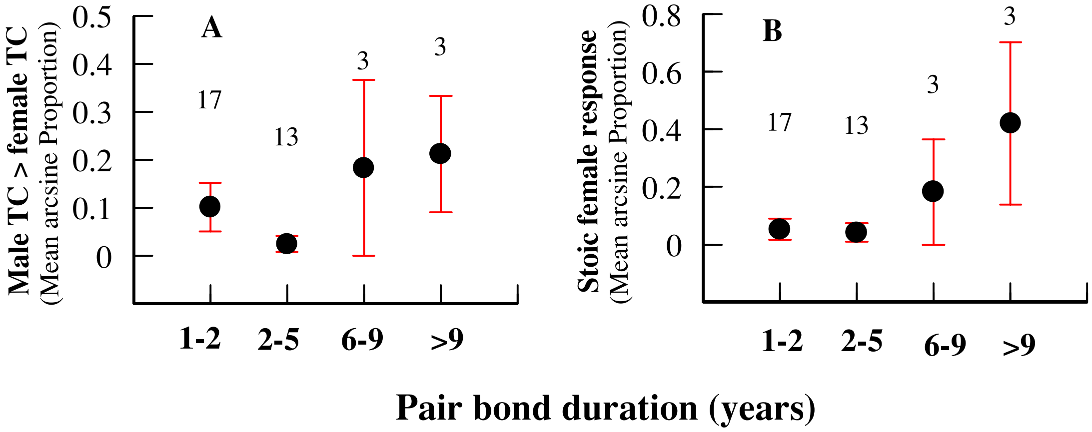


Fig. 6: The mean (arcsine) proportion of A. the males' triumph ceremony being more intense than the females and B. 'no response behavior' by the female in relation to pair bond duration. Males displayed more intense triumph ceremonies when they were paired to a female for more years ($\chi^2 = 12.1$, df = 4, P < 0.025), in particular males that were paired 2 - 5 years displayed the more intense triumph ceremony less often than males that were paired 6 - 9 years (t = 3.03, df = 14, P < 0.01) or more than 9 years (t = 2.3, df = 14, P < 0.05). Females showed more stoic responses when paired for longer ($\chi^2 = 3.64$, df = 4, P < 0.02). Females that were with their mate for 1 to 5 years showed less stoic behavior than birds that were together for more than 9 years (1 - 2 / > 9: t = 2.8, df = 18, P < 0.01 and 2 - 5 / > 9: t = 2.8, df = 14, P = 0.02). Standard errors and sample sizes are indicated.

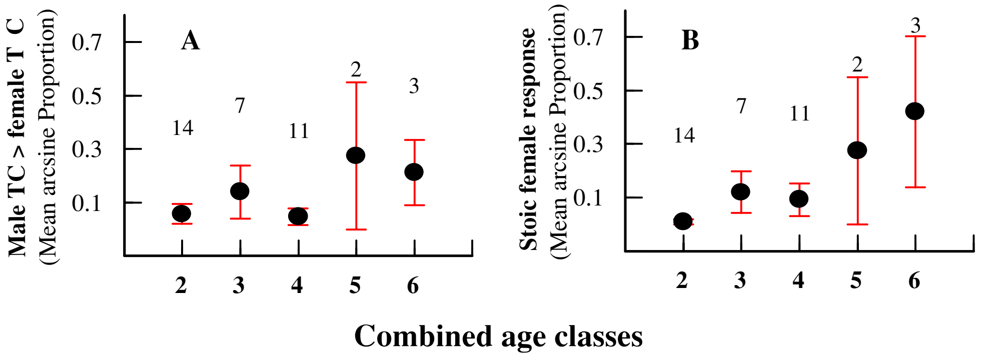


Fig. 7: The mean (arcsine) proportion of A. the males triumph ceremony intensity being stronger than the females and B. the stoic response by the female in relation to the combined age of the partners (A: $\chi^2 = 9.9$, df = 4, $P < 0.05$ and B: $F = 3.88$, df = 4, $P < 0.02$). Standard errors and sample sizes are indicated.

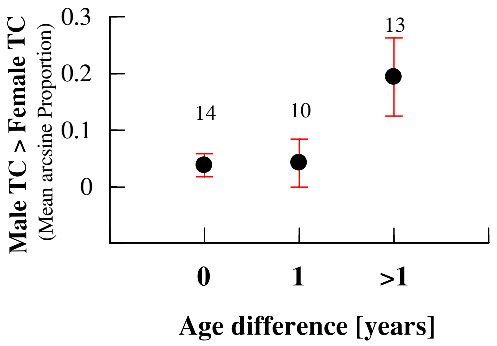


Fig. 8: Mean (arcsine) proportion of the males' triumph ceremony being more intense than the females in relation to the partners age difference in years ($\chi^2 = 11.88$, df = 2, $P < 0.005$). Males with a large age difference from their partner showed a higher proportion of more intense triumph ceremonies than males with a small age difference from their partner ($t = 3.0$, df = 25, $P < 0.001$). Standard errors and sample sizes are indicated.

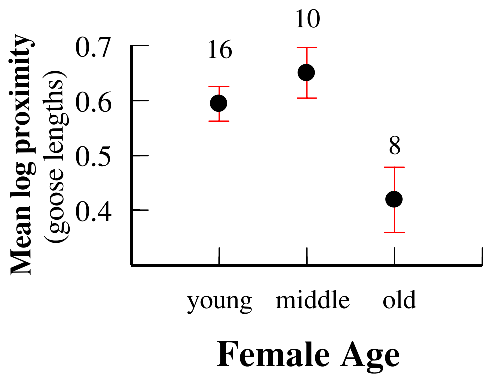


Fig. 9: The mean log proximity (in goose lengths) between partners in relation to female age. Old females were closer to their mates ($F = 4.78$, df = 2, $P < 0.02$). Male age did not influence proximity. Sample sizes and Standard errors are indicated.

To find out which parameters explained most variation in the social display behaviors, I fitted them all to the same model. None of the size parameters stayed in models that included age parameters, indicating that age effects were stronger than size effects. For some behaviors male age and pair bond duration and the interaction between both was significant (Tab. 1), indicating that age effects in males were most significant in long pair bond durations. Old males in long pair bonds initiated triumph ceremonies more often than their partners, and those pairs displayed less triumph ceremonies of the same intensity. Female age was not significant.

Table 1: GLIM model on the effect of male age and pair bond duration on various behaviors during triumph ceremonies. Female age had no effect. The x indicates an interaction term.

Behavior:		male initiates		female initiates		same TC intensity	
	df	F	P <	F	P <	F	P <
pair bond duration	3	3.88	0.02	3.6	0.05	3.2	n.s.
male age (years)	1	0.85	n.s.	0.79	n.s.	0.25	n.s.
male age x pair bond duration	3	4.07	0.02	3.69	0.05	3.57	0.05

Distance between partners

The distance between partners in the previous non-breeding season was a function of female age; older females were closer to their mates (Fig. 9). Variables such as male age, male and female size, pair duration, combined age or age disparity did not have an effect on proximity. Females followed males more during displays in pairs that maintained greater distances (Fig. 10). The females that followed their mates less during displays were closer to their mates and of mixed age (4 young, 2 middle-aged and 2 old).

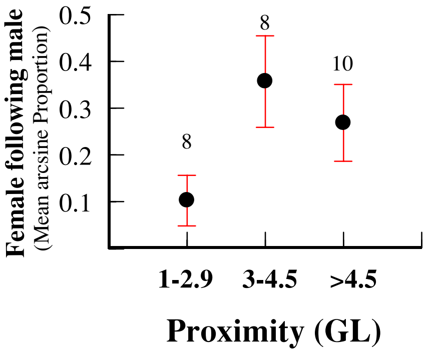


Fig. 10: The mean (arcsine) proportion of the female following the male during the triumph ceremony in relation to their proximity in the previous non- and pre-breeding season ($\chi^2 = 6.39$, df = 2, $P < 0.05$). In pairs that stayed within a mean of 2.9 goose lengths (GL's) of each other, males lead less often than in pairs that stayed at 3 - 4.5 GL's. Standard errors and sample sizes (number of pairs) are indicated.

Breeding success comparisons

Pairs with males that performed less intense displays than their mates were more likely to have a clutch of eggs (Fig. 11). Hatch success was lower in females displaying more stoic responses than females with fewer stoic responses (Fig. 12). There was no effect of distance on number of eggs laid or hatched.

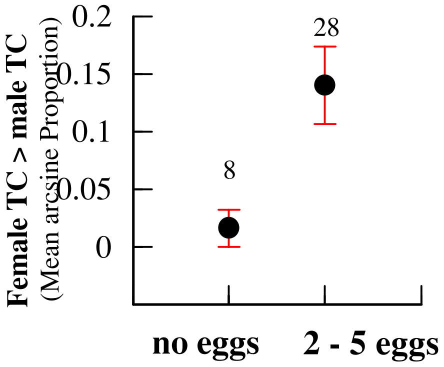


Fig. 11: The mean (arcsine) proportion of the female displaying a triumph ceremony of higher intensity than the male in relation to clutch production. Females that displayed more intense triumph ceremonies than their mates had a higher proportion of egg-laying ($\chi^2 = 6.1$, df = 1, $P < 0.025$).

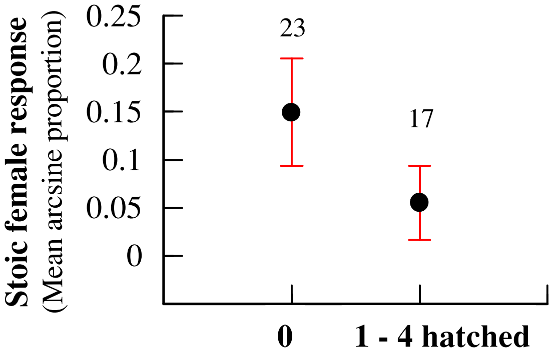


Fig. 12: Females that hatched one to four young had a lower mean (arcsine) proportion of non-responsiveness ($F = 4.7$, df = 4, $P < 0.05$). Standard errors and sample sizes are indicated.

DISCUSSION

Sex differences in display behavior

Males were generally more active in social display than their mates. They were liable to escalate into exaggerated displays when encouraged by the female, but some escalated without female encouragement. Some females were not able to cope with the overt aggressive nature of the display and fled. Others did not respond.

Males may display their strength and dominance to the female to ensure that she remains interested in him as a partner. Encouraging the male in his social display may be the females' tool to achieving her daily energy requirements, and surplus requirements for breeding. Through the display she encourages him to take action, to create space around them in which to forage in an uninterrupted fashion. This may be a visual signal to neighbors. Some females join their mates in physical encounters with neighbors (Black and Owen 1989b, Black *et al.* 1996). In Canada and Barnacle Geese, families and pairs had a higher success in aggressive encounters when the gander was involved. When separated from their mates, females were less successful in aggressive encounters, were threatened more frequently and spent less time feeding (Akesson and Raveling 1982, Black and Owen 1989b). Female Bewick's Swans paired to dominant males were able to spend more time feeding, thus increasing their reproductive fitness (Bowler 1996). Female geese without mates are at the bottom of the pecking order (Lamprecht 1986a, b).

There may be a trade-off for the female in terms of stress caused by overt male behavior and benefits she gains from male protection. When paired with a less overt male, females may have to encourage the male more to turn his signalling and protective behavior on. Females paired to overt males, on the other hand, may have to put up with more male harassment, but will hardly need to invest in encouraging responses and rarely need to join in any battles with neighbouring flock members.

Changes of pair synchrony with age and pair bond duration

After choosing a mate, animals in long-term pair bonds may adjust their behavior to the other so that the pair bond is strengthened (Nelson 1965, 1972, Pickering 1989). Mate familiarity may result in more efficient energy expenditure and resource procurement, yielding reproductive advantages. Some studies have shown that reproductive success declines when birds become old (reviewed in Black 1996), thus reducing the advantages of mate familiarity. In my study, the fine-tuning of pair members' cooperative, behavioral repertoire decreased with pair duration resulting in overt male behavior and stoic female responses. Old males showed a higher proportion of overt behavior and females paired to old males initiated less triumph ceremonies and showed more stoic responses.

Females might not respond to old males because reproductive success declines in old males whereas some old females had a high success (Chapter 7). Old males might be less attractive to females because they can no longer win aggressive encounters to secure feeding areas and nesting territories (Black and Owen 1995), thus explaining the stoic female response. Reproductive success initially increased with pair duration but then decreased, which could be attributed to a decline in male quality (Chapter 7). With the alternative being divorce, old males might try harder to maintain the pair bond by signalling more intensely.

Another explanation for the non-responsiveness of females paired to old males may be that females that have been with their mates for a long time might not need to encourage their mates anymore. The older males get, the more proficient they may become in the display. In Barnacle Geese the proportion of soft calls decreased with pair duration, whereas the proportion of louder calls increased (Black *et al.* 1996). The soft calls are thought to help maintain the pair bond (Hausberger and Black 1990); they might not be necessary in long-established bonds as older pairs are unlikely to divorce (Ens *et al.* 1996).

Old, experienced females were closest to their mates, but responded less to male overt behavior. Females might learn to stay close to their mate and benefit from more secure food resources and uninterupted feeding time thus increasing their probability of survival. Female Bewick's swans that stayed close to their mate won more aggressive encounters than females that kept a larger distance (Scott 1980). Old, more experienced females might be able to better cope with the males. Young females might keep a distance from the males to avoid stress.

Size

A large size disparity between partners did cause a behavioral disparity. Large males showed most overt behavior. Regardless of their own size, females paired to large males showed stoic responses and rarely initiated a display. By not responding, females avoided to encourage the male, thus reducing further stress. It is not clear why females endured large, overt males because, unlike in other waterfowl species, they did not have a higher reproductive success (Black 1996, Scott 1980, Chapter 7). Maybe no other mates were available.

Display behavior and reproductive success

Females that showed stoic responses to overt male behavior had a lower hatching success. In contrast, when the male displayed less intensely in relation to the female, pairs were more likely to have a clutch. Overt males may stress females and thus inhibit the flow of reproductive hormones (Greenberg and Wingfield 1987). Stressed females may not be able to accumulate sufficient body reserves for breeding and may, as a consequence, have to take longer incubation recesses in order to feed. By leaving the nest unprotected for longer periods, eggs are more likely to be predated or become chilled (Prop *et al.* 1984).

Could dominance explain differences in display behavior?

The intensity of the triumph ceremony appears to change with dominance status. In geese, families are dominant over pairs and singles (Black and Owen 1989). Triumph ceremonies associated with aggressive encounters were more intense by ganders of families as compared to pairs and singles (Raveling 1970). In Bewick's swans more dominant birds displayed more intense ceremonies (Scott 1978), in addition, the display intensity was dependent on the dominance status of the opponent's rank.

It is likely that mates can assess each others' dominance rank during mate choice (Choudhury and Black 1993) and that when having the choice, they choose to pair with the higher ranking individual. One possible explanation for the variation in pair behavior in Hawaiian Geese may be that in terms of dominance a bird may be paired to a higher, lower or similar ranking mate. Dominance relationships within a pair might influence triumph ceremony behavior, and thus involve a demonstration of rank between partners (Scott 1978).

In cichlids, the size of the female relative to the male's, and her aggressiveness relative to his were predictors of pair stability (Lamprecht and Rebhan 1997). In agreement with the so-called parity hypothesis, pairs were compatible only when the female's aggressiveness compensated for her smaller size. Similar studies are needed for Hawaiian Geese, to explain the role of dominance and aggression in pair behavior.

Conclusion

Males and females varied the intensity of triumph ceremony displays according to their relative age, size and duration they were paired to a mate. Females that showed stoic responses to overt male behavior had a lower hatching success, maybe indicating a behavioral mis-match. Females that displayed more in relation to the male were more likely to have a clutch.

Future research

To further our understanding of the observed differences in pair behavior, studies on pair compatibility in relation to dominance rank within and between pairs are needed. Through measuring stress hormone levels in droppings, we could find out how stressed females of overt males are. Furthermore, we need more information on how the behavior between partners changes over their life time, and how this affects their life-time reproductive success. Finally, behavioral studies after partner change, e.g. after divorce or death of a partner, would reveal if the characteristics of a new partner influence an individuals' behavior.

SUMMARY

To test varying compatibility in Hawaiian Goose pair bonds, I studied the behavioral fine-tuning of partners in social displays in relation to the relative age, size and pair duration of partners as well as to the distance with which partners associated. Males were more active in the display than females. Males displayed more with increasing age and pair bond duration, females displayed less. Old, more experienced females stayed closest to their mates. Large males were overt, but females did not respond with the same behavior. Females that showed stoic responses to overt male behavior had a lower hatching success. In contrast, when the male displayed less intensely in relation to the female, pairs were more likely to have a clutch. Proximity between partners did not affect reproductive success or social display. Pair behaviour varied in relation to age, size and pair duration of the partners, and was linked to a pairs' reproductive success.

Chapter 9: Concluding remarks on reintroduction

Many non-migratory island species have become extinct or are threatened by extinction, the most prevalent causes being habitat alteration and the introduction of ground-dwelling predators (Magin *et al.* 1994). With the exception of small and remote islands, it is difficult to reverse habitat alteration, or to remove introduced ground predators entirely. Although faced with environmental and demographic stochasticity and loss of genetic variation (Caughley and Gunn 1996), some island species that are surviving today appear to have adapted to a changing environment. It is this plasticity, apparent in many species, that can be used to advantage when restoring threatened populations.

Hawaiian Geese are a prime example for this adaptability. They moved away from their release sites in dense vegetation to breeding areas in sparsely vegetated scrubland, where predator densities were lower. Birds released in the lowlands or at higher elevations moved to mid-elevation sites where average rainfall and subsequent food availability was highest. The geese adapted to new, introduced plant foods and prosper in habitats very different to those they originally evolved. Throughout their annual cycle, Hawaiian Geese use grasslands created by humans. There are signs that some species will evolve new behavior in response to environmental change (Goss-Custard and Sutherland 1997). Berthold's example on the new migratory pattern of blackcaps provides a fascinating example (Berthold *et al.* 1992). Historically, blackcaps overwintered in the Mediterranean and Africa, but some birds now spend their winters in Britain, where food is plentiful. In a similar fashion, the behavior we observe in reintroduced Hawaiian Geese may already be a result of an adaptive response to a changing environment.

Behavioral decision making by individuals has population consequences (Goss-Custard and Sutherland 1997) and may be of high importance for the conservation of a species. Individual Hawaiian Geese varied in their ability to exploit available resources and in their propensity to move. In terms of reproductive success, individuals that grew up in the wild performed better than the majority of released birds. Wild birds may have gained some experience in early life that released birds are lacking. In captivity, age and size differences of the partners affected a pair's behavioral compatibility, and ultimately their reproductive success. To manage the wild population of long-term monogamous species effectively, we have to consider not only individuals but partner combinations.

The Hawaiian Goose is among many bird species that have been released in areas where wild populations have declined or disappeared. The establishment of a self-sustaining population, based on the reintroduction of a species from captivity into the wild, has rarely been achieved in endangered species management. Beck *et al.* (1994) calculated an only 11 percent success rate for 145 reintroduction projects using captive-bred animals. Out of 13 reintroduction attempts of 10 endangered waterfowl species, only one has been successful (Table 1, Callaghan *in press a*). Reintroduction of captive-bred animals should only be undertaken if reasons for their endangered nature have been removed. The reason why many

Table 1. Fate of reintroduction projects for threatened waterfowl taxa (from *Anseriformes* Action Plan, Callaghan *in press a*).

Species/subspecies	Country	Success?*	Reference
Hawaiian Goose (*Branta sandvicensis)*	USA	No	Black & Banko (1994)
Aleutian Canada Goose (*Branta canadensis leucopareia)*	USA	Yes	Byrd *in press*
Lesser White-fronted Goose (*Anser erythropus)*	Sweden	No	Wilson & Stanley Price (1994)
Blue Duck (*Hymenolaimus malcorhynchos)*	New Zealand	No	Williams (1988)
Brown Teal (*Anas chlorotis)*	New Zealand	No	Williams & Dumbell (1996)
Hawaiian Duck (*Anas wyvilliana)*	USA	No	Browne *et al.* (1993)
Mexican Duck (*Anas diazi)*	USA	No	Wilson & Stanley Price (1994)
Marbled Teal (*Marmaronetta angustirostris)*	Pakistan	No	Green (1993b)
Ferruginous Duck (*Aythya nyroca)*	France	No	Callaghan (in press b)
	Italy	No	Callaghan (in press b)
	Spain	No	Callaghan (in press b)
White-headed Duck (*Oxyra leucocephala)*	Spain	No	Anstey (1989)
	Hungary	No	Anstey (1989)

**A project is considered successful when a self-sustaining wild population of 500 individuals or more was established (following Beck et al. 1994).*

reintroduction projects fail is that reintroduction criteria are not met (Black 1991, Kleiman *et al.* 1994). For example, when Hawaiian Geese were first reintroduced, all criteria seemed to be met, but today, with our increased knowledge, crucial environmental conditions criteria are not met (Table 2, Black 1998a).

On Hawaii and Maui, environmental conditions that limit population recovery, such as poor habitat quality and predation, were operating throughout my study, but some management efforts appeared to be successful. In Hawaii Volcanoes National Park, predator control and grassland management increased productivity. However, there was an indication that some habitats in the National Park may be saturated (also see Black *et al.* 1994). Hatching success declined with increasing population size, suggesting that the carrying capacity of some areas may be reached. To increase populations on Hawaii and Maui, management of the wild habitat with the goal of increasing carrying capacity, including grassland management and predator control, are the best way forward. The population on Kauai thrives on lowland pastures and, in absence of introduced mongooses, seems to recover without further releases (Banko *et al. in press*). Further releases into the current range of the species seem therefore less than prudent. The range of the population could, however, be expanded by reintroducing birds onto smaller, properly managed islands, such as Kahoolawe, Lanai or Niihau. Small islands seem ideal for reintroduction as they allow intensive management including the removal of introduced predators and subsequent monitoring.

Table 2: An assessment of the criteria for reintroduction/translocation for Hawaiian Geese for past and current perspectives (scale = 5 is best). From Black (1998a).

	1960s perspective	**1990s perspective**	**Comments/comparison**
Condition of species			
1 Need to augment wild popn.	Yes	Yes	Still declining?
2 Available stock	Yes	Yes	Improved/best available
3 No jeopardy to wild popn.	?	?	
Environmental conditions			
4 Causes of decline removed	Yes?	No	New evidence
5 Sufficient protected habitat	Yes?	No	New evidence
6 Unsaturated habitat	Yes	No	New evidence
Biopolitical conditions			
7 No negative impact for locals	No	No	Could benefit
8 Community support exists	1	4	Education needed
9 GOs/NGOs supportive/involved	Yes?	Yes	Improving
10 Conformity with all laws/regulations	Yes	Yes	
Biological and other resources			
11 Reintroduction technology known or in development	Yes	Yes	Still refining
12 Knowledge of species' biology/ecology	2	4	
13 Sufficient resources for program	No	No	
Recommended reintroduction/translocation?	Yes	No	Habitat enhancement, predator control and maximize genetic diversity

Well-known examples for the introduction of birds onto small islands come from New Zealand, where numerous bird species have been released into predator-free environments (e.g. Clout and Craig 1994).

The translocation of Hawaiian Geese to smaller, predator-free islands could be successful if natural food resources are available year round. The process of evaluating the carrying capacity of a habitat before release has been well documented for the Little spotted Kiwi in New Zealand (Jolly and Colbourne 1991), e.g. islands have to be protected and predator free, need to have abundant foraging and nesting habitat, and be of adequate size. An accelerated rate of climate change might effect populations on small islands more than on larger islands. Larger islands often have more varied microclimates that allow animals to move if conditions become unfavorable. The genetic diversity of a species needs to be maintained, to give it a chance to adapt to changing environmental conditions.

Recent discussions in conservation biology have been concerned with the contrast between strategies that focus upon species and those that focus on habitats or communities (Hutto *et al.* 1997, Seal *et al.* 1992). Although in many cases more species can be saved by protecting large areas of habitat, the ecosystem approach may not be effective in saving species or populations with precariously small numbers (Black 1998a). Furthermore, rare species that have adapted to man-made habitats would not receive any protection through the ecosystem approach. Endangered New Zealand Brown Teal, for example, inhabit ponds in pastoral habitat which is void of other threatened bird species, which represents a special challenge for conservation politics (Williams and Dumbell 1996). In a similar fashion, Hawaiian Geese use pastures existing of introduced grass species, that are not utilized by any other endemic island species. Managing pastures adjacent to nesting areas, however, is a rather quick and comparatively inexpensive means of providing Hawaiian Geese with food and, in addition, is beneficial for adjacent native ecosystems. Corridors with short grass sward serve as firebreaks and so protect native plant communities that are not adapted to fire. Although the restoration of native communities should remain a long-term goal, we can achieve much by pursuing new approaches to management.

MANAGEMENT RECOMMENDATIONS

The management of Hawaiian Goose habitat is of greatest importance for the survival of the species. The development of new predator control techniques is underway, involving aerial drops of poisoned bait to remove predators from large areas. I suggest that it may be even more important to provide the geese with long-term, sustainable, good quality forage. Conditions that would improve the birds' breeding success in the wild should be introduced. The main management recommendations from my work are:

1. Grazing pressure declined in grass taller than 11 cm. Mowing or grazing grass higher than 11 cm optimizes pastures for the geese.

2. The geese used some areas less during drought periods. Irrigation could be a useful management tool in drought periods, especially during the breeding season.

3. Geese grazed more in areas with grass sward than in areas with bunch grasses. Repeated mowing favors grass sward growth and reduces bunch grasses.

4. Geese grazed more in areas with plants high in protein. Fertilizer application is likely to improve pasture quality.

5. Carrying capacity of the wild habitat could be increased through grassland management.

6. Planting additional scrublands with Mamaki would provide additional forage.

7. Berry picking by people should only be allowed in areas not utilized by the geese.

8. Parental contact was important not only during rearing but after release. Whenever possible, extended parental contact should be incorporated in the reintroduction methodology.

9. Wild birds should be encouraged to nest in predator-free enclosures in wild habitat. Fostering additional goslings into families were both parents can fly could be explored as a way of increasing the wild population where necessary.

10. Hawaiian Goose pair members were compatible to a varying degree. For young birds to find a compatible mate, enough young birds have to be available to choose from. Concentration of management efforts in a few core areas would ensure that enough birds are recruited every year to allow mate choice.

Many of the results of my work have been incorporated into the U.S. Fish and Wildlife 'Nene Recovery Plan', which is currently being rewritten, and will set specific conservation objectives. Some of the lessons learned from this long-running reintroduction program hopefully will be relevant to the management of endangered species elsewhere. The longer I spent working on my thesis, the more questions arose, and there is clear scope and necessity for further research on the ecology and reintroduction of the Hawaiian Goose.

FUTURE RESEARCH

Research has contributed significantly to Hawaiian Goose conservation in the past (reviewed by Black 1998a) and should continue to be closely linked with the management of the species.

Predicting the consequences of habitat change and habitat loss on animal populations is important for making management recommendations. In recent times many conservation scientists have taken a modeling approach to predict changes, including interference between and depletion of food by foraging animals (Sutherland and Allport 1994, Goss-Custard *et al.* 1995, Percival *et al.* 1998). The young lava flows used by Hawaiian Geese for nesting and summer flocking, together with the associated grasslands are among the most variable habitats in the world, susceptible both to variable weather patterns and to frequent cover by new lava flows. A volcanic eruption could easily wipe out half or more of the current habitat, which makes the population at Hawaii Volcanoes National Park extremely vulnerable. Additional modeling would be useful to predict future scenarios and perhaps to increase carrying capacity in areas which are less likely to be covered by lava in the near future.

Studies on the survival and life-time reproductive success of Hawaiian Geese in Hawaii Volcanoes National Park are needed to find out how important the different rearing and release methods, release sites and dominance status are. To explain effectively the distribution of individuals, long-term studies of dominance relationships should be undertaken and the results incorporated into analyses of the movements of the birds. Social regulation of distribution and access to food and nest sites will contribute to determining how many Hawaiian Geese will fit within management areas.

Detailed observations on gosling foraging behavior, similar to my foraging studies on adult geese, are needed to ensure that grassland areas provide nutritious gosling food plants. Detailed nutritional analyses are necessary to identify which nutrients the plants are lacking, especially for young goslings. Low fertility soils contributed to the poor nutritional quality of the Kakapo's herbivorous diet (Powlesland *et al.* 1992). Most soils at Hawaii Volcanoes National Park are acidic, which makes them low in Calcium. Lack of Calcium in the soil and in plants may explain smaller clutch sizes at Hawaii Volcanoes National Park when compared to the less acidic Haleakala National Park. Lack of certain minerals in the food plants may also be responsible for poor gosling growth rates and survival. Furthermore, the importance of native food plants for Hawaiian Geese should be explored, including growth and feeding trials, as well as nutritional analysis of the food plants.

I conclude my thesis with the insight that biological systems are incredibly complex and that everything varies in a multidimensional way. In Hawaii, an individual's decision when and where to feed and to nest is complicated by an extremely fluctuating environment. Statistics helped me to understand some of this complexity but there is still much to be discovered!

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Diplomarbeit: Ökologie der Hawaiigans in verschiedenen Habitaten des Haleakala Nationalparks auf Maui (Hawaii/U.S.A).

Promotion: 1994 - 1999 über die Verhaltensökologie ausgewilderter Hawaiigänse (Universität Hannover). Wiederholte Forschungsaufenthalte in Hawaii, Datenanalyse beim Wildfowl & Wetlands Trust in Slimbridge, England.

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Werkvertrag zur Bestandserfassung der Brutvogelpopulation in Kiesgruben Oberschwabens (Bad Wurzach) an der Universität Hohenheim, Institut für Zoologie

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1993: Mitarbeit in der Resources Management Division des **Hawaii Volcanoes National Park.** Monitoring der Hawaiiganspopulation, Prädatorenkontrolle, Training von Mitarbeitern im Gebrauch einer neuen Datenerfassungsmethode

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Abhalten zahlreicher wissenschaftlicher und populärwissenschaftlicher **Vorträge**, Poster

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