The Galapagos hawk: an eco-geographical study with special reference to its systematic position. 1973

Vris, Tjitte de.
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THE GALAPAGOS HAWK

an eco-geographical study with special
reference to its systematic position

to Dr. W. G. Reeder

with my best greetings

THE GALAPAGOS HAWK

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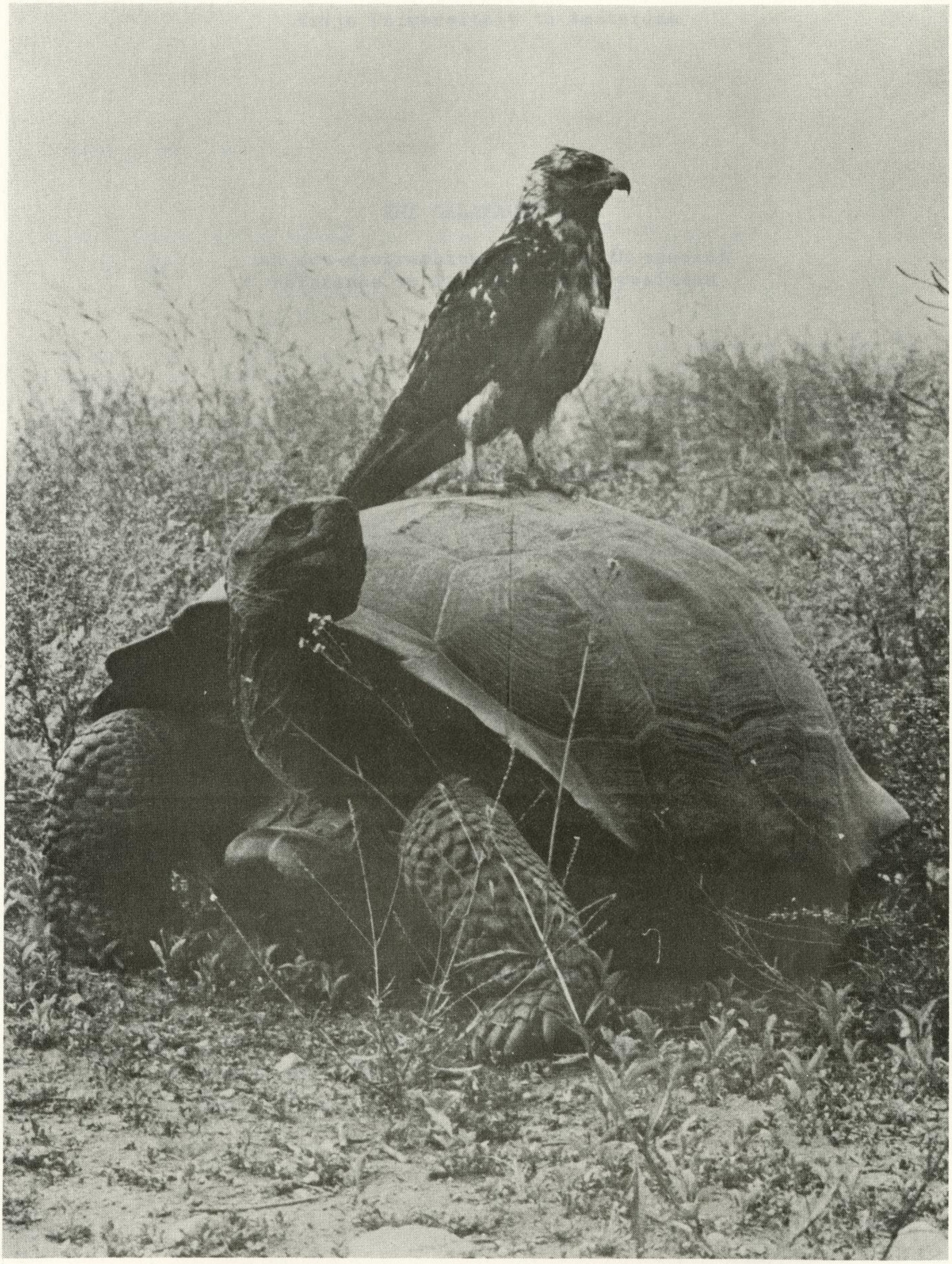

Vrije Universiteit te Amsterdam

THE GALAPAGOS HAWK

an eco-geographical study with special reference to its systematic position

academisch proefschrift

ter verkrijging van de graad van doctor
in de wiskunde en natuurwetenschappen aan de
Vrije Universiteit te Amsterdam,
op gezag van de rector magnificus
Mr. I.A. Diepenhorst,
hoogleraar in de faculteit der rechtsgeleerdheid,
in het openbaar te verdedigen
op woensdag 27 Juni 1973 te 13.30 uur
in het hoofdgebouw der universiteit, De Boelelaan 1105

door

Tjitte de Vries

geboren te Niawier

PROMOTOR: PROF. DR. K.H. VOOUS

STELLINGEN

I

Galapagos is geen Hof van Eden maar een Archipel van Disharmonie.

II

Veelmannerij bij de Galapagos Buizerd is een gevolg van de relatieve talrijkheid van kleine prooidieren.

III

Het verschil in lichaamsgrootte van het mannetje en het vrouwtje van de Galapagos Buizerd is een aanwijzing voor de juistheid van de hypothese van Reynolds.

R.T. Reynolds, 1972. Condor 74:191-197.

IV

De hypothese van Reynolds geeft geen verklaring voor het feit dat bij roofvogels juist het vrouwtje altijd groter is dan het mannetje.

V

Ashmole's mening, dat het voorkomen van verwante zeevogelsoorten op verschillende breedtezones mede veroorzaakt wordt door het feit dat geen twee nauw verwante soorten op dezelfde broedplaats populaties kunnen vormen, is in strijd met de door Harris geconstateerde reproductief geisoleerde populaties van dezelfde soort op hetzelfde eiland.

N.P. Ashmole, 1971. In D.S. Farner et al. Avian Biology I:223-286.
M.P. Harris, 1969. Proc. Calif. Acad. Sci. 37 (4):96-166.

VI

Het voorkomen van Geospiza conirostris op Española is veeleer een gevolg van de aanwezigheid van Mimosaceae dan van de afwezigheid van Geospiza magnirostris.

D. Lack, 1969. Evolution 23:252-263.

VII

Expansiedrift en eigenbelang van Europeanen zijn nog steeds oorzaak van het uitroeien van de inheemse bevolking van Amerika.

L. Bodard, 1971. Massacre on the Amazon. Stacey, London.

VIII

In verband met een doeltreffende natuurbescherming verdienen oecologische studies aan predatoren een grotere prioriteit.

IX

Bevordering van toerisme naar de Galapagos Eilanden kan een bijdrage vormen tot het natuurbehoud in dit Nationale Park van Ecuador.

X

Zolang de eis tot conformisme het controle instrument is waarover een bevoorrechte, op eigen belang gerichte, minderheid beschikt zijn hervormingen slechts door revoluties te bereiken.

C. Torres, 1969. Revolutie: christelijke opdracht. Bruna, Utrecht.

XI

Het feit dat revolutie zowel immorele omwenteling als constructieve verandering kan betekenen is een aanwijzing dat een harmonische oplossing voor sociale ongerechtigheid mogelijk is door middel van een gesprek.

XII

Het feit dat de voortplantingsphysiologie van zoogdieren een geringe rol toeschrijft aan het mannetje met betrekking tot het verzorgen van nakomelingschap, in tegenstelling tot die van vogels waarbij de enige activiteit waarvoor mannetjes niet zo goed zijn aangepast als vrouwtjes het leggen van eieren betreft, is een overkomelijke, doch vaak onderschatte, barriere voor de verwezenlijking van de emancipatie van de vrouw.

XIII

Kousbroeks kritiek op Aafjes' Ooka is verwant aan twisten omtrent de couleur locale van Melville's Oberlus.

XIV

De mogelijkheid om met de handschoen te promoveren dient niet a priori te worden afgewezen.

XV

De hersenen van Homo sapiens hebben de functie van overlevingsorgaan niet verloren.

Amsterdam, 27 Juni 1973 Tj. de Vries

para el Sr. Don Camilo Calapucha

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Roosbroecks kritiek op Keijses' boek is vermomd een twisten omtrent de confuse Insula van Melville's Oberlus.

XIV

De mogelijkheid om met de handschoen te promoveren dient niet à priori te worden uitgesloten.

XV

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Amsterdam, 27 Juni 1973 ,   Tj. de Vries

CONTENTS

INTRODUCTION

The Galapagos Islands are situated in the Pacific Ocean, under the Equator, some 600 miles (1000 kilometres) off the coast of Ecuador, to which country the Archipelago politically belongs. The total land-area consists of 7800 square kilometres, half of which comprises the island Isabela. Four other islands are in the range of 500-1000 km^2, eight are from 500-5 km^2, six from 5-1 km^2, forty smaller than 1 km^2, the rest (some 45) are considered exposed rocks (see Table 1 for further details, and English and Spanish names of the islands). The waters between the islands cover some 40.000 km^2. The distance from the most northern island, Darwin, to the most southern island, Española, is 350 km. The highest volcano is 1700 metres.

Oceanic islands are in an outstanding position when compared with continental conditions, since such isolated islands have relatively simple ecosystems. The presence of only one resident diurnal bird of prey in the Galapagos provides an unique opportunity to study the ecological niche which the hawk occupies here, particularly in relation to the other, mainly nocturnal avian predators, the Short-eared Owl *Asio flammeus galapagoensis* and the Barn Owl *Tyto alba punctatissima*. There are no indigenous land predators in the Galapagos.

Detailed food observations were undertaken and breeding cycles followed over several years (1966-1970) in order to obtain information on the variety of prey taken and on the relative importance of the various prey species to decide on the ecological place of the Galapagos Hawk. This ecological part of the study was mainly undertaken on the four islands Santa Fe, Española, Pinzón, and Santiago.

The Galapagos Islands, which are geologically speaking of recent volcanic origin (the oldest exposed rock sofar known dates back some two million years, in the Pliocene, Williams 1966), must have been colonized by hawks coming somewhere from the American continent. The Galapagos Hawk is obviously the result of a process of geographical species formation, but its direct relative on the American continent is not apparent and therefore unknown. Facts on food and hunting habits in conjunction with comparative plumage studies may demonstrate the similarities and distinctions with regard to other species of *Buteo*. The scanty data on continental species of *Buteo* are included for comparison and an attempt is made to link this endemic species with mainland forms.

There is a certain confusion regarding the common names of *Buteo* species. In this paper the established name Galapagos Hawk is used, which is considered a synonym for Galapagos Buzzard.

MATERIAL AND METHODS

The Charles Darwin Research Station at Academy Bay on Santa Cruz served as headquarters during my five years stay (October 1965 - February 1971) in the Archipelago. The square-rigged motor vessel Beagle II, local yachts and fishing boats made inter-island transportation possible. Base camps were made ashore, at times it was necessary to establish additional camps further inland; these have always been made outside the territory of the pair of hawks under study at the time.

Some of the field observations were made with the aid of binoculars of 8 x 30, 10 x 50 or a telescope of 30 x magnification. A hide was placed some 5-10 metres from the nests; in this way almost all prey items could be identified. I tried to have at least a spell of eight hours per day watching the nest, totalling 100 observation hours over a twelve day period. Transects for studying the density- activity pattern of potential prey species were checked as regularly as possible. Traps for rodent studies consisted of live-traps, indigenous rats Oryzomys bauri were released, Black Rats Rattus rattus killed.

The systematic study was undertaken in various museums; the wing measurements refer to the flattened wing from the bend of the folded wing to the tip of the longest primary.

Measurements for the claw (nail) are in straight line from the dorsal side of the base to the tip, for the bill from the cere to the tip.

DISTRIBUTION

3.1 Distribution, habitat

The Galapagos Hawk is endemic to the Galapagos Archipelago, where in previous times it was widely distributed on most islands except the northern smaller islands Genovesa, Wolf, and Darwin (see Figure 1). The hawk occurs in all areas from coast to summit, including such different topographical areas as the intertidal zone, barren lava fields, open shrub, open mixed deciduous-cactus forest, closed deciduous forest, and grassy areas. Nesting,however, is restricted to the dry zones.

The hawk is sedentary. Adults rarely leave their territory (one pair on Santa Fe was for five consecutive years encountered only within its territory). No ringing records have proved that birds have moved from one island to another, though concentrations of juvenile hawks and the occurrence of single stragglers suggest that some leave their natal island. However, three hawks ringed as juveniles on Santa Fe were breeding later on this same island.

Another indication that the hawks are attached to their original island is the absence of recolonization on islands where they have been exterminated, and where at present the circumstances are again suitable for breeding (Daphne, North Seymour). Stragglers to these islands are very uncommon.

Juvenile hawks were seen in the last 30 years only twice on Floreana, situated only 65 km away from Santa Fe and Española (pers. comm. Sr. Eliezer Cruz, Mrs. Margaret Wittmer).

In Academy Bay (Santa Cruz), 20 km away from Santa Fe, only two hawks were seen in five years (pers. comm. Miss Tui deRoy), which yet could have been birds from the few pairs breeding on northern Santa Cruz, rather than coming from Santa Fe.

One juvenile hawk was observed on Plaza Island on 21 June 1971 (pers. comm. M.P. Harris), the first definite record despite frequent visits of birdwatchers in the last years to this island. Observations are known of hawks flying from Rábida to Santiago, a distance of 5 km; while hawks nesting on Gardner-near Hood used a part of Española as hunting ground, flying over a bay of 1 km.

3.2 Decline, present status

Due to human persecution the hawk vanished from Floreana, San Cristóbal, Baltra, North Seymour, and Daphne, while on Santa Cruz its

presence has been reduced to a few pairs.
It must be admitted that no definite former record for Floreana exists, but this was the first island to be colonized by man (in 1832), and it seems likely that its hawk population was exterminated soon afterwards.
Hawks were still abundant on Santa Cruz during the expedition of the California Academy of Sciences in 1905/06 ("Indefatigable was the center of abundance of the Galapagos Hawk.." Gifford, 1919). During the first years after human settlement at Santa Cruz (in 1926) hawks were killed in great numbers; some colonists killed up to 70 daily (pers. comm. A. Rambech). It was said that during the first two years at an average some 20 birds a day were easily killed with a stick, which would mean close to 15.000 birds.

Exaggerated as this might seem, 250 breeding pairs in those days on Santa Cruz seems not unlikely; at present 2 pairs are left. The comparative scarcity of the species on the largest island (Isabela) cannot wholly be attributed to direct activity by man. Isabela is composed of five large shield-volcanoes and has a permanent human settlement on the southern part only. However, cats have been introduced and have run wild at least for half a century, covering now the whole of the island. It is likely that this land predator competes with the hawk for food.
Lizards, doves (and probably centipedes) are now scarce; indigenous rats have never been recorded on this island.

The total hawk population throughout the Galapagos Islands amounted in 1970 to 130 pairs, divided over the nine islands were they still occur as follows:

Santa Fe		17 pairs	(7 polyandric)
Española		10	1 "
Pinzón		5	1 "
Santiago	approx.	50	many "
Santa Cruz		2	
Isabela	approx.	25	
Fernandina		10	
Pinta		6	
Marchena		5	

The Galapagos Hawk has been protected by Ecuadorian law since 1959, and is listed on a white sheet in the Red Data Book of I.U.C.N. (1966).

PLUMAGE AND DIMORPHISM

4.1 Plumage, moult

The adult plumage is dark-brown to sooty black; with increasing age birds appear to become sooty black, rather than dark-brown. The colour of the plumage in both sexes is alike. The feathers of mantle, back, and belly are edged with paler brown of buff, with white bases showing only when plumage is in disorder.

The tail is dark-brown to grey-brown with buff and white (inner flag is lighter than outer flag) and has 9-10 dark-brown bands. Primaries and secundaries have 6-7 dark-brown bands, forming in flight a contrast with the dark-brown wing coverts.

Juveniles are dark-brown, much variegated with buff and white, giving the bird a spotted and sometimes streaked appearance. Recently fledged young have the ground-colour chestnut brown rather than buff and white, which appears after half a year as a result of fading rather than of moult. Between the second and third year a 'sub-adult' stage is distinguishable in which the head is already dark-brown, breast- and belly-feathers have considerably more brown than in earlier stages, but buff and white are still present.
Males were noticed breeding in this 'sub-adult' plumage.
The adult plumage is now gradually appearing through when body moult is slowly progressing. Some primaries and tail-feathers have probably been replaced three times before the definitive stage of plumage has been reached.

For detailed plumage description, see Friedmann (1950).

In the juvenile plumage moult of the primaries is descending. In adults it is more complicated and often primaries 9 and 10 (p. 9 and p. 10) are still old while p. 8, p. 1, and p. 2 are new and p. 3-7 old (counting from the inner-most primary as no. 1). It seems, as pointed out by Stresemann & Stresemann (1966) for other hawks, that in adults the outer primaries do not moult regularly and what appears to be two centres of moult actually might represent the same cycle in which p. 8 (7)-10 are postponed. The moult of the tail-feathers is complex and often irregular; in some cases according to the formula 1, 2, 6, -, -, -, or 1, 6, 2, -, -, -, (counting from central outwards). Moult of secondaries and body-feathers were not studied in detail.

4.2 Sexual size dimorphism

When wing length is taken as a measurement to express difference in size, the male Galapagos Hawk is 91 per cent the size of the female (average of male 388 mm, average of female 425 mm). In weight the proportion is 73 per cent (male 1000 grs, female 1366 grs); in length of hind claw (as a measure of killing power) this is 81 per cent (male 29.0 mm, female 32.6 mm).

Sexual dimorphism in birds of prey has been discussed by several authors (Amadon 1959, Cade 1960, Perdeck 1960, Selander 1966, Storer 1966, Reynolds 1972). Sexual dimorphism may be considered to be the result of sexual selection; it might become more divergent through ecological factors. In birds of prey body size generally reflects predation power. The difference in size of the sexes contributes to a more efficient use of the available prey and alleviates inter-sexual competition for food. Natural selection likely favoured the female to become the larger of the sexual partners, probably due to mastering the male at critical periods. In many species specialized greeting ceremonies occur often before copulation, as well as just before and at the time the male arrives with prey on the nest. It seems obvious that these are related to preventing the aggressive drive from becoming violent, since in other hawks it has been observed that males hastily drop the prey at the nest (as if being wary for the female in this situation) and harriers have food change-overs away from the nest, in the air. In Peregrine Falcons greeting ceremonies at the nest occur as well as food change-overs in the air (Cade 1960).

In addition to differences in prey size corresponding with the larger size of the female there must be also differences in hunting methods, but this cannot always be easily detected.

During my study I found that female Galapagos Hawks catch more centipedes and feed more on carrion than males, and this might indicate that the size and structure of the male renders it in a more favourable feeding position than the female. According to this view male Galapagos Hawks are then in a better competitive situation when the habitat as a whole is taken into consideration. If the above holds true then the larger size of the female could be explained by her dominating role in keeping the pair bond, while polyandry, which in this species often occurs, could result from direct inter-sexual competition for food, since more males would survive.

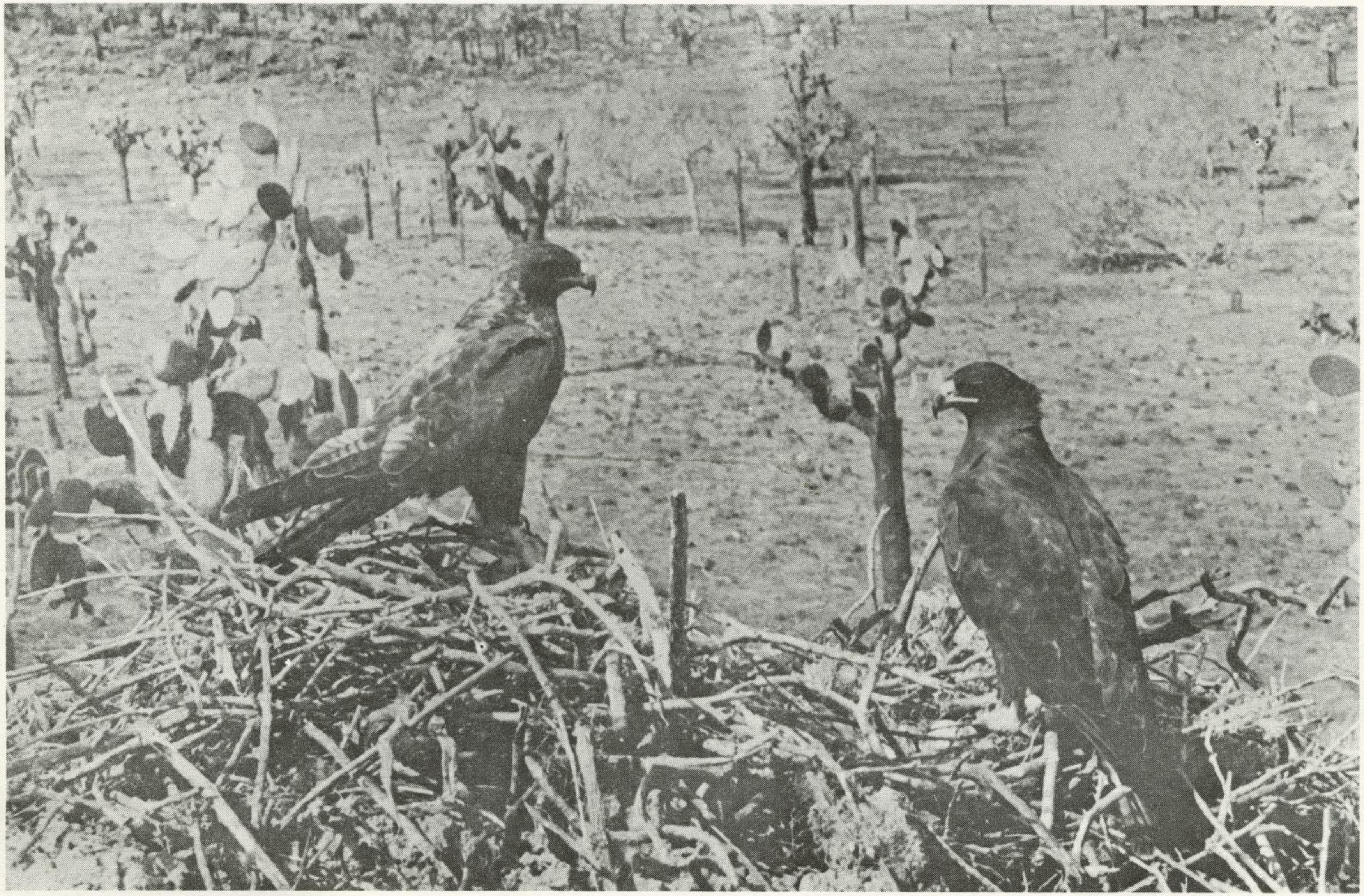
The fact that the Galapagos Hawk is a sedentary bird is certainly of importance in this respect. A pair bond of a long duration in the same territory diminishes the effect of inter-male competition for territories, since an established pair will attack jointly any persistent intruder.

BREEDING BIOLOGY

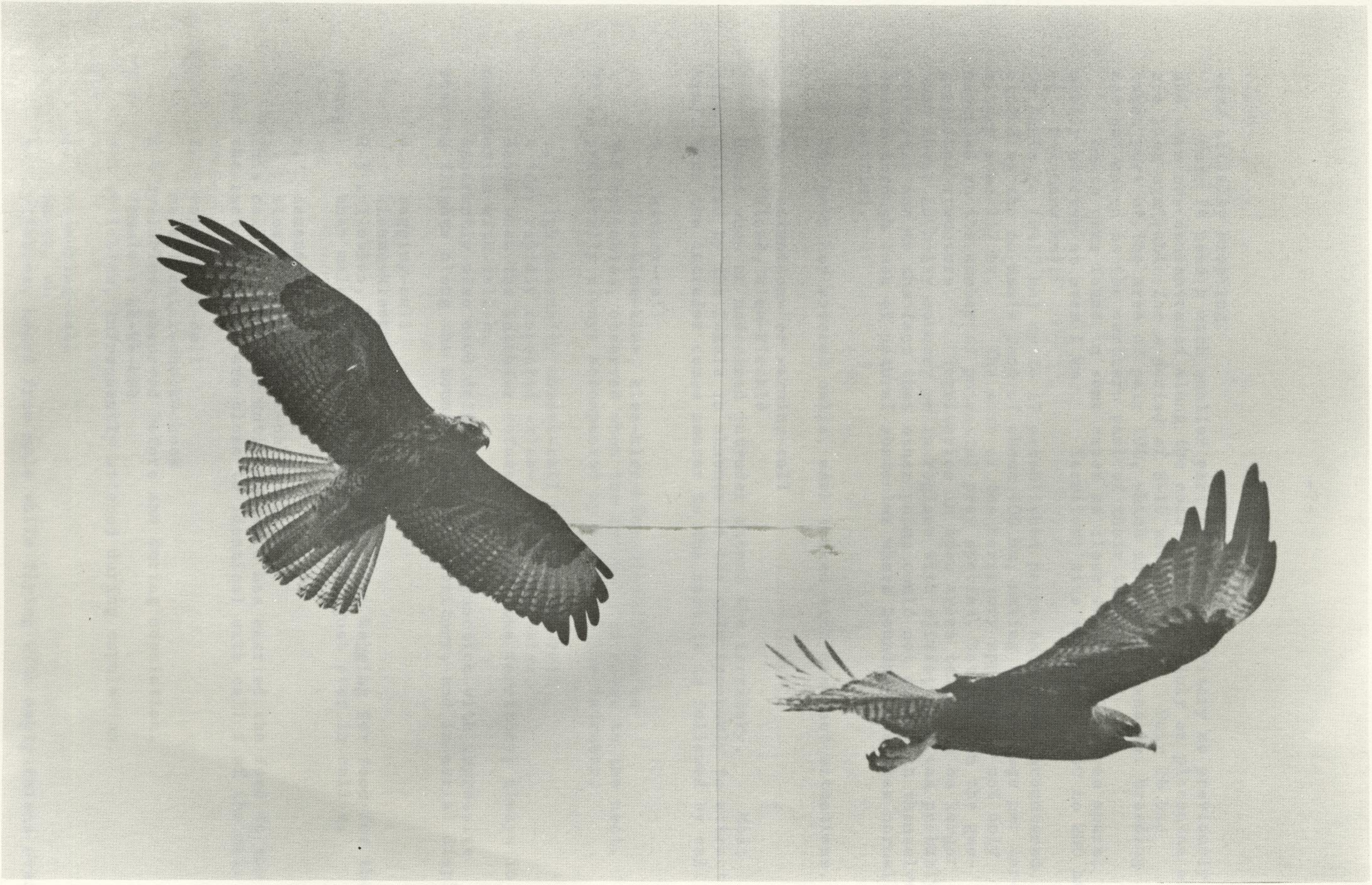
5.1 Territory, call

The Galapagos Hawk is extremely sedentary, and defends its area even outside the actual breeding period. Neighbours have been seen fighting furiously on many occassions.
One instance was observed on Santa Fe (31 August 1969), where the boundary was disputed at a point where a cliff was parted at a dry streambed.
Both were polyandric pairs, one being diandric, the other triandric.
It was during the actual breeding period (pair 5 had eggs in August and November, pair 44 in September). The three hawks of pair 44 would stay in the air more or less on the same spot, while the pair of four (pair 5) would line up and attack, one after the other, in the centre of the three soaring hawks rather than let it come to a direct individual fight.
This was repeated twice.
By the third time one was gripped by the claws and 'wheeled' down, loosing the grip some twenty metres above the ground. All ended up with the four sitting on the cliff on one side of the streambed and the three of the other pair on the other side, all loudly screaming with the attack- and exciting-call. However, during the breeding period most pairs have been observed living peacefully near each other, their territories apparently having established the boundaries, respected by both pairs. Most boundaries were formed by natural obstacles or barriers (cliff, hill) or in any case included some strategic points (e.g. rocky outcrop).

Any other passing hawk, adult as well as juvenile, was immediately attacked at entering the territory. When the male was unable to accomplish the task alone the female left the nest and joined the male in driving the intruder away. At times an unfortunate intruder might subsequently be attacked by two or three different pairs in places where occupied territories are close together and no free flyway was left to flee.
I formed the opinion that these territories were elastic and adjusted to the available prey and number of breeding hawks present.
The following instances clearly demonstrates this view. In 1969 the total number of established pairs on Santa Fe was 17 (see Figure 2), of which 13 were actually breeding; only in the north-eastern and south central part some 'no man's land' remained where often juveniles were encountered. In 1970 only 8 pairs (of which 7 were the same as in 1969)



Open cactus forest with pair 33 (female left) at its nest, Santa Fe



A juvenile (left) and an adult hawk in flight were actually breeding.

Pair 14 used a much smaller part of their territory as previously and were now concentrated along the coast, living mainly on placentae of sea lion available for a period of 8-10 weeks only. Pair 24 had taken part of the area of pair 104, which on its turn was not breeding and had moved to the northern part of their territory.

Nests were found in some cases as close as 300-400 metres apart, mostly however at over 1 km. Territory size varied from 50 to 200 ha ($\frac{1}{2}$ - 2 square km).
On Santa Fe (2413 ha) up to 17 established pairs have been encountered, excluding the no man's land of about 400 ha, making the average per territory some 117 ha. The size of the territory apparently not only depended on the number of potential prey species, but also on the geographical structure. Territories in open areas tended to be larger than those in hilly country or in regions with cliffs; this was probably primarily due to the fact that other pairs could not establish themselves nearer through lack of natural obstacles where boundary disputes normally were settled.

The hawk has several calls, each linked with distinct situations.

a. attention- or warning-call
kleeè, klee-kleeklè
Heard when an undesired intruder enters the territory. Most often uttered by the female in absence of the male (probably to attract him). When the intruder comes nearer to the nest it is followed by call b.

b. attack-call
klee-klee-klee, klee-klee-klee-klee-klee-klee
3-6 syllables, observed when the intruder is close to the nest. It is practically always accompanied by diving at the intruder.

c. high intensity threat-call or exciting-call
A very rapidly repeated -klee-, 12-15 syllables.
Heard when the intruder refuses to leave the territory; always in combination with call b.
Apparently also used defensively in conjunction with impressive soaring flights along the boundary of the territory, and in aerial display.

d. begging-call
kleeuu-kleeuu
2-3 syllables, heard from the female when begging for food for the young. When male nears with prey this call goes over in call e.

e. demanding-call
kleeuu-kleeuu-chick-chick-chick
This call last as long until the male has carried the food to the nest; the last syllables are close to identical with call f of the male

f. copulation-call
male : chick-chock-chock
2-4 syllables, observed before and during copulation.
female : kè-kè-kèè
2-4 syllables, infrequently uttered during copulation.

g. reasuring-call
uh-uh, uh
1-2 syllables, heard from male while flying with empty talons over

the nest. Mostly after the female has been calling a longtime, begging for food.

h. low intensity threat-call
be-be, or mu-me-be

2-3 syllables, a very soft purring or muttering.
Uttered in 'frozen position', often in bow-posture, by an individual (adult as well as juvenile) when feeding in a large flock. It seems to express a low intensity threat in a social encounter when individual dominance is still unsettled.

i. hunger-call
-klee-

2-10 syllables; higher pitched than of adults.
Uttered by young and juveniles begging for food.

j. stress-call
pree-pree-

Uttered in a long sequence by young exposed to strong sunshine.
A call not much dissimilar is used by juveniles being unable to escape quickly when attacked by adults.

For details of certain calls see the sonagrams in figure 3.

5.2 Display, pair formation, pair bond, polyandry

The aerial display is a simple soaring-circling-spiral flight, the male, recognized by its smaller size and more slender appearance, often in a position above the female. The male sometimes dives at the female which then usually turns around to present her claws.

Both soar and circle at times with dangling claws, the male eventually coming as close to the female as if trying to touch her. All of a sudden the male may start a series of 2-5 undulating flights, with or without the exciting-call. The female then is the first to glide downwards, settling in the top of a cactus-tree or on a rocky outcrop. The male follows also gliding, or in a criss-cross slant when coming from great height with up-turned wings hanging backwards in the air, or in a plunging dive with closed wings, striking near or straight on top of the female, and copulation may follow. In many cases the display in the air was not immediately followed by copulation so aerial display may be more an advertisement to surrounding hawks, indicating that the area is occupied, rather than being only a necessary prelude for copulation. Before copulation male and female were usually observed sitting on the ground or in a tree, the male presenting himself to the female in a characteristic 'bow-posture' with a special call.
The female paid no obvious attention, or flattened herself slightly, or in other instances 'froze' for a while in bow-posture, apparently indicating peacefulness, after which copulation followed, lasting 3-6 seconds. This performance was observed at least a hundred times. In certain pairs, which did not yet have eggs, copulation was observed 5-10 times a day. In diandric or triandric pairs often all males copulated with the female, one after the other in a period of five minutes or less. Where pairs have nested side by side for many years, aerial display is less frequent presumably because territorial boundaries are well known, but any stranger straying into a territory causes an immediate increase in display. This kind of behaviour apparently is not closely associated with sexual display. In one instance where a certain territory on Santa Fe had been occupied in 1965, 1966, and a pair with a

deserted egg (nest 5) was observed in March 1967, no birds were seen in 1968 and not until April 1969 was an adult seen, whilst by the end of May two adults (male and female) were present, and nest 5 encountered with fresh nest material. By the end of July the adult male was gone and not seen further, but two males in sub-adult plumage were present. Since the same nest was used it is possible that the males joined the same female, in which case the female decided upon the locality of the nest-site.

In the third week of August a clutch of 2 eggs was laid. In September a third male in sub-adult plumage joined this pair. The nest was not successful, one egg disappeared, the other was abandoned by the end of September (a close to hatching embryo was inside this egg). In November a clutch of 3 eggs was laid in nest 67 (the same territory), and this time the triandric pair raised one young.

It is certain that in this polyandric pair the other males were not young fledged from the same nest and subsequently joining their parents. Polyandric pairs were more frequent in dense hawk populations than in places with relatively few breeding pairs : on Santiago 8 out of 11 (73%), on Santa Fe 7 out of 17 (41%), on Pinzón 1 out of 5 (20%), and on Española 1 out of 10 (10%). This may have been the result of a stronger inter-sexual competition for food in places with many hawks, aggravated by the sedentariness of the birds.
The Galapagos Hawk probably mates for life, and even the pair bond in polyandric pairs was found to last for several years. One monogamic pair on Santa Fe was encountered for five consecutive years in the same territory. Two diandric pairs, which were all ringed, remained together for the three years they were under observation.

Polygamy is known to occur only in a few other birds of prey. It seems not uncommon in Hen Harriers Circus cyaneus, but in this species concerns polygyny. For the Hen Harrier Brown & Amadon (1968) state: "Bigamy and even polygamy occurs and has an adverse effect on breeding success". That polyandry in the Galapagos Hawk has a positive effect on the breeding success is probably only true in periods of low prey densities. During the breeding period practically all food is gathered by the male. In diandric pairs both males share this task, but in spite of that I did not find the prey frequency (prey items per time unit) doubled. In defending their territory polyandric pairs were usually in an advantage in comparison to monogamic pairs, but I know of one or two instances in which a monogamic pair was the more successful, as will be discussed later.

5.3 Nest, nest-site, egg, clutch-size, incubation

All nest found were bulky affairs, with sticks (often branches of Bursera or drift-wood of mangrove) of 0.5 metre or up to one metre in length, lined with small twigs, grass, lichens, and often with green leaves (Rhizophora, Scalesia, Castela). Nests were normally 50 cm - 1 m high, 80 cm - 1 m in diameter, in some extreme cases up to 3 metre high; obviously the larger nests had been in use for many seasons. The inner-diameter of the nest usually was about 30 cm. larger, generally 35-40 cm, on Española. Nests were constructed in trees or on rocky outcrops, in practically all cases located in such a position that the breeding bird could overlook a large part of its territory. A still higher vantage point was alway present in the vicinity (the only noted exception to this rule was an old deserted nest on Eden, situated at the sheer summit of this islet).

On Santa Fe, Española, and Pinzón all nests (a total of some 150)

were ground-nests, constructed on rocky outcrops. On Santa Cruz, Isabela, Fernandina, Santiago, Pinta, and Marchena most nests were tree-nests, ground-nests occurred at places of barren lava only. Trees used as nest-sites were mainly 'Palo Santo' Bursera graveolens, the commonest tree in the arid zone. Sometimes Opuntia, Erythrina, Pisonia, Piscidia, Psidium, and Zanthoxylum were used.
Within a territory the same pair used various nests in different breeding seasons, sometimes over 10 nests were found in the same territory. Change of nest was more frequent in a territory with ground-nests than in a territory with tree-nests, in a few instances a change of tree-nest occurred because the tree had fallen down or the nest had become heavily overgrown with a milkweed Sarcostemma angustissima. Mostly before the breeding period several nests were rebuilt and new nests constructed. The reason for this behaviour was not clear. Surprisingly few actual nest constructing was observed. Only once it was seen that a male broke a branch of a Bursera tree and brought it to the nest. I assume that half finished new nests were constructions of males, since they often used these sites as outlook posts, and that it was actually the female choosing eventually the site for breeding, but no direct evidence exists for this supposition.

Nests were kept very neat and clean during the breeding period, prey remains and pellets were removed by both adults, while regularly fresh nest material was brought, in most cases by the female. The use of green leaves at the nest may be of importance primarily as a source of humidity, rather than having the function of shading the eggs (see Amadon 1965), since in all cases observed the leaves were put near and not on top of the eggs. Moreover, leaves were also brought when there were already young.

The egg is greyish to greenish white, often marked with reddish-brown blots or spots
Measurements (Santa Fe) : 55.5 x 43.6 mm (n=36); with the extremes 66.5 x 43.4, 51.1 x 41.6, 53.1 x 40.6, and 58.4 x 47.7. The hawks from Española are slightly larger; consequently the eggs also average slightly larger, 57.3 x 45.2 (n=5), but remain within the extremes of the measurements found on Santa Fe.
The fresh weight of an egg of 54.0 x 43.6 (Santa Fe) was 55 grs :

egg-shell	5.9	grs	(10.8 %)
albumin	37.8	grs	(69.0 %)
yolk	11.1	grs	(20.2 %)

The thickness of this shell was 0.55 mm (average of 3 measurements).

One addled egg of 54.6 x 42.6 mm (Santa Fe) has been analysed at the "Instituut voor Veterinaire Farmacologie en Toxicologie" of the State University, Utrecht by Mr. J.H. Pennings. In this egg a trace of DDE (dichloro-bis-(p-chlorophenyl-ethylene) was found at a concentration of 0.12 ppm., the origin of which being unknown. This quantity is according to current views not considered fatal or otherwise of influence on the embryonal development of the chick. Weight of this egg-shell was 5.4 grs, thickness of the shell 0.437 mm (average of 10 measurements) (pers. comm. Dr. J.H. Koeman).

Clutch-size varied from 1-3; average 1.96 (n=49), 10 with c/1, 31 with c/2, and 8 with c/3. Incubation was shared by both sexes. While observations were made at the end of incubation period the female of a diandric pair was breeding most of the time. During 37 hours of observation at this nest (5 days; Santa Fe, nest 14, 17-21 August 1969) incubation frequency by the three nest-partners was recorded as follows:

female	:	28 hours	10 min.	(76.0 %)
male *orange*	:	7	31	(20.4 %)
male *blue white*	:	0	12	(0.6 %)
unoccupied	:	1	07	(3.0 %)

During this period 7 preys were brought to the female by the males (male *orange* : 1 *Nesopelia* nestling, 1 *Scolopendra*; male *blue white* : 4 *Geospiza* nestlings, 1 *Tropidurus*).

In the late afternoon only the female was found on the nest, suggesting that it is she who broods during the night.

Eggs were laid with intervals of 2-3 days. In some cases the female was found to be sitting on the first egg, in other instances she would be standing at the nest and sit infrequently until a second egg was laid, but I did not collect detailed data on this subject.

The incubation period (time of actual brooding of the eggs) could be determined exactly in two cases and lasted 37-38 days. The first egg from a clutch of 3 (Santa Fe, nest 48, August 1969) hatched 41 days after it was laid, and that from a clutch of 2 (Santa Fe, nest 43, August 1970) 39 days. The first young hatched 42 days after another clutch of two eggs had been found (Santiago, December 1969), but in this case the age of the eggs was unknown and the adults incubated infrequently, being often off the nest, which may have delayed hatching. During hot, sunny days adults would often stand at the nest and shade the eggs rather than brooding them.

5.4 Climatic data, breeding period, breeding season, breeding cycle

The Galapagos Archipelago, situated under the equator and with the cold Humboldt Current passing the island, has climatic conditions which conveniently can be divided in a hot season (end December - April) and a cool season (May - November). The distinction hot and cool reflects actual weather conditions of the seasons better than do wet and dry, since the period of December to April always will be the hotter time of the year, but not necessarily the wettest.

In many years the heavy tropical rainfall fails to arrive, and then most of the precipitation will fall as a drizzling rain in the 'garua' season (May - November). In figure 4 monthly totals of rainfall records, registered at the Charles Darwin Research Station on Santa Cruz, demonstrate the irregularity over a period of six years, 1965-1970. The years 1965 and 1969 have given heavy rain showers in the early part of the year, associated with high sea water temperatures, presumably due to a failing of the Humboldt Current to reach as far north as the Galapagos.

The relative constancy of day length and the impredictability of the rainy season make the Galapagos a good place to study the factor responsible for the timing of breeding cycles. In Figure 5 the breeding records over the years 1966, 1967, and 1968 are shown, indicating the months in which eggs were laid.

During these three years little precipitation was recorded in the hot season, and breeding was found to occur in all months of the year.

The amplitudes in the diagram are no indication for the total numbers of breeding hawks, since in the first years not all nests had been found.

For the years 1969 and 1970 climatic data are given in Figure 6a and the number of occupied nests in Figure 6b. Figure 6a shows the monthly average of daily sunshine in hours, and the monthly average of the daily maximum temperature in centrigrades recorded in the arid zone on Santa Cruz at the Charles Darwin Research Station. The general trend of these data is representative for other arid parts in the Archipelago; however, locally weather conditions may differ considerably. Figure 6b shows that the distribution of breeding records over these two years had a distinct maximum for 1969 in June and for 1970 in June/July. The breeding peak in June 1969 was apparently the result of the heavy rainfall in March, first effecting the prey species and then their predator, as will be discussed later under prey densities.

The situation on Santa Fe was studied in some more detail. On this island two distinct maxima of breeding activity occurred in 1969, one in June and a lower one in November. The breeding season in October/November proved to be to represent the start of a second breeding period by the same birds (hatched in Figure 7). This season of second clutch breeders did not appear in 1970.

For six pairs on Santa Fe the breeding periods could be followed over various years, giving an indication for the long-term breeding cycle. In Figure 8 an arrow shows the time the pairs were ringed. The extrapolation carried out in the figure seems justified, since prior to the ringing the pairs were regularly encountered together in the territory concerned; of the following pairs none or only one partner was ringed (for nest numbers see map in Figure 2) :

Nest 79,56, adults not ringed, but female could be recognized by a scar on the cere.

Nest 13, 14, 16, 26, 43, change of a male; second male (<u>blue white</u>) disappeared between January-March 1970, while the female lost successively her two colour rings and might therefore have been replaced since June 1969.

Nest 22, 12, 24, 102, only the two males ringed, but a female was always observed in this territory, hence, a change seems unlikely, though not impossible.

The breeding cycle was completely irregular.
The shortest interval between two successful breeding periods observed was 5 months (nests 79,56, May-November 1969), the longest interval was 26 months (nests 22, 102, June 1968 to September 1970). In another case 6 clutches (5/2 and 1/1) were laid within 18 months, two of which were successful (nests 16, 14, 26, 43, February 1969 - July 1970).

5.5 Young, juvenile, growth, fledging period

Newly hatched young had snowy white down, which soon became dirty grey-white. After one week to ten days the second down appeared forming a somewhat curled roseate-grey coat. The primaries become visible after 21-25 days, the tail feathers some 3-4 days later, and both seemed to be fully grown after about 50 days. The scapulars appeared after 33-34 days, after which body feathers also gradually appear on abdomen, breast and back.
Head and thigh feathers were the last to appear, after some 40 days.
The fledging period was 50-60 days.

A one day old hatchling (Santa Fe, nest 33, July 1969) had a weight of 40 grs. After seven weeks young had reached 900-1450 grs, depending on food and feeding conditions. No information was obtained whether differences in body weight at this stage were related to sex.

Two days old hatchling, hawk-egg, and a Darwin's finch as prey, Santa Fe

A juvenile hawk at 10 months of age; hawks were colour ringed for identification

In Figure 9 the growth curves are given of 8 young from 4 nests; the screened-in food list will be discussed further in Section 6.3.

Nest 79, with 3 young, had one young which was clearly under-weight. There was some evidence that this young did not survive, since later in the season only two juveniles were seen together in this territory.

Nest 57, with 2 young, reared both of them successfully, while nest 33 reared only one from a clutch of two.

Nest 80 succesfully reared the only young observed here, but had a clutch of 3 eggs.

The death of the young of nest 33 was caused by its sibling. When an adult arrived with prey the elder young attacked its companion prior to being fed, mainly aiming at its head. The female remained completely indifferent. The elder young did not start feeding until the younger had moved away, often over the edge of the nest. When there was no other escape, the younger chick would put its head under the body of the elder chick, which would then start pulling and pecking in the down feathers of back and body. Within 4-5 days the youngest one's head was as a result completely defeathered and had changed into a bloody mess. The young was not eaten by its elder sibling, in spite of its efforts, probably because its skin was too tough to be torn apart. The female was seen carrying the carsass away.

A similar procedure was noticed in another instance (Santa Fe, nest 39, 15 September 1968), where a female carried away a dead young, but returned within five minutes, which was too short a time for her to have eaten it. She may have dropped it somewhere, but this could not have been observed from the hide.

Fledlings remained for some months dependent upon the adults for food. In one instance (Santa Fe, nest 7, December 1967; observed again August 1968) a juvenile of ten months old was encountered in the territory, but it was not certain whether it was still fed by its parents, and it was not seen begging for food. In another case (Santa Fe, nests 79, 56, November 1969) a juvenile of 5 months old was still begging for food from the male, while the female was sitting on eggs again.

The Galapagos Hawk can breed at an age of two to three years. A juvenile male, ringed on 30 December 1967 in a gathering outside a territory, was later encountered (August 1969) breeding in a sub-adult plumage at an age of at least 25 months. Another breeding male (*orange*; nest 14, June 1969) had been ringed as an independent juvenile (19 August 1967; age 5 months or more) and therefore must have reached breeding age by at least 29 months. Male AJ 24846 (independent juvenile at 30 December 1967) was first noticed breeding in July 1970, at an age of at least 38 months. One bird, colour ringed as downy chick (Santa Fe, nest 22, August 1968, black right / blue left) was seen and photographed several times afterwards at the beach on Santa Fe. In January 1971 it was photographed by Peter Kramer. The colour slide shows the bird still in sub-adult plumage, at an age of 30 months.

5.6 Breeding success, mortality

The total number of breeding records observed in 1969 was almost twice as high as in 1970 : forty-eight to twenty-six. For Santa Fe, where all breeding birds were known for those two years, the records were twenty-four to ten.

In 1969 eighteen young (38.3 %) were reared from 47 eggs

(24 clutches) observed on Santa Fe, or 0.75 young per nest. Three young died before fledging. From the 26 addled eggs 4 contained a dead embryo, 8 were not fertilized, the state of 14 remained uncertain. The exact hatching success is unknown, as not all nests were observed from the initial stages onwards, but it must have been at least 45 per cent. In July 1970 a gathering of 6 juvenile hawks (and 2 sub-adults, 4 adults) was encountered near a dead goat, thus, assuming that on this island no large scale wandering has occurred, a mortality of 66.6 % for the first year could be suggested.

In 1970 seven young (41.2 %) were reared from 17 eggs (10 clutches) on Santa Fe, or 0.70 young per nest. One young died before fledging. From the 9 addled eggs 2 contained a dead embyo, 4 were not fertilized, 3 remained uncertain. Hatching success was at least 47 per cent.

In table 2 the breeding records are divided over three periods : Januari-April (hot-season), May-September (cool season, main breeding season), September-December (cool season, 'second clutch' season).

The mean clutch-size varied slightly. However, contrary to the general trend in birds (see Klomp 1970), in 1969 second clutches were on average not smaller than first clutches. When analysed in further detail it appeared that the second clutch-size from previously unsuccessful nests had remained the same or had increased (1-1, 2-3; 1-3), while from previously successful nests the second clutch-size was the same or smaller (2-2, 2-1, 3-2). It is noticeable that during the hot season of 1969, and over the whole of 1970, no clutches of 3 eggs have been found.

Fledging success of the main season of 1969 was distinctly higher than that of the 'second clutch' season of 1969 (50 % against 31 %); and slightly lower in comparison to the main season of 1970 (50 % against 58 %). In 1970 two of the seven young were encountered dead in the field, just after they had fledged, thus bringing the ultimate breeding success at 42 per cent.

On Santa Fe a total of 4 nestlings was ringed with a metal number ring in 1967 (2 in May and 2 in December); one was still alive there at an age of 5 months, another at an age of 10 months. None was seen afterwards. Two birds ringed (metal) as independent juveniles in December 1967 on Santa Fe were subsequently found breeding on this island.

Eight juveniles were ringed on Santa Fe in August 1967 with plastic colour rings; one of these was later found breeding on the island. Unfortunately this record cannot be used for calculating post-fledging success as it became clear that birds were losing rings of this type of plastic.

In 1969 no birds were ringed, but available information suggest that from the eighteen birds raised no more than six (33.3 %) survived their first year.

5.7 Predators, parasites

The Galapagos Hawk has but one predator, the mockingbirds (<u>Nesomimus</u> spp.). These birds are well known as egg predators in seabird colonies (boobies, Swallow-tailed Gulls, albatrosses, stormpetrels), of the Galapagos Dove, and of oystercatchers; they have also been observed devouring hatchlings (Harris 1968, and pers. observation). I observed mockingbirds on Santa Fe pecking furiously at an unattended hawk-egg (nest 3, October 1969). As an experiment a chicken-egg was placed in the same nest. Within ten minutes the egg was attacked for 5 minutes in succession, after which the mockingbirds lost interest, but returned later to start over again. There were two birds involved, which returned to continue hammering at the egg, and pecking under and at the sides of the egg as if trying to roll it away. This behaviour was observed for two hours, but the shell was apparently too thick to be broken by the birds. However, two days later the egg had disappeared and pieces of egg-shell were laying near the nest.

I have no evidence of rice rats (Oryzomys spp.) and snakes (Dromicus spp.) eating hawk-eggs. The Barrington Rat Oryzomys bauri is, contrary to general thought, not strictly vegetarian and might be a potential egg predator. I have seen tooth-marks of this rat on several deserted hawk-eggs, but the eggs were not broken.

In some instances (nest 14, 5, 47) eggs disappeared from the eyrie during the incubation period. Mockingbirds may have been responsible, but accidental breakage, and hawks eating their own eggs, cannot be excluded.

The disappearance of hatchlings from eyries at Punta Suarez (Española) and Punta Espinosa (Fernandina) seems likely to have been caused by mockingbirds. At Punta Suarez one few days old chick was found laying a metre beside the nest, the female sitting on the empty nest without paying attention to the peeping young. This young could never have moved so far, either it was thrown out of the nest by the parent carelessly leaving the nest, or it was taken from the nest by mockingbirds at an unattended moment. I placed the young in the nest again, and watched at a distance to see the female returning. However, three days later the young had disappeared. Mockingbirds on Gardner-near-Hood even stole prey remains from a hawk's nest (August 1969); at time the birds were seen waiting within a metre distance from the nest with an adult hawk in attendance on it.

Two species of Mallophaga are known from the Galapagos Hawk, Colpocephalum turbinatum and Degeeriella regalis; and one Hypoboscid fly Icosta nigra. I collected all of them except Degeeriella (identification by Miss Th. Clay).

"Colpocephalum turbinatum Denny, 1842 (Menoponidae) has a wide distribution on the Falconiformes and has been taken from a number of species of Buteo including B. galapagoensis and B. jamaicensis; its occurrence on any particular hawk seems to be of little systematic significance.

Degeeriella regalis regalis (Giebel, 1886) (Philopteridae) is found elsewhere in the New World only on Buteo swainsoni and B. jamaicensis. However, the specimens taken from these hawks appear to the same species as is found on the species of Milvus, Haliastur indus, and Haliaeetus leucoryphus - which makes a strange distribution. Some of it could be geographical and some phylogenetic.

Icosta (Ornithoponus) nigra (Perty) is wide-spread through the neotropical region and into the Nearctic, Hawaiian Islands and Galapagos. There are many records from Buteo, but large number from other Accipitridae, Falconidae, and non-birds-of-prey" (pers. comm. Th. Clay, British Museum, London).

HUNTING AND PREDATION

6.1 Description of islands and prey species

Priority was given to observing prey brought to the nest, so detailed studies on the density of prey species were not nade.

In Table 3 the available prey species are presented for five islands. The distinction is made as to species being present, rare, of restricted occurrence, and not present, respectively. The total number of prey species present on any one island varies from 9-15 (considering 21 prey species). As will be seen later the density of the hawk population on certain islands depends more upon a few prey species present in high numbers than on a broad variety of prey species occurring in low numbers.

In the following sub-sections a succinct description of the islands concerned is given with information on whatever I could find of the population size (more exactly density-activity patterns) of some of the prey species.

6.1.1 Santa Fe

Santa Fe is one of the small islands of the central group. It is roughly rectangular, about 7 by 4 km (2413 ha), and a relative low island, with the whole central plateau and two further hills above five hundred feet (150 m). The highest peak is 259 metres. The island has many cliffs and steep ridges. Tree cactus Opuntia and Palo Santo trees Bursera graveolens constitute the dominant vegetation, with low shrubs of Cordia lutea, Lantana peduncularis and Encelia hispida, the last restricted to soils of a loose texture such as red cinders. Scalesia is now confined to cliffs, out of reach of goats. Locally along the shore, and at the sites of temporary freshwater pools, bushes of Cryptocarpus pyriformis, Maytenus octogona, and a tree-form of Cordia lutea are present.

Rice rats

Almost nothing is known of the life history of the indigenous rice rats Oryzomys and during this present study only fragmentary information was obtained on the population fluctuation of Oryzomys bauri on Santa Fe. Rice rats or signs of their presence were found over the whole island. The highest numbers were noticed when they were attracted while camping near the shore at places with Cryptocarpus and Maytenus bushes. They emerge after dark and remain active towards about mid-night. A second and much shorter period of activity was found to occur an hour before twilight. Normally, rice rats are not active at day time. In fact during the five years of study rats were seen running during the day only during the period from June to September 1969, and never more than 1-3 individuals during a day's walk. During those months they were a nuisance in the hide while observing a hawk's nest, as at least one or two rats would gnaw on anything present. In early evenings 50-60 rats were counted in and around our tent in a clearing of five by five metre close to the shore. Hence we removed our camp to more open terrain further inland, where incidentally instead of by rats we were visited by 10-15 Short-eared Owls hunting in and around the camp.

In Table 4 the average is shown of three over-night catches from 20 live-traps, placed in two parallel rows of ten traps, each one metre apart and covering an area of 10 square metres. This simple method of trapping in an area where rats are widely dispersed gives no information on actual density; but the numbers of rats caught are indicative for their density-activity pattern. High numbers of rats (activity pattern of 2 rats/m^2) occurred in coastal areas with Cryptocarpus bushes and in rocky inland areas with Cyperus grasses (Large Pool Area). During the same month less rats were caught (activity pattern 1 rat/m^2) in open, less rocky areas with Castela shrub (Cerro 33). After a long period of drought numbers were growing very low, and the activity figure dropped to 0.5 rats/m^2.

An attempt was made to get information on the population size by marking the animals caught. This was discontinued as too many rats died as a result of capture operations. Various rats were killed through heavy fighting, especially when 4-6 rats had been caught in the same trap. The first night 25 September 1969, Cerro 33) 12 males and

5 females were caught; marking demonstrated that after four nights 32 individuals (20 males, 12 females) had been involved.

Doves, mockingbirds, and finches.

Breeding activity of doves, mockingbirds, and finches was closely linked with the amount of rainfall. In years with little rainfall finches of the arid zone may start nest building, but few lay eggs and rarely do they rear young. In the extremely dry year of 1970 only two dove nests with eggs were found on Santa Fe (in 1969 about 50, found without any difficulty), and a few finches were seen nest building, but no breeding was observed.

Doves Nesopelia galapagoensis occurred over the whole island, and were normally seen feeding in small groups on the ground. Nests were built under stones, in hollow trunks, between cactus pads, or in deserted nests of mockingbirds. The total population fluctuated considerably over the years. In August 1969 over 100 birds (e.g. 30 August : 35 adults and 92 juveniles) were commonly seen at early morning and late afternoon drinking at the Large Pool, which held standing water from March-September 1969. At various other places foraging groups of 10-30 birds were encountered. In September/October 1970 groups were much smaller (3-12) and were almost restricted to the central and western part. These are the higher parts of the island and in the cool season more clouded by fog and frequently wetted by drizzling rain. Here doves and finches were seen taking water drops from the grasses, following with the beak along dead stems or leaves; they were also observed drinking from standing water collected in small holds in the rocky surface.

Mockingbirds Nesomimus parvulus usually kept to their territories and did not form bands (10-15 birds) outside the breeding season as they do on Española near sea bird colonies. Rarely more than four birds were seen together, normally a pair with their offspring. One pair occupied an area of 2-5 ha, making a total of at least 500 pairs for the entire island.

Darwin's finches were represented in fair numbers, but only Geospiza fuliginosa and G. scandens were common. During 1968-1969 G. fortis virtually disappeared for reasons yet unknown, while G. magnirostris was seen less than five times over the last five years. Camarhynchus psittacula was observed only once, and C. parvulus, if still a resident, occurred in less than 5 pairs, Certhidea olivacea in less than 15 pairs. Almost nothing is known of the density of the finches in previous years, but the paucity of tree finches (Camarhynchus spp., Certhidea) is very likely due to the devastating effect of grazing and browsing goats. The disappearance of G. fortis may have been the combined effect of overgrazing and a long period of drought resulting in a shortage of seeds of sufficient variety.

During 1969 G. fuliginosa and G. scandens had an extended breeding season, from April to December; no nests of other finches were encountered.

In 1970 no breeding was observed, only G. fuliginosa was seen nest building, but no young were reared. In Aug/Sept 1969 flocks of feeding finches were considerably larger (20-100) than in Sept/Oct 1970, when they rarely exceeded ten individuals.

During the early morning hours of August 30, 31, September 1, and 30, 1969 a census was undertaken in areas of 2 ha each in the hawk territories 57, 79, 33, and 14, respectively (Table 6).

Description of territories

Territory 57 had stands of large cactus trees, with many side-branches and pads full of buds and fruits; at that time this was certainly one of the most luxuriant cactus forests of the island. In the census plot the following floristic components were counted : 400 *Opuntia* trees (with brown trunk) 20 young *Opuntia* (still with spiny trunk), 100 *Bursera* trees (no saplings of *Bursera* occur as a result of grazing goats), 25 tall bushes of *Cordea lutea*. The soil is composed of solid red rock or broken cinder, with about a 10 % coverage of *Encelia*, *Castela*, *Coldenia*, and *Boerhavia*.

Territory 79 covers an extensive terrain with boulders and grasses. In the census plot were counted : 175 *Opuntia* trees with trunk, 25 young *Opuntia*, 65 *Bursera* trees, 5 *Maytenus*, and 1 tall *Cordia lutea*. The soil is of broken cinder, with about a 30 % coverage of *Encelia*, *Castela*, and *Cordia lutea*.

Territory 33 is more open with a few rocky hills; dry streambeds (forming an ephemerous torrent only after a down-pour, at places standing water remaining for several months) with deep canyons leading to the sea. The entire coast is a 50-60 metre high cliff. Within the census plot occurred : 250 *Opuntia* trees with trunk, 40 young *Opuntia*, 35 *Bursera* trees, and 5 tall *Cordia lutea* bushes. The soil consists of broken cinder, solid rock and boulders, with a ground coverage of less than 5 % of the creeping shrub *Castela*.

Territory 14 is crossed by ridges, and includes a dome-shaped, reddish-brown cinder-hill, several rocky hillocks, and areas strewn with boulders. The terrain gives an open impression, with dispersed occurrence of *Opuntia* and *Bursera*, but at places an intertwined undergrowth of *Cordia lutea* and *Lantana peduncularis* prevails. The coast has a rocky fore-shore with a small, sandy beach. Within the census plot occurred : 140 *Opuntia* with trunk, 50 young *Opuntia*, 80 *Bursera* trees. Fine dark soil and boulders were for 40 % covered with *Cordia lutea* and *Lantana peduncularis*.

Lava lizards and land iguanas

Lava lizards *Tropidurus albemarlensis* were the most common reptiles.

Censuses were undertaken by means of transects of 3 metres wide over a length of 500 metres. All lizards within this area (0.15 ha) were counted during the morning hours (8.00 - 11.00); males, females, and juveniles being separated. Transects were laid down in the central north eastern part (4 transects, I-IV), in an area with undergrowth of *Cordia lutea*, *Lantana*, and at places with *Encelia*; near Cerro Colorado (transect V), in an open area with red cinders and scattered bushes of *Encelia*; and south of Cerro Colorado (transect VI), in an open area with *Castela* shrub, and checked as regularly as possible. The transect are indicated in the map (Figure 10) and the results are presented in Table 8.

The area of red cinders proved to have the greatest numbers of lizards, especially females. The soils of loose texture there may well serve as the main nesting habitat.

Land iguanas *Conolophus pallidus* are widely spread over the island, concentrated at areas with red cinders, in which we found many of their burrows. The total population was estimated at about 2000 individuals. Small juveniles were rarely seen and were extremely shy.

Snakes and centipedes

Snakes (*Dromicus* sp.) were encountered in the whole island, although they were never met frequently; up to three individuals have been seen during a day's walk. But during my whole stay in the Galapagos only once one small snake was found as prey remain at a hawk's nest.

Centipedes *Scolopendra galapagoensis*, to the contrary, were frequently observed as hawk's food, but were very rarely met with in the field, and then one or two during wet or cloudy days only.

Marine iguanas and sea lions

The coast of Santa Fe consists mainly of high cliffs; only in a few places the rocky fore-shore is accessible. A major flat area exists in the south-east corner of the island, part of which forms the territory of hawk pair 14; along a stretch of this coast a census of marine iguanas and sea lions was undertaken during hours of high tide.

Marine iguana Amblyrhynchus cristatus, 25 September 1969 : 6191 iguanas counted over a stretch of about 2 km; on 13 October 1970 : 3291 over 1 km.

Sea lion Zalophus californianus wollebaeki, 25 September 1969, the census over 2 km resulted in : 49 males, 278 females (probably including some juvenile males), 84 juveniles, and 36 puppies; on 13 October 1970 over 1 km : 103 puppies (57 males, 169 females), and on 6 November over 1 km : 129 puppies (32 males, 179 females); juveniles were not counted.

In 1969 and 1970 young sea lions were born on Santa Fe from September to mid December, with a peak in October/November. Mostly 1-3 placentae (or parts of these) were lying on the beach in those months.

Sea birds

In general can be said that sea birds form an insignificant part of the avifauna of Santa Fe. Less than 20 pairs of Masked Boobie Sula dactylatra are nesting along the south-eastern coast. Blue-footed Boobies Sula nebouxii do not breed on this island, but at times several hundreds roosted in various parts of the sea cliffs, as did Fregate Birds Fregata magnificens. Swallow-tailed Gulls Creagrus furcatus nested in less than hundred pairs in a few scattered places, Brown Pelicans Pelecanus occidentalis in less than 5 pairs. Audubon's Shearwaters Puffinus lherminieri were regularly seen in groups of 20-50 birds flying along the cliffs and almost certainly nested there.

6.1.2 Española

Española is the most southerly island of the archipelago. It has a length of 14 km and is at the broadest part 7 km wide, narrowing at its eastern and western ends to points known as Punta Cevallos and Punta Suarez. The area is 6048 ha. The whole southern coast consists of a high cliff. In the north is an extensive sandy beach with the islet Gardner (55 ha) at one mile distance. The island is relatively low, with five hills of over five hundred feet (150 m). The highest point is 195 metres.

Extensive areas are covered with vegetation of acacia shrub (Prosopis, Desmanthes, Acacia spp.). A few Opuntia and Bursera trees are still standing, mostly at places where Lantana peduncularis and Cordia lutea form the commonest undergrowth. Some 1000-2000 goats roam over the island. In the north east an area with boulders and soft soil collects water during the rains in a temporary pond with many inlets fringed with Cyperus-grasses.

Rice rats

Rice rats do not occur in Española.

Doves, mockingbirds, and finches

Doves occurred over the whole island, nesting under rocks. Breeding activity was initiated by the rains. Apparently several thousands of doves must breed here during years of optimum rainfall. After a period of drought the numbers decrease considerably. Influx of doves noticed on the nearby island Floreana (where doves are scarce due to wild cats and Black Rats) do suggest inter-island wanderings (pers. comm. E. Cruz).

In August 1969 doves were seen in very small numbers (groups of 2-3 birds) on Gardner, but no nests were found. At Punta Suarez larger groups (5-10 birds) were observed, as well as recently fledged young and nestlings. Doves were more numerous in 1970 than in 1969 although the breeding conditions for doves measured in the amount of precipitation, seemed better in 1969; apparently a period of two years is needed to reach a peak in the population.

In April 1970 it was apparent from the remains of standing water and the greening of the vegetation that more rain had fallen on Española than in the arid zone of Santa Cruz (Figure 4). This higher amount of precipitation was reflected in the profuse breeding of the land birds on Española, contrary to Santa Fe where it remained dry and birds did not breed at all or in very small numbers only.

When breeding doves were accidentally disturbed mockingbirds were always alert to devour the unprotected eggs or even the young.

The Española Mockingbird Nesomimus macdonaldi was considerably less numerous than the Galapagos Dove and was mainly encountered near the sea bird colonies at the western and eastern extremities of the island. It is certainly the most active and persistent mockingbird species of the archipelago in attacking eggs and young of other birds, including doves. It is not improbable that this habit was originally stimulated by the presence of large sea birds colonies. A band of twelve mockingbirds was observed feeding from the placenta of a sea lion.

Three species of finches were found ; Geospiza fuliginosa and G. conirostris were most common, Certhidea olivacea occurred in fair numbers. The following data on actual numbers was collected:

On 9 August 1970 a feeding flock of about 115 G. fuliginosa, 30 G. conirostris, and 3 Certhidea was encountered inland from Gardner Bay, in an open stretch of a hundred metres length (0.2 ha).

On 20 August 1970 in an area of 10 ha at Punta Suarez; 182 Nesopelia, 70 G. fuliginosa (including 9 black males), 13 G. conirostris (incl. 4 black males), 2 Certhidea, and 24 Nesomimus.

Lava lizards and land iguanas

Lava lizards are less numerous on Española than on Santa Fe. The Española Lava Lizard Tropidurus delanonis is the largest of the species of Tropidurus in the archipelago. Males grow up to 40 cm and have a weight of 90 grs. In an area of 10 ha at Punta Suarez with dominant vegetation of Cryptocarpus, Maytenus, Lantana, and Atriplex, 14 males, 17 females, and 23 juveniles (total 54) were counted on 20 August 1970.

Along a transect of 500 m (0.15 ha), including a colony of sea lions, on Gardner-near-Hood were noted:

13 August 1969 :	5 males,	4 females,	2 juveniles	(total 11)
9 October 1969 :	9	8	5	22
10 August 1970 :	1	1	17	19

Land iguanas are not indigenous in Espanola, but one single male is known to live near Gardner Bay; this animal is considered to have been introduced by man.

Marine iguanas and sea lions

Marine iguanas are common along the coast of Española. At Punta Suarez several thousands were usually present. On the south and east coast of Gardner-near-Hood 428 iguanas were counted on 10 August, and 417 on 9 October 1969. The colony of sea lions, along the same stretch of coast, consisted (9 Oct) of 92 males, 275 females, 113 pups (juveniles were not counted), in addition 5 remains of placentae were noticed. In August 1969 and August 1970 young were born (13 Aug 1969 : one placenta observed; 10 August 1970 : 3 placentae observed; colonies not counted).

Sea birds

Sea birds are common on Española and young are present throughout the year, often in high numbers.

The Waved Albatross Diomedea irrorata breeds in open areas all along the southern part of the island. In 1969 breeding success was very low, almost all eggs were deserted, contrary to 1970 when many young were reared; the total breeding colony was estimated at some 13000 pairs (Harris, in prep.). The population has an annual breeding cycle with small young from mid June to early August.

Large colonies of boobies occur at Punta Suarez (several hundred pairs of Sula nebouxii and S. dactylatra)and at Punta Cevallos (also both species, but S. dactylatra in much greater numbers, about 1500-2000 pairs). Sula dactylatra has an annual breeding cycle with small young from February to May. Sula nebouxii breeds almost continuously over the year, but peaks of egg-laying occur at intervals of less than a year.

On 20 August 1970 at Punta Suarez the situation for S. nebouxii was as follows : 2 displaying, 3 with eggs, 9 small downy young, 28 large white downy young, 106 young with primaries and tail feathers visible, and 7 full grown young. Only 2 displaying birds of S. dactylatra were present at this time.

The Swallow-tailed Gull Creagrus furcatus breeds in several thousands of pairs along the cliffs at Punta Suarez and Punta Cevallos. It has a non-annual breeding cycle.

The Red-billed Tropicbird Phaethon aethereus is present in several hundreds of pairs; little is known about their breeding cycle. Elsewhere in the archipelago it breeds annually as well as at any time of the year with peaks of less than twelve months intervals.

Though Oceanodroma castro is known as a breeding bird, its breeding cycle on Española is unknown, but birds have been heard calling in their burrows at Punta Suarez in August 1970.

6.1.3 Pinzón

Pinzón is one of the smaller islands (1815 ha) of the central group. It is more or less circular with a diameter of 5 km and a height of 450 metres. The island is strewn with boulders and numerous scattered, sharp-edged stones,while spiny shrubs (Prosopis, Acacia, Parkinsonia, Scutia, Castela, Zanthoxylum), at places intertwined with Cordia and Lantana, is covering seven-eight of the island. Pinzón is the only island of the archipelago where Bursera trees are absent for reasons yet unknown; a few low growing Pisonia (a typical transition zone tree) occur in the more central parts. The top is mostly concealed in misty clouds; here Zanthoxylum predominates with clusters of bromeliads growing on the rocks. The caldera floor, situated in the north west, has dead stands of tall Cordia bushes and a barren, reddish soil only greening after a period of heavy rains. South of the caldera is a flat area with Opuntia trees and a small temporary pond.

Black Rats

The Black Rat Rattus rattus has been introduced to Pinzón and was first found by the Hopkins-Stanford Galapagos Expedition in 1898-99. Indigenous rats Oryzomys have never been recorded.

During my infrequent visits to Pinzón I placed live-traps in two regions : a series of ten in a coastal area and a further ten inland in tortoise nesting country. In both cases the traps were placed 10 metres apart over a stretch of hundred metres. An average of 8 rats (4-11) was caught per catching period of 3-4 days in the coastal area, an average of 2 rats (0-4) in the inland region (see Table 8). Virtually all rats were caught in the first and second night after the traps had been placed and it seems as though Black Rats on Pinzón never reached such densities as did rice rats on Santa Fe (density-activity pattern in my samples : 0.013 Black Rats/m^2 on Pinzón, as compared to 3.2 rice rats/m^2 on Santa Fe).

Black Rats are known to dig into tortoise nests and eat eggs as well as the emerged young tortoises. It is of interest that during our study rats were never as numerous in tortoise nesting country as they were in a coastal area.

All five hawk territories were situated in the south and west parts of the island, including a coastal stretch, in all of which Black Rats probably were abundant.

Doves, finches, flycatchers, and warblers

Doves were rare on Pinzón, probably as a result of nest predation by Black Rats. During a day's walk over the island rarely more than 2-6 doves were seen; we never did find nests. At dusk up to ten doves were seen flying over our base camp to an islet off Pinzón, probably to enjoy a rat-free night.

Geospiza fuliginosa was commonly seen, but flocks never exceeded ten birds; G. fortis and G. scandens were less numerous, while Certhidea olivacea was rare. Other finches reportedly occurring on this island were not noticed; neither were mockingbirds.

The Large-billed Flycatcher Myiarchus magnirostris and the Vermilion Flycatcher Pyrocephalus rubinus were both not uncommon and were seen in exposed places typical for flycatchers; this habit may make them more vulnerable to avian predators, but their agility and keen eye must make them a difficult catch for a buzzard.

The Yellow Warbler Dendroica petechia occurring from the inter-tidal zone to the island's summit, was present in fair numbers, feeding on the ground and in bushes.

Lava lizards and tortoises

Lava lizards Tropidurus duncanensis occurred locally in low numbers. In open areas and in terrain of red cinders 2-5 lizards were seen per stretch of 100 m. But along a trail through thick brush cut over several kilometres lizards were rarely encountered.

Land iguanas do not occur on Pinzón.

The total population of tortoises Geochelone elephantopus ephippium has been estimated at 150-200 individuals. The last fifty years no juvenile tortoise has been observed; only once (July 1969) one yearling was found near a rat trap, attracted by bananas used as bait. Eggs and young tortoises were apparently eaten to such an extent by rats that few young survived.

Marine iguanas and sea lions

Marine iguanas were present in small groups all around the island; high cliffs prevented proper censusing.

Sea lions were scattered around the rocky shores in moderate numbers; a colony of some hundred animals was present in a bay on the north-eastern part of the island.

Sea birds

Audubon's Shearwaters were seen in groups of 10-30 birds, calling along the cliffs at several places, doubtlessly breeding there. Boobies and fregate birds were roosting, as did Swallow-tailed Gulls, the last ones probably breeding in small numbers. Except for an odd Brown Pelican and some Noddy Terns *Anous stolidus* no other sea birds are known to breed.

In general it can be concluded that Pinzón is poor in land birds and lizards; sea birds are few, and rats are much less numerous than on Santa Fe.

6.1.4 Santiago

Santiago is the fourth largest island of the archipelago, about 36 km long and 25 km at the broadest part, making a total area of 58.464 ha. To the east and south it consists mainly of barren lave. Eruptions have occurred within historic times. The north-western region has a high and humid area of some 4000 ha with a summit of 890 metres height. *Zanthoxylum* and *Psidium* formed the dominant trees, which largely have now been destroyed by goats and pigs, transforming the forest into grassy areas. During periods of drought extensive areas here are nothing but dust bowls. South and south-west of this is dense *Psychotria* scrub. In the east is Sullivan Bay with a small island Bartholomew (122 ha), and more to the south a group of islets, the Bainbridge Rocks, including Sombrero Chino (22 ha) and Roca Flamenca (18 ha). In the west lays James Bay with a long sandy beach partly overflown by a kilometre wide, black, barren lava stream, originating some five kilometres inland. Two conspicuous cones dominate the surrounding park land of *Acacia* and *Bursera* trees and tall bushes of *Cordia lutea*. To the north is Buccaneer Cove with Buccaneer Mountain rising steeply from the shore and the deepest gully, eroded in tuff-stone, I have met with in the Galapagos. Freshwater springs, attractive to birds and mammals, are found on the outer slope of the larger cone at James Bay and along the inner slope of Buccaneer Mountain, in fact they are the only spots where freshwater still could be found after long periods of drought.

Rice rats and Black Rats

The James Rice Rat *Oryzomys* (*Nesoryzomys*) *swarthi* from Santiago is known from four specimens collected by the California Academy of Sciences Galapagos Expedition of 1905-06. The species is now considered extinct, probably due to introduced Black Rats which already were established on Santiago at the time of Darwin's visit in 1835.

In analogy to Santa Cruz, where Black Rats were accidentally introduced by colonists, rice rats must have been abundant on Santiago before buccaneers beached their boats. (The same holds true for San Cristóbal, the only island where Darwin collected rice rats and commented on their abundance; later Black Rats were introduced and rice rats became extinct).

On my infrequent visits to Santiago I never encountered many rats; they were never a nuisance at the camp, and numbers appeared to be even lower than on Pinzón. (On 6-9 June 1966 and 15-23 January 1967 each 2 Black Rats were caught in our series of ten traps near Buccaneer Cove).

Doves, finches and other land birds

Doves are said to be sometimes numerous near James Bay and Buccaneer Cove, particularly in periods following heavy rains. I have never observed large groups here, in fact they rarely exceeded 5-10 birds.

In the arid zone of the west the most common finches were Geospiza fuliginosa, G. fortis, and G. magnirostris, while Certhidea olivacea was regularly seen, but in small numbers.
During June 1966 very few finches were present; no breeding occurred.
In January 1967 a flock of 15-20 ground finches was observed daily near Buccaneer Cove; no breeding was noted during this period.

Mockingbirds were always around, and we were rarely out of the range of their calling, but they did not occur in large bands.

Both species of flycatchers occurred. The Vermilion Flycatcher, normally restricted in the Galapagos to the humid zone, was commonly seen as far down as the coast of James Bay.

The Yellow Warbler was frequently seen in mangroves as well as in bushes of Cordia, Clerodendron, and Chiococca around James Bay and Buccaneer Cove. It was present over the whole island, from the algae-green rocky intertidal zone to the epiphytic growth at the island's summit.

Lava lizards, land iguanas, and tortoises

A census of lava lizards Tropidurus albemarlensis was undertaken along a 250 metres long beach at Buccaneer Cove with a small colony of sea lions (and consequently their faeces attended by swarms of flies), while just above the highwater mark there were many ledges and crevices in tuff-stone layers, ideal for lizards to hide. These may be reasons that densities here were higher than noted elsewhere (almost one per five metres, for details see Table 9). Further inland numbers were lower, but at a certain ridge of Buccaneer Mountain 17 were counted over 20 metres (22 January 1967). At that time these high numbers were thought to be associated with the presence of numerous pterophorid moths, but the stomachs of 2 lizards examined did not reveal those insects.

Land iguanas were common in Darwin's time, but feral pigs have caused their extermination.

Some 300-500 Giant tortoises Geochelone elephantopus darwini are still surviving on Santiago, particularly in the east central parts.

Marine iguanas, sea lions and fur seals

Marine iguanas are nowhere abundant on Santiago.
At Cape Trenton 2 adults and 7 juveniles were counted over a length of 1 km of coast-line (7 February 1966). Some 15-30 were regularly seen at rocks near the beach at Buccaneer Cove.

Sea lions were found in many places around the island.

There is a colony of fur seals Arctocephalus australis galapagoensis near James Bay, (18 males, 34 females, 38 juveniles; 3 April 1968), while smaller groups were found in a few other places. Little is known of the reproduction, but they likely give birth in caves (in which they also hide for the heat of the day) so that the placentae cannot be a source of food for scavenging hawks.

Sea birds

Audubon's Shearwaters were common around the island, while Swallow-tailed Gulls were present in small numbers and in a few places only. Except for a remnant population of Dark-rumped Petrels Pterodroma phaeopygia nesting in burrows in the upland humid zone, and Noddy Terns and Stormpetrels, mainly on Bainbridge Rocks, no further sea birds are known to breed on this island.

Introduced large mammals

Goats were found all over the island, but so far nobody has seriously tried to estimate their numbers. In most cases they occurred in herds of 20-50, but we observed groups of up to 200 and at times we could walk for hours and find goats scattered around everywhere. It is thought that at present well over 20.000 roam over the island. Feral pigs were present all over the island, except in the rough rocky regions of the east. Three National Park Officials killed 1500 over a four month' period in 1970. Probably some thousands were still left. Of freshly killed goats and pigs hawks only fed on the eyes, the skin being apparently too tough to tear apart. They were feasting, however, from any butchered corpse.

6.1.5 Fernandina

Whereas the Galapagos have been termed one of the most active volcanic fields in the world (Simkin & Howard 1970), Fernandina is their most active volcano. It is a shield volcano, roughly quadrangular of about 25 by 25 km extent within the centre an elliptical caldera measuring 4 by 6.5 km across and about 900 metres deep. The summit is nearly 1500 m above sea level. As a result of the frequent volcanic activities most parts of the island consist of barren lava. The latest volcanic activity was the spectacular caldera collapse with ash-emission in June 1968, changing the whole inner aspect of the crater (Simkin & Howard 1970), destroying all wild life there. Prior to this explosion there were at least two other eruptions in the sixties with lava flowing from the flanks.

The total area of Fernandina is 64.248 ha, making it the third largest island of the group. A relative small area (about 5 %), situated on the southern slopes, is covered with humid and transition zone vegetations as Psidium, Pisonia, and Psychotria. Where in the arid regions plant growth occurs scattered Bursera, Opuntia, and persevere clumps of tiny Brachycereus cactus. Locally tall solitary candelabra cactuses of the genus Jasminocereus jut out over Lippia and Macraea bushes which sparsely cover old lava flows. Around the crater rim Scalesia, Waltheria, and man-high Cyperus grasses are most conspicuous among the vegetation. The crater holds the largest freshwater lake of the archipelago, where before the eruption of 1968 probably the largest population of Galpagos Pintails was found.

Rice rats

The Narborough Rice Rat Oryzomys (Nesoryzomys) narboroughi is recorded from several places (Punta Espinosa, Cape Hammond, pers. obs.; Punta Mangle, halfway to the crater rim, and near the cone in the caldera prior to the 1968 collapse, pers. comm. R. Perry).

In October 1969 a few rats (less than five) were bothering us at our camp site near the shore at Cape Hammond. But both in August 1966 and September 1970 none were caught in the traps placed in the mangroves at Punta Espinosa (practically the only vegetation here for many miles); however, rats were numerous around this place in 1971 (pers. comm. Miss D. Boersma). This rather scanty information indicates that the rat population fluctuates here considerably.

Doves, finches and other land birds

Land birds formed but an insignificant part of the avifauna, not only at Punta Espinosa, but probably also throughout all coasts with barren lava.

Doves were present, but generally scarce and single birds or pairs were regularly seen in the hawk's territory at Punta Espinosa.

From the finches only few Geospiza fuliginosa were observed at Punta Espinosa, solitary searching for ticks on marine iguanas or feeding in the intertidal zone. Certhidea olivacea was present in the mangroves on all occasions that we were looking out for it (though absent in 1971, pers. comm. M.P. Harris). Yellow Warblers were here the commonest birds.

Mockingbirds Nesomimus parvulus were present in just an available odd pair, never amounting to large bands. The Large-billed Flycatcher was observed regularly; a few times a Vermilion Flycatcher was noticed as well.

Lava lizards and land iguanas

Lava lizards Tropidurus albemarlenis were present in small numbers, but were dispersed over places associated with mangroves and sea lions. So it could happen that we saw 2-5 lizards within ten or twenty metres and met with only one or none for an additional stretch of several hundred metres.

Land iguanas were numerous in the higher regions of the island, totalling several thousands. Once in a while an individual was encountered at Punta Espiñosa which must have crossed many miles of barren lava and which was probably a wanderer from overcrowded populations somewhere higher up.

Marine iguanas, sea lions and fur seals

Punta Espinosa is famous for its thousands of marine iguanas, clustering on the rocks. At places I counted 25 iguanas per square metre and calculated for the actual point of Punta Espinosa a total of about 3500 (November 1965). Within the limits of the hawk's territory numbers reached probably ten thousand.

Small colonies of sea lions existed along places with gentle slopes of smooth rocks, small beaches or stands of mangroves.

The south and west coasts of this island have probably the largest colonies of Galapagos Fur Seals.

Sea birds

Audubon's Shearwaters were regularly observed feeding in large gatherings off the coast at Punta Espinosa, often with stormpetrels, terns, and pelicans. Brown Pelicans, which here have a non-annual breeding cycle, nested in the mangroves in a few small groups of 2-5 pairs. A few Lava Gulls were mostly present (no breeding known here), Swallow-tailed Gulls were rarely seen near Punta Espinosa, but a colony of several hundred pairs exists in the west of the island.

The flightless Cormorant Nannopterum harrisi nested everywhere along suitable coasts of flat lava slabs in small groups (2-7 pairs), totalling within the limits of the hawk's territory at Punta Espinosa about 25 pairs.

The Galapagos Penguin Spheniscus mendiculus probably reached in this area some 50 pairs, nesting in holes under lava.

Cormorant and penguin eggs have been found in many months of the year. Hence, though little exact information is available, it is likely that peaks of breeding activity occur in non-annual cycles.

A breeding colony of several hundreds of Masked Boobies is known not far from Punta Mangle, and Blue-footed Boobies nested near Cape Douglas.

6.2 Hunter, scavenger, hunting methods

The Galpagos Hawk is an active hunter as well as a scavenger. Hunting methods proved to be variable. Most common was a soaring, inspection flight, 50-200 metres high, slowly gliding along with an occasional wing-beat; at times it was seen hovering. Occassionally it glided to a lower level and repeated the inspection flight, which was either terminated by a stooping dive at a prey or else it broke off and alighted on a rock. Galapagos Hawks can dive from considerable height. I saw an adult hawk stoop from at least hundred metres at an angle of some 45 degrees to the ground, but it failed to catch anything. These rather peregrine-like stoops have also been noticed near sea cliffs, where a hawk soared along the edge and suddenly made a not too steep dive to the bottom of the cliff. However, such tactics were never seen to result in a kill.

A selection of incidental observations may give an impression of the variability of the Galapagos Hawk's hunting techniques :

A juvenile hawk was seen pursuing a finch (Geospiza fuliginosa) between the branches of a Bursera tree, hopping from one branch to the other without being successful in getting the bird, which eventually managed to escape by flying away from the tree top. The same hawk was seen gliding from a cactus tree to the ground, forty metres away, to what hardly could have been anything else but a lava lizard. It missed, but dug various times with the claws in the loose soil and cinders as if still trying to grip the prey.

On Pinzón I saw an adult hawk following a grasshopper in the air, catching it with the claws and eating it straight away while in flight.

Sr. Camilo Calapucha told me that when men in Santiago were killing doves with a stick, hawks would take the escaping dizzy doves in mid-air.

A single adult hawk was seen diving at a goat with a week old young. The kid was hiding under the mother and both did not move. After a few fruitless attempts the hawk flew away. While killing female goats on Santa Fe for nature management purposes I have seen several times how adult hawks were striking down on the heads of fleeing kids, picking out their eyes and eventually killing them in this way.

Sitting in the top of a mangrove (Punta Espinosa, Fernandina), an adult hawk was watching for an hour in succession a group of some 200 marine iguanas. When eventually a dive was made a lava lizard was taken, a metre away from the basking iguanas which paid no attention.

In another instance an adult hawk was flying over a cluster of marine iguanas, allowing the hawk just a square foot to land. The bird was watching for some five minutes, flew up and settled on the head of a 70 cm long iguana, which offered surprisingly little resistance : the hawk started eating his living prey on the spot without any preparatory attempt of killing.

Yet another encounter between hawk and marine iguana, also at Punta Espinosa, was a struggle lasting for several hours (pers. comm. R. Silberglied, F. Sulloway). Here an adult hawk grabbed a 50 cm long iguana, which was able to escape several times by diving and swimming through a tide-pool, but at emerging the hawk took it immediately again and pulled it back into the mangroves.

That full grown marine iguanas are not the prey which hawks do know to handle very successfully was also noted by Amadon (1965) : "During our stay (1964) on Punta Espinosa the egg-laying period of the iguanas commenced. The females trudge about on the sandbars and eventually begin to dig a nesting burrow. On the morning of February 3 as we were watching half a dozen or so thus occupied, an adult hawk came flying by. Immediately intrigued by this display of exposed iguanas away from the lava to which they can cling, it lit on the sand among them, then ran about four metres and seized one by the back with both feet. The presumably painfully astonished iguana rushed away, dragging or carrying the hawk. The latter, evidently accustomed to carrying its prey rather than the reverse, released its grasp and flew to a lava outcrop a few feet away. After surveying the situation, it flew off".

So presumably only the weaker full grown marine iguanas are taken, or individuals returning from feeding excursions in the sea and still too cold and therefore too lethargic to defend themselves properly.

On Santa Fe there is evidence that even adult land iguanas are taken. How the birds are able to kill reptiles over a metre in length with a weight of 3500-4000 grs, is not clear. Even if seized in the back by surprise a land iguana could be considered to run for his life and escape in a burrow nearby. Still I found two corpses of land iguanas in an early enough stage to allow me to see that the sides of the neck and part of the troat were the first parts to have been eaten by two or three hawks present at the scene.

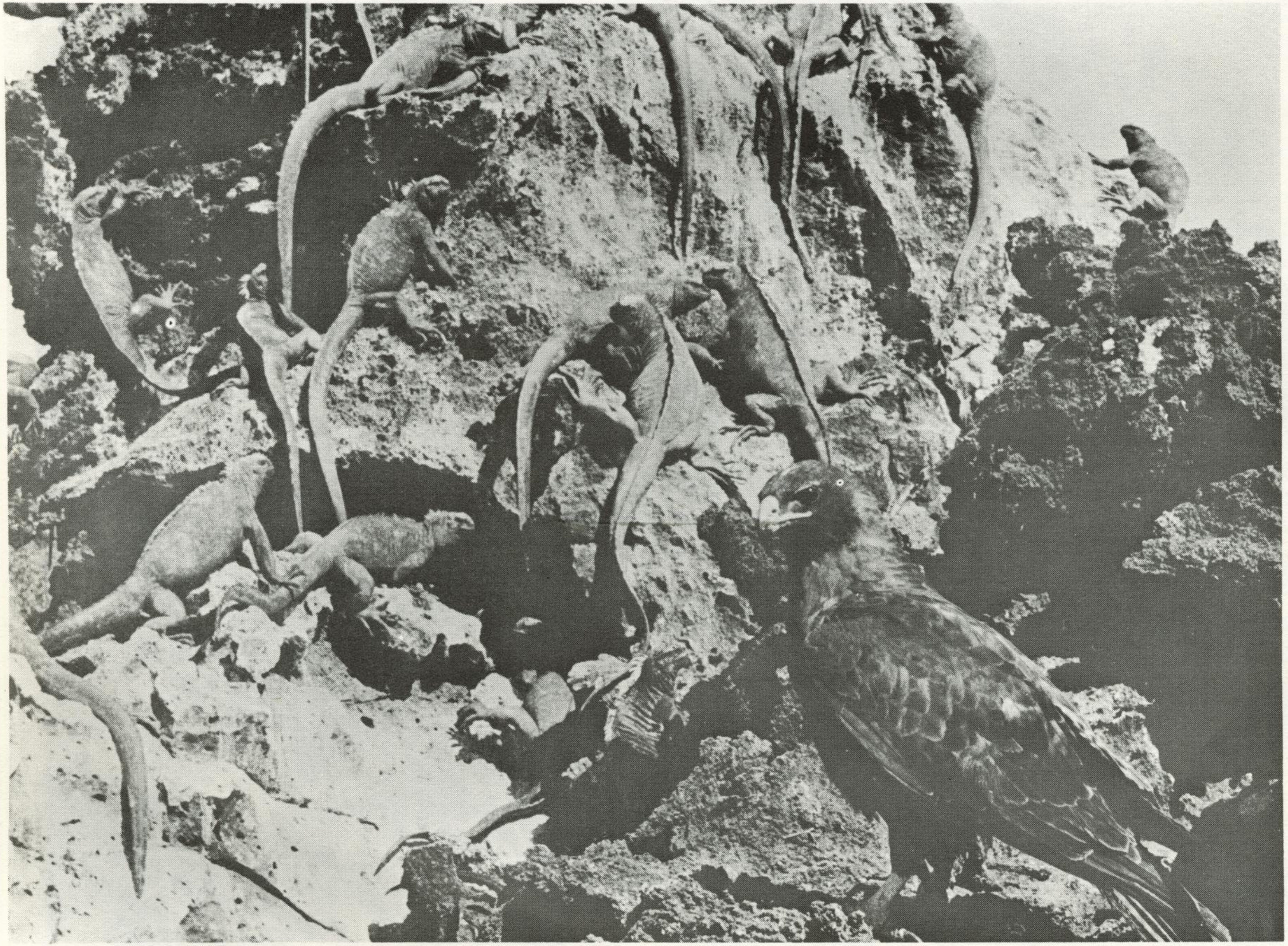
Caterpillars were eaten and these were taken from the leaves with the bill. Once I observed on Alcedo (Isabela) two hawks walking through a vegetation of Datura and jumping once in a while to reach the large sphingid larvae.

Also on Alcedo a juvenile hawk was seen turning a large tortoise dropping with its bill and pecking quickly at the ground, probably in pursuit of dung beetles.

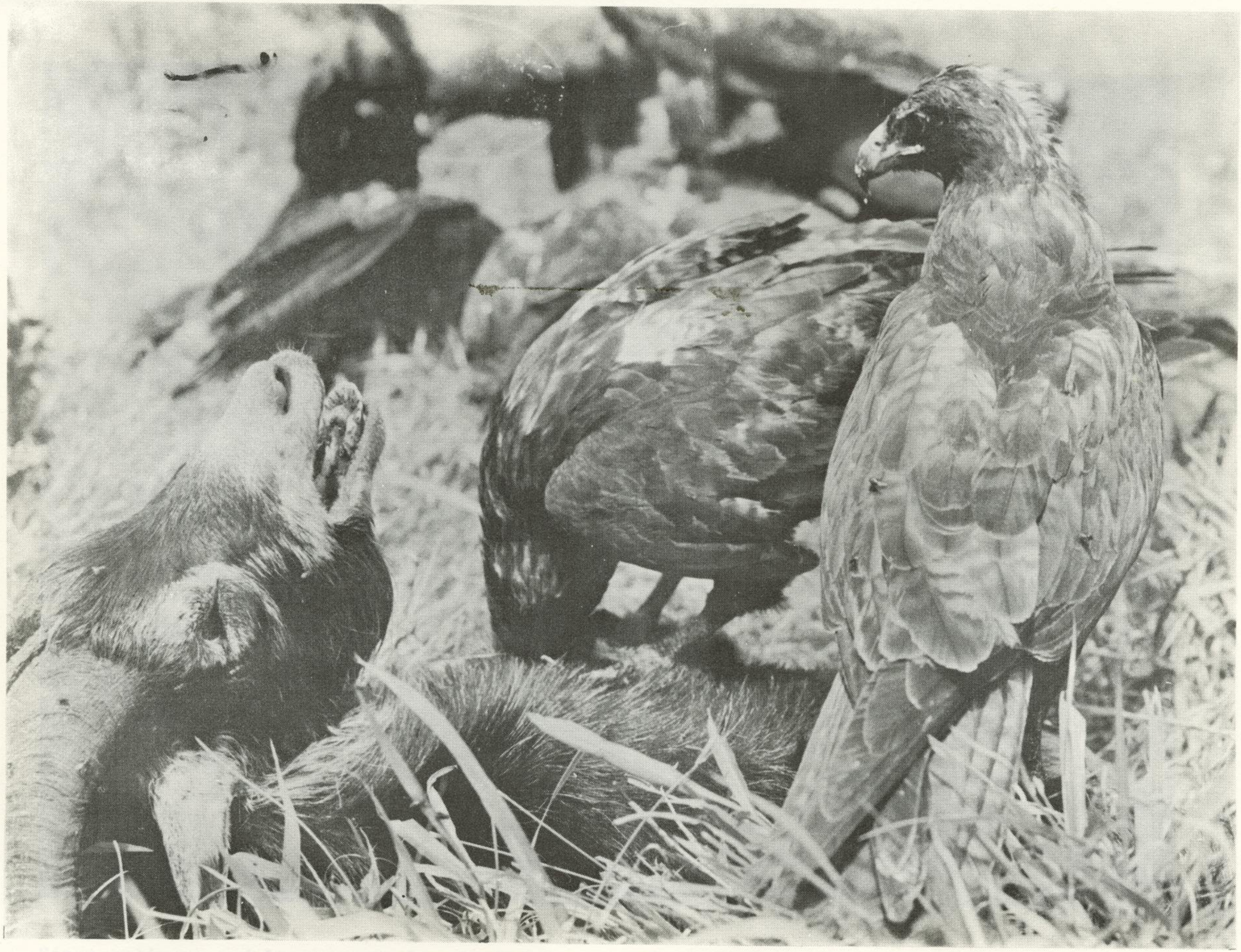
On Santa Fe several finch nests were found destroyed, half of the nest taken away or torn apart. This was probably hawk's work, as a complete finch nest was once found by me in a hawk's nest.

As a scavenger, hawks took to placentae of sea lion and remains of fish left by fishermen, and entrails and other remains, and goat and pig killed by man.

A gathering of 1 juvenile Brown Pelican, 8 Lava Gulls, and 5 juvenile Galapagos Hawks was seen near a placenta of a sea lion (Santiago, James Bay, 1 October 1968). A few times the female sea lion attacked the scavengers; the gulls were the boldest but the pelican snatched the



An adult hawk amidst marine iguanas at Punta Espinosa, Fernandina



Galapagos Hawks feasting on goat carcasses in the highlands of Santiago

Since vultures and hyenas are absent, feral pigs and buzzards set the scavenging scene

The Galapagos Hawk allows to be fed from the hand; two adults (right) fight for the best feeding spot biggest part, while the hawks were merely watching at a distance.

Taking advantage of these scavenging habits I was able to ring in December 1970 in the humid zone of Santiago in three days 71 hawks, attracted by goat carcasses.

The sex and age ratios of the hawks caught on this occassion are of interest : 22 adult and 18 juveniles females, 5 adult and 26 juvenile males. During this period no breeding occurred and it is possible that males stick more to the breeding territory (in the arid zone) than do females. Non-breeding females, which might have difficulties in finding sufficient food in the arid zone, may extend their foraging area further into the humid zone living there on centipedes and carrion. At the gathering mentioned above more juvenile males than juvenile females were present. This might indicate that indeed more males are surviving, but no additional direct evidence was collected for supporting this supposition.

6.3 Prey brought at the nests

For obtaining exact information on the bulk of food taken by the Galapagos Hawk it proved to be necessary to watch various eyries with young. As a consequence and as an inevitable disadvantage the data gathered was restricted to the breeding periods. Nests were generally kept so clean that pellets and prey remains formed no more than indications of the prey brought to the nest. They proved insufficient for a comparative and quantitative study. Therefore, in most cases an eyrie with young had to be watched from a hide for a 100 hours' period, distributed over 12 consecutive days, to assess direct information on the preys brought.

6.3.1 Santa Fe

During July and August of 1969 three occupied hawk nests were observed; nest 33 simultaneously with nest 79 in July, and nests 33 and 57 in August (Figure 9). A comparison between the preys brought to nest 33 in July (2 small young) and in August (only the oldest young surviving) demonstrates that the numbers of preys in both periods were almost the same, except of <u>Geospiza</u> which had increased fourfold (from 6 to 23, adults as well as nestlings). In this period no increase of breeding activity of the finches could be established, but 14 of 23 finches mentioned above were brought in two days (17-18 August), 7 of which were nestlings brought the same day. It seems therefore that 2 or 3 nests had been emptied systematically, a supposition which is corroborated by the fact that three nestlings were brought within a period of 15 minutes (08.55, 09.00, 09.10; the other four at 09.40, 11.35, 15.25, 15.40, respectively).

A total of 29 lava lizards was brought, 13 of which were males, 7 females, and 9 unidentified. The majority of males was probably connected both with their conspicuous behaviour (territorial display on exposed places), and with the fact that their larger size forms a bigger target for an avian predator.

The biomass of food (for female + young) was practically the same in the July and August periods of 100 hours of observation, viz. 2041 and 2060 grs, respectively.

The preys brought to nest 33 and 79 differed in many ways. Even when realizing that pair 79 reared 3 young and pair 33 had 2 young the differences were still considerable, not only quantitatively but also in prey items. To nest 79 were brought more than twice as many rats, ten times more finches, and a strikingly high number of centipedes.

The biomass of food (for female + 3 young) calculated per 100 hours period of observation was 4520 grs.

Comparing nest 33 with 57 the main differences are the high numbers of dove-nestlings (28 against 7) and the low numbers of lizards (2 against 15). To both nests more *Geospiza scandens* (full grown) than *G. fuliginosa* were taken, while the reverse was true for nest 79 to which, moreover, no nestlings were brought at all.

The preys recorded at the nests reflect to a certain extent the relative abundance of potential prey species present, but divergences do occur, indicating that at times the Galapagos Hawks hunt selectively. Though density and availability of prey species apparently were the most important factors, location of nest sites and specialization or skill also played a role. While availability of prey species will be discussed below, the hypothesis of a 'searching image' as a hunting method (see L. Tinbergen 1960, Croze 1970) employed by the Galapagos Hawk, will be discussed in Chapter 9.

There was no evidence that *G. scandens* had a longer breeding season than *G. fuliginosa* (rather the contrary was true), in fact *fuliginosa* was more numerous than *scandens*. Yet, however low the figures were, there was a trend of larger numbers of *scandens* than of *fuliginosa* caught in the territories 33 and 57. One wonders how this difference is brought about and the following considerations may be worth wile.
G. scandens generally known as the Cactus finch, feeds on nectar of cactus flowers and on cactus fruit, as well as on insects on trunks and large branches of *Opuntia*, and therefore is more exposed.
G. scandens is a larger bird and thus a bigger target; it may be clumsier as well. On the other side *G. fuliginosa* feeds on seeds on the ground and is less exposed to avian predators, at least in a close cactus forest.

In territory 79 few finches were breeding, but mixed flocks (20-30 birds) of *G. fuliginosa* and *G. scandens* were feeding on the ground, most probably on grass seeds. The finches brought to this nest as prey reflect almost the 3:2 proportion of the available species. This now indicates that the hawk takes finches from a feeding flock on the ground at random.

In territory 79 most centipedes were caught by the female (55 out of 60 brought to the nest; Table 10). This is an unusual activity of a female hawk, in most other cases observed the females did hardly participate in supplying food to the young. Nest 79 was located in a rocky area where probably many centipedes were at home, but the human eye did rarely observe them; in fact not one was noticed by us during the week the nest was watched while half of the territory was crossed twice a day to reach the hide. This female was most of the time standing at the nest, at times shading the young, but apparently she was hunting very effectively, for she returned with a centipede often within five minutes after having left the nest.

Observations at nest 14, occupied by a diandric pair give information on differences of prey brought to the nest by two males (Table 10). Male 'orange' caught more finches and centipedes, and less doves and marine iguanas than male 'blue-white', while both caught almost the same amount of rats, lizards, and nestlings of finches. These males did not have different hunting routes; they were seen hunting closely together in the air and they did not seem to have the territory divided in separate hunting grounds, but there is the possibility that one remained longer in one part of the territory than the other. It is of interest to note that there is a differentiation in certain prey species and not in others. We could imagine that rats form a basic staple food for the hawks to such an extent that these will be taken whenever they are available. On the other hand centipedes, marine iguanas, and to a lesser extent finches and doves are prey items for which only certain hawks have developed a skill of catching them, more than occassionally. This would mean that only few hawks receive sufficient strong stimuli after having obtained experience in capturing certain preys to enable them to hunt with a broad scala of imprinted 'searching images'.

The observations at nest 14, from the end of August to October, were divided into two periods to evaluate possible differences between the time shortly after hatching and at a later stage of the young. During this time the number of rats increased from 9 to 20 (Table 11), an increase for which no explanation is at hand (no rat traps were placed in this territory, but the increase is contrary to information on the density-activity pattern of rats obtained elsewhere).

Whereas the biomass of food over the two periods observed by nest 33 did not increase, by nest 14 it was augmented from 2000 to 2560 grs in the periods of 100 observation hours in Aug/Sept and Sept/Oct (Table 11).

On 26 September and again on 3 October the female returned on the nest with clustered fresh blood on toes and tarsi and almost certainly had been eating from a placenta of sea lion. She did not bring pieces along for the young, nor did the males, which were not noticed with blood-stained tarsi at that time.

There were not only differences of preys brought to the nests by *different* pairs over the *same* period, but also differences by the *same* pairs (in the same territory) over *different* periods (Tables 10 and 11).

The change of food was particularly clear when the pair of nest 14 moved to nest site 43 (1 km south of nest 14) where placentae of sea lion became the dominant food.

Unfortunately one of the males ('blue-white') disappeared between January and April 1970, thereby interrupting our observations on prey preferences of males in the same territory under changed conditions. The remaining male ('orange') switched successfully to another prey item, placentae of sea lion, which incidentally had been also available during the end of the breeding period 1969, but at that time had remained unexploited by both males. Male *orange* kept preying upon finches, and caught one marine iguana.

More *Geospiza fuliginosa* were caught than *G. scandens* (10 against 5), but 9 *fuliginosa* were caught on two days (1-2 October). Presumably the hawk had profited from wandering flocks of ground finches passing through this territory. On 2 October, while returning from the hide, I counted 23 *fuliginosa* and 5 *scandens*; the next days and weeks no more than 2-5 were seen, mainly *fuliginosa*. All but one *G. fuliginosa* caught, and all *G. scandens*, were in juvenile or female plumage.

Doves were neither seen in the territory nor brought at the nest.

At the nests of the monogamic pair 79-56 (nest sites 79 and 56 were located ca 100 metres apart) a decrease of rats and centipedes brought at the nests was recorded during both of the breeding periods of 1970 (Table 11). The smaller number of rats brought to the nests runs parallel with the decrease of rats caught in our live traps. Still, this was the only pair on Santa Fe that in January 1970 successfully reared young. Apparently the male managed to catch a sufficient amount of rats and doves, but not of finches. During this period no finch census was undertaken.

Later in the year (October 1970) mainly doves and finches were brought to the nest. This time more *G. scandens* were caught than *G. fuliginosa*. As ground finches did not breed in this territory and therefore did not show conspicuous inter-specific differences in feeding habits no direct explanation can be given for the reversed proportion of species caught. It is of interest to note that of 8 *fuliginosa* caught, 2 were black males and 6 were in juvenile or female plumages, whereas of

11 scandens 9 were black males and 2 in juvenile or female plumages. The numerous black males of G. scandens caught is an interesting feature and may furnish an explanation for the high total numbers of scandens brought to the nest as prey. Black birds are more conspicuous against a background of grey or green vegetation or of red cinders, but this is also true for G. fuliginosa of which not a higher proportion of males was caught.

When discussing the breeding cycle (Section 5.4) it was demonstrated that pair 79 and pair 5 had a successful breeding season at a time that their neighbours, pair 44, were not successful, in previous periods pair 5 had its turn of being unsuccessful, whereas its neighbours (44) succeeded. This raises the question whether in dense hawk populations the failure of a certain pair may be caused by the presence of another pair. As an example pair 44 had bred under rather unfavourable food conditions in September 1968, when they reared one of the two young hatched. The lack of success of this same pair in 1969 could probably be attributed in some way to the presence of Short-eared Owls which were particularly numerous (but only active at night) in a large part of the hawk territory, especially in the area of the Large Pool. Several times at moonlight nights the warning call of hawks was heared, from pair 44 as well as from pair 5, which hardly could have meant for anything else than owls. In addition there were many boundary disputes between 5 and 44 (pair 5 was a newly established pair), but less so between 79 and 44, so at least the continuing failure of 44 in 1969 and 1970 to breed successfully (twice an egg deserted) may have been caused by intraspecific fighting. Certainly the pairs 44 and 5 were much meddling with each other, and kept both their grounds, while 44 surely did not occupy the smallest territory. It may be reminded that 79 was a monogamic pair, 44 a diandric pair and 5 a triandric pair. Whatever the reason, food shortage cannot have been the cause of the failure of 44, for rats, doves, finches, and lizards were in 1969 available in very high numbers and in 1970 in good numbers.

The same story held true for pair 22 which did not breed at all for 26 months. One wonders whether apart from external factors also internal regulating factors have been involved.

6.3.2 Española

Gardner-near-Hood is a small islet (55 ha) one mile off the coast of Española. Still it contained a hawk's nest, which I observed 10-14 August 1969 when it contained a six weeks old young. Though I observed the male of this pair several times flying over the bay to the mainland of Española and saw it hunting there, I did not witness it carrying prey from the main island to its eyrie of Gardner-near-Hood. The female was mainly standing at the nest, at times shading the young, or watching and preening on a nearby rock-pile. She was for short times away (probably did not leave the islet), and during my observations she brought only 2 centipedes and 1 piece of placenta to the young.

The main prey items over the observed period were pieces of placenta of sea lion, and to a lesser extent lava lizards. It is most likely that the placentae were taken from the sea lion colony at the southern and eastern parts of Gardner, since the male carrying this food came always from that direction. Actually a hawk was frequently encountered there and twice it was seen eating from a placenta on the spot. The biomass (for female + 1 young) brought to this nest (over 100 observation hours) amounted to 4190 grs. This is twice as much as calculated for a female and her young on Santa Fe. On 9 August the young had a weight of 1470 grs and on the 14th it was 1410 grs; the male was 1110 grs and the female

1460 grs. These weights are higher, particularly for the male, than known for Santa Fe. This may explain the fact that a larger amount of food was brought to this nest.

In August 1970 2 young (about 2 weeks old) were present in nest 9 on Gardner, probably from the same pair as in 1969, but adults were not ringed. Many blood clusters on the nest indicated that placentae again formed a large part of the prey, but no nest observations were made.

A pair at Punta Suarez with abundant sea birds in its territory was unsuccessful in rearing young. (Three pairs near sea bird colonies at Punta Cevallos were less accessible and consequently less frequently visited; here also eggs and young disappeared.) The following on this failure was observed:

23 July	1963,	one downy young (D.W. Snow, notes in Charles Darwin Research Station card index). No information on fledging.
18 August	1964,	one egg; nest empty in September following without any indication of a young having been reared (J.B. Nelson, CDRS card index).
	1965,	no information.
	1966-1968,	no eggs observed; the island was infrequently visited by me, but apparently no young had fledged.
20 June	1969,	two eggs, but these were gone on 10 August with no sign of a young.
7 October	1969,	one few days old young was present, but this had disappeared by the 9th.
8 August	1970,	two eggs. It was observed that the male incubated irregularly, often leaving the nest before the female had arrived.
December	1970,	nest empty with a dead adult male hawk at the foot of the rock-pile under the nest site; cause of death unknown (pers. comm. M.P. Harris)

Four hawks were noticed in the area and several disputes were seen over what seemed to be establishing a new pair bond and the occupation of the territory.

The new established pair proved also to be not successful in rearing young (pers. comm. M.P. Harris) :

11 May	1971	two eggs.
14 June	1971	one few days old young and one egg.
9 July	1971	nest empty.

All in all, this territory apparently favourably situated near sea bird colonies was unsuccessful in rearing young for at least the last nine years in succession. Whatever the causes, food shortage could not have been one of them.

During August 1970 a nest with one young (about 3 weeks old) of a diandric pair was watched, situated 2 km east of Punta Suarez.

1450 grams. These weights are higher, particularly for the male, than known for Santa Fe. This may explain the fact that a larger amount of food was brought to this nest.

In August 1970 2 young (about 2 weeks old) were present in nest 9 on Gardner, probably from the same pair as in 1969, but adults were not ringed. Many blood clusters on the nest indicated that placentas again formed a large part of the prey, but no nest observations were made.

A pair at Punta Suarez with abundant sea birds in its territory was unsuccessful in rearing young. (Three pairs near the colonies at Punta Cevallos were less accessible and consequently less frequently visited; here also eggs and young disappeared.) The following failure was observed:

27 July 1965; one downy young (D.W. Snow, notes in Charles Darwin Research Station card index). No information on fledging.

18 August 1965; one egg; nest empty in September following without any indication of a young having been reared (J.B. Nelson, CDRS card index).

1966; no information.

1967-1968; no eggs observed; the island was infrequently visited by me, but apparently no young had fledged.

20 June 1969; two eggs, but these were gone on 10 August with no sign of a young.

7 October 1969; one few days old young was present, but this had disappeared by the 9th.

8 August 1970; two eggs. It was observed that the male incubated irregularly, often leaving the nest before the female had arrived.

December 1970, nest empty with a dead adult male hawk at the foot of the rock-pile under the nest site; cause of death unknown (pers. comm. M.P. Harris).

Four hawks were noticed in the area and several disputes were seen over what seemed to be establishing a new pair bond and the occupation of the territory.

The new established pair proved also to be not successful in rearing young (pers. comm. M.P. Harris):

11 May 1971 - two eggs.

15 June 1971 - one few days old young and one egg.

9 July 1971 - nest empty.

All in all, this territory apparently favourably situated near sea bird colonies was unsuccessful in rearing young for at least the last nine years in succession. Whatever the causes, food shortage could not have been one of them.

During August 1970 a nest with one young (about 3 weeks old) of a diandric pair was watched, situated 2 km east of Punta Suarez.

Black Rats formed probably a principal prey item during August-October 1966 (and for nest 7 in Jan-Feb 1966). This conclusion, however, is based only upon information from pellets collected at the nests. A list of pellets and prey remains (Table 14) has been included since the figures of Table 13 do not give a complete picture of preys taken on Pinzón. Further studies will have to reveal the importance of rats as prey item on this island.

6.3.4 Santiago

Observations on Santiago were of particular interest as the largest population of the Galapagos Hawk is surviving on this island. Santiago is a large and high island and possesses a wide array of climatic altitudinal belts and corresponding arid and humid vegetation zones. The situation on this island could be compared with the small, low and exclusively arid island of Santa Fe. Lack of means of quick inter-island transportation prevented me from accomplishing these comparisons more satisfactorily. It is particularly unfortunate that no observations could be made on Santiago in a year of heavy rainfall (e.g. 1969) during which land birds would have been plentiful. It is of interest that in those dry years during which I had the opportunity to collect data, lizards formed the main prey (Table 15). This supports the view expressed already as a result of observations on Santa Fe (nest 33), that, when not enough rodents and birds are present, the Galapagos Hawk switches over to catch lizards.

In areas of barren lava as in the territory at Cape Trenton, where lizards were rare, hawks eat mainly marine iguanas and Audubon's Shearwaters (Table 15). This territory (and may be the same pair) had young or eggs in the following months :

February 1966, one young
August 1966, 2 eggs, result unknown
August 1967, one fledged young
No information for 1968
July 1969, one downy young
July 1970, one downy young

Thus the Galapagos Hawk rear young in territories where marine iguanas and shearwaters are the only available prey.

In keeping with the above conclusion are the following sea bird remains found at a long-deserted (at latest mid-1950's) nest site on North Seymour on 3 June 1966 : 71 Puffinus lherminieri (number based on 71 right and 55 left humeri), 1 Pterodroma phaeopygia (skull), 1 Creagrus furcatus (skull). But most other prey remains would not have lasted this long, and this sample is thus certainly biased.

The young of nest 4 in the saltmine crater at James Bay was probably much suffering from heat. The female was infrequently seen on the nest, and left the young unshaded. At the fourth day of observations (6 Feb 1970) the young was laying almost unconcious in the nest and it had disappeared the next day. The maximum and minimum temperatures on 6 February were 90° F (32.2° C) and 75° F (23.9° C). From 6-15 February the average maximum temperature measured in the sun was 95.2° F (84-110). Though the amount of food brought to the young was low (1200 grs over 100 observation hours, i.e. 150 grs per day), lack of food dit not seem to have been the cause of death. This then was another instance that a young hawk had died during the hot season.

6.3.5 Fernandina

Barren lava fields must by any standard be a marginal habitat for hawks, unless marine iguanas are abundant along the coast. This is the case at Punta Espinosa on Fernandina, where also a mangrove thicket is present and where further lava lizards, cormorants, penguins, and sea lions add to the diversity of wild life and potential food. No observations were made to assess information on the number of marine iguanas and sea birds taken over a certain period, but hawks often appeared unsuccessful in rearing young in this place as the following data may illustrate:

1962 : 28 February, one young ringed (R. Lévèque, CDRS card-index); never recorded again.
1963 : no information.
1964 : 26 January, nest was found with one egg and fresh leaves; the pair was defending the nest but did apparently not breed (Amadon 1965).
1965 : no information.
1966 : 10 August, 2 eggs.
10 September, 2 young of about fourteen days old; adult with medium-sized marine iguana in talons flying to the nest; iguana was dropped and hawk started attacking the observer furiously (pers. comm. B. Schreyer); not known if both young fledged.
1967 : 12 July, 2 fledged young, one ringed; remains of marine iguana and several centipedes on the nest.
5 August, "5 buses, une des buses est un jeune à cri aigu; pas observé bagues" (in litt. D. Weber).
1968 : 4 June, nest empty; copulation; no further information.
1969 : 25 July, one fresh egg (pers. comm. M. Castro); no evidence of young reared.
1970 : 11 July, 2 eggs, no young reared.
1971 : 17 February, one young just hatched and one chipping egg (pers. comm. R. Lévèque).
24 February, nest empty (pers. comm. M.P. Harris).
26 June, 2 eggs.
13 August, 2 half grown young, ringed (pers. comm. M.P. Harris).

In two cases observed the first week of the young for reasons yet unknown seemed to be the critical period, but death caused by a too long lasting exposion to the sun seems the most likely explanation, rather than lack of food or nest predators.

6.4 Relation with other predators

Two other avian predators occur in the Galapagos, both endemic subspecies : the Galapagos Short-eared Owl <u>Asio flammeus galapagoensis</u> and the Galapagos Barn Owl <u>Tyto alba punctatissima</u>. There are no indigenous land predators, but cats and dogs have been introduced and now run wild on various islands.

Detailed data on the ecological differentiation of hawks, owls, and cat will be presented elsewhere. As conclusive note the following seems to be relevant to the present study.

Cats and Short-eared Owls are diurnal as well as nocturnal hunters, the Galapagos Hawk is active only at day time whereas the Barn Owl is strictly nocturnal. Where all three avian predators still occur alongside each other (Santiago), the Galapagos Hawk is the predominant diurnal hunter, the Barn Owl the nocturnal one, whereas the Short-eared Owl is present in very small numbers only and is rarely or not seen at day time.

On islands where Buteo and Asio occur alongside each other (Santa Fe, Española, Pinzón, Pinta, Marchena), the Short-eared Owl is strictly nocturnal. Every time Short-eared Owls were flushed by me on Santa Fe they were instantly attacked by a hawk. The owl escaped by rising higher and higher, gaining height above the hawk, until even with 10x50 binoculars it was not to be seen anymore. The hawk would follow it for some distance but soon would give up and continued soaring for some time before returning to his roost. Still Short-eared Owls were found a few times as hawk's prey on Santa Fe. The absence of Barn Owls on Santa Fe is probably due to lack of caves and hollow trees for roosting and nesting.

On Fernandina Buteo and Tyto occur alongside each other, Asio probably being only a straggler. On Fernandina the humid habitat is relative small and with already a day and a night hunter present, the Sjort-eared Owl apparently cannot hold its ground.

The Galapagos Hawk was found in all cases to be the stronger except where cats were present, but this might be due to competition for food. I have no evidence of cats taking young hawks. Doves are scarce on all islands where cats occur (Isabela, Santa Cruz, Floreana, San Cristóbal), but the scarcity may also be the result of human slaughter as all these islands have human settlements. However, to quote another example, the whole of northern Isabela is free of man but roamed by cats and here the paucity of doves (as well as of lava lizards) was equally evident, which seems to suggest that cats have a more destructive effect on the dove population than man.

In the humid highlands of Santa Cruz, where hawks have now almost become exterminated (though once non-breeders were common; pers. comm. A. Rambech), Asio and Tyto occurred alongside each other. The Short-eared Owl is abundant and diurnal as well as nocturnal in this situation. It is striking that near large colonies of stormpetrels and shearwaters Asio, and not Buteo or Tyto, had its hunting ground.

Only the lava gull Larus fuliginosus is a potential competitor as a scavenger with the Galapagos Hawk. Encounters seem to occur only incidentally. On Santiago once a pig was seen feeding on goat carcasses amidst a gathering of about 30 hawks (November 1970).

Two species of migrant birds of prey have occassionally been observed in the archipelago, the Peregrine Falcon Falco peregrinus and the Osprey Pandion haliaetus. On Santa Fe three hawks were once seen driving a Peregrine away successfully. The falcon flew rapidly away, remaining above the hawks. An encounter between an Osprey was quite different. A male hawk (its female was sitting on eggs, nest 56, Santa Fe, November 1969), using warning and exciting calls, kept more or less at the same height with the Osprey, at a distance of about 20-30 metres. Both were soaring slowly over the hawk's territory. I lost sight of the Osprey when it was above the sea, the hawk returned and hunted for a while before settling in a cactus not far from the nest.

6.5 Ecological place of the Galapagos Hawk

In the previous sections of this chapter the activity-density pattern of various potential prey species were given followed by information on the actual prey taken and the relation with other predators. From these components the ecological place (habitat and niche) will have to be deduced.

In all cases observed the nesting habitat was in the arid zone, sometimes in the lower transition zone. Hunting and feeding was extended into the humid zone by non-breeders. I have never observed that breeding hawks leave their territory to hunt in the humid zone, and it seems very unlikely that it ever occurs.

Doves and indigenous rats proved to be the most important prey items, furnishing 34.5 and 21.4 per cent of the total prey weight, respectively. Finches, lava lizards, placentae of sea lion and marine iguanas form an equal part of the remainder with 6.9, 7.0, 8.1, and 7.3 per cent of the total prey weight, respectively (Table 16).

Besides the prey species mentioned in Table 16 the following incidental food items have been recorded, the list having been based on prey remains and field observations collected during my investigations and from data in the literature :

Capra capra, kids and carcasses
Zalophus californianus wollebaeki, only once noticed at a recently dead puppy

Sula sula, adult
Sula nebouxii, adult and young
Creagrus furcatus, adult
Phaethon aethereus, juvenile
Spheniscus mendiculus, recently fledged young
Nannopterum harrisi, eggs (pers. comm. D. Boersma); possibly young (Snow 1966)

Butorides sundevalli, juvenile (Amadon 1965)
Dromicus spp, in litt.; only once found as prey remain during my investigation

Fish remains, left by fisherman on the beach
Grapsus grapsus (Gifford 1919), but I found no further evidence for this

Manduca sp., larvae (Sphingidae, Lepidoptera)

The Galapagos Hawk is an extremely adaptable predator. The main preys are doves and indigenous rats, but it raises its young with Audubon's Shearwaters and marine iguanas as well, as with placentae of sea lion; at other sites lava lizards can form the most important prey. However, it has been unable to extend its breeding ground into the humid zone.

TAXONOMIC RELATION

7.1. Earlier opinions

The history of the opinions on the systematic position of the Galapagos Hawk is interesting in that, unlike in other cases the hawk's habits have played an important role. Gould (1837), who described the species on specimens collected by Darwin, commented on these as follows: "Where I not assured by Mr. Darwin that the habits of this bird strictly coincide with those of the Caracara (Polyborus Brasiliensis), its mode of flight and cry being precisely the same, I should have been induced to regard it as rather belonging to the genus Buteo than to Polyborus; but as I have satisfactorily ascertained by a close investigation, it forms a beautiful intervening link between these genera, as is evidenced by the scaling of the tarsi and the produced form of the beak; while its habits place it within the limits of the latter genus. It is on the authority of Mr. Darwin also that I rely for the assurance of the two birds... being the male and female of the same species, so great is the difference between them both in size and colour". Apparently, Gould was not content with this compromise, as he later placed the Galapagos Hawk in a separate genus, Craxirex, while Darwin was not certain of himself whether to place this genus in the Buteoninae or in the Polyborinae.

Darwin in turn refers to Gould's taxonomic interpretation as follows : "Mr. Gould was partly led to institute this genus Craxirex from the facts communicated to him by me regarding the habits of the following species, which is found in the Galapagos Archipelago, and there supplies the place of the Polybori and Milvagines of the neighbouring continent of America.

If a principal of classification founded on habits alone, were admissible, this bird, as will presently be shown, undoubtedly would be ranked with more propriety in the sub-family of Polyborinae, than amongst the Buzzards. To the latter it is closely related in the form of its nostrils; in the kind of plumage which covers the head, breast, and shoulders; in the reticulation of the scales on its feet and tarsi, and less closely in the form of its beak. To the Polyborinae it manifests an affinity in the great strength and length of its toes and claws, and in the bluntness of the latter; in the nakedness of the cere, in the perfectly uncovered nostrils, in the prolongation and bulk of the bill, in the straightness of the line of commissure, and in the narrow shape of the head. In these several respects, taken conjointly with its habits, this bird supplied a most interesting link in the chain of affinities, by which the true buzzards pass into the great American sub-family of carrion-feeding hawks. I am, indeed unable to decide, whether I have judged rightly in placing this genus, as first of the Buteoninae, instead of last of the Polyborinae. ... These birds (Galapagos Hawks) will eat all kind of offal thrown from the houses, and dead fish and marine productions cast up by the sea.

They are said to kill young doves, and even chickens; and are very destructive to the little tortoises, as soon as they break through the shell. In these respects this bird shows its alliance with the buzzards.

Its flight is neither elegant nor swift. ... It is also a noisy bird, and utters many different cries, one of which was so very like the shrill gentle scream of the N. chimango, that the officers of the "Beagle" generally called it either by this name or from its larger size by that of Carrancha, - both names, however, plainly indicating its close and evident relationship with the birds of that family" (Gould 1841).

From the above we learn that even Darwin was not infallible; he was obviously misled by observing the Galapagos Hawk only near the shoreline or near the campsite, not seeing it actually hunting in its territory.

Amadon (1965), when discussing the habits of the Galapagos Hawk, remarks : "After reading of the tameness of the Galapagos Hawk and of how it eats centipedes and carrion, I had expected a sluggish, inoffensive bird. During the breeding season, at least, it is actually a vigorous, noisy species and, ... it catches some large prey. In these respects it is to be compared with such a species as the Red-tailed Hawk, Buteo jamaicensis".

Since its first description, the Galapagos Hawk has been placed in the following genera: Polyborus (Caracara), Craxirex, Astur (Goshawk), Dromolestus, and Buteo (Buzzard) in the following combinations:

Polyborus galapagoensis (in Gould 1837)
Craxirex galapagoensis (in Gould 1841)
Buteo galapagoensis (in Gray 1844, original not seen; courtesy D.W.Snow)
Astur (unicinctus) gallapagoensis (in Kaup 1847; name spelled as gallapagoensis and gallopagoensis) (see also Friedmann 1950, p.274)
Buteo galapagensis (in Sundevall 1871)
Dromolestus galapagoensis (in Sundevall 1874)
Buteo (Craxirex) galapagoensis (in Ridgway 1875).

Since 1875 the species was consistently considered to belong to Buteo.

According to Brown & Amadon (1968) the genus Buteo consists of 25 species, 17 of which occur in North, Central or South America and adjacent islands; the remaining eight species are found in the Palearctic, Africa, and Madagascar. The genus may have evolved somewhere in South America.

The Galapagos Hawk was placed by Ridgway (1875) in the subgenus Craxirex together with Buteo poliosomus [=B. polyosoma], B. erythronotus [=B. polyosoma], B. albicaudatus, B. swainsoni, and B. pennsylvanicus [=B. platypterus], based on the fact that all these birds have three outer primaries notched (most other Buteo's have four outer primaries notched).

Amadon (1965), in discussing the systematic position of the Galapagos Hawk, removed B. platypterus from this Craxirex group, following Johnson & Peeters (1963) who placed this species (in spite of having only three outer primaries notched) in the group of small woodland buzzards (B.magnirostris, B.ridgway, B.lineatis, B.nitidus, B.platypterus).

In the overall arrangement of the genus Buteo Amadon starts with the woodland group, followed by the Craxirex group, and ending with the more advanced, "four notched" group, including all the Old World species and such New World ones as B. jamaicensis and B. regalis. In Brown & Amadon (1968) the sequence of species of Buteo is : nitidus, magnirostris, leucorhous, ridgwayi, platypterus, brachyurus, swainsoni, galapagoensis, albicaudatus, polyosoma, poecilochrous, albonotatus, solitarius, ventralis, jamaicensis, buteo, oreophilus, brachypterus, lagopus, rufinus, hemilasius, regalis, auguralis, and rufofuscus.

Referring to Buteo galapagoensis Brown & Amadon state : "The feet and talons are strong like the closely related B. polyosoma and B. albicaudatus, not weak as in B.swainsoni. To the latter it is usually compared, though less closely allied".

Finally, Mayr & Short (1970) conclude : "The hawks Buteo albicaudatus, B. polyosoma, B. poecilochrous, and B. galapagoensis are closely related.. and comprise a superspecies probably related to B. swainsoni".

7.2 Taxonomic relation with other American *Buteo* species

Most earlier authors have looked among the species of the *Craxirex* group for the immediate relatives of *Buteo galapagoensis*.

Therefore in this chapter *B. galapagoensis* will be compared with the species of this group, as well as with the North American migratory Red-tailed Hawk, *B. jamaicensis*, and its southern South American relative *B. ventralis*, as well as with the Hawaiian Hawk *Buteo solitarius*, whose closest relative is still unknown.

Ultimately an attempt will be made to reconstruct the geographic origin of the Galapogos Hawk, which, to manifest the problem succinctly, may be one of the following possibilities :

(a) colonization by a present or former North American migrant, e.g. *B. swainsoni* or its immediate ancestor;

(b) colonization by a present or former North or Central American resident, partly migratory, or may be previously migratory, e.g. *B. jamaicensis* (*c.q. B. ventralis*), or its immediate ancestor;

(c) colonization by a present or former South and Central American migrant or vagrant, e.g. *B. albicaudatus* or its immediate ancestor;

(d) colonization by a present or former South American resident, e.g. *B. polyosoma*, *B. poecilochrous*, or their immediate ancestors.

In Table 18 mensural data are presented, with the statistical details given in an Appendix.

The following series of sixteen characters has been compared in eight American species :

1. Colour of adult plumage
   - 1a dark brown or with a dark brown to dusky black phase
   - 1b not dark brown
2. Colour pattern of the tail in adult birds
   - 2a red or brown, with or without bands
   - 2b white with narrow grey bands and one black subterminal band
3. Colour of mantle in adult birds
   - 3a with reddish brown
   - 3b not reddish brown
4. Colour of the abdomen in adult birds
   - 4a white, with or without tiny grey bands
   - 4b various shades of brown, never white
5. Colour of downy chick
   - 5a white
   - 5b grey or buffy-brown
   - 5c salmon pink
6. Wing depth in females
   - 6a 250-265 mm
   - 6b larger than 280 mm
   - 6c smaller than 220 mm
7. Length of wing tip by females
   - 7a smaller than 50 per cent of wing depth
   - 7b larger than 50 per cent of wing depth
8. Shape of wing or wing formula
   - 8a type A
   - 8b type B
   - 8c type C

9. Shape of primaries
   - 9a outer three primaries notched
   - 9b outer four primaries notched
10. Length of tail of adult birds
   - 10a smaller than 70 per cent of wing depth
   - 10b 70-80 per cent of wing depth
11. Length of inner and hind claws
   - 11a smaller than 25 mm
   - 11b larger than 25 mm
12. Length of bill in relation to inner claw
   - 12a bill relatively short
   - 12b bill and inner claw of about the same length
   - 12c bill relatively long
13. Length of tarsus
   - 13a smaller than 70 mm
   - 13b larger than 70 mm
14. Length of middle toe
   - 14a smaller than 40 mm in males, than 45 mm in females
   - 14b larger than 40 mm in males, than 45 mm in females
15. Voice
   - 15a a relatively short -keeu- or a high -ke-several times repeated
   - 15b a rather prolonged hoarse scream or a squeak
16. Food
   - 16a mainly insects, small birds and small rodents
   - 16b small rodents and medium-sized mammals, birds reptiles, and insects
   - 16c medium-sized mammals

Ad. 1. A dark brown to dusky black plumage occurs in all species except _B. poecilochrous_. I have seen no dark specimens of _B. ventralis_, but this species has been added under 1a on the authority of Johnson (1965) and Brown & Amadon (1968). The complete dark forms (dark brown plumage, or grey with red-brown) of _B. p. polyosoma_ are more common (at least in museum series) in the Falkland Islands and Patagonia than elsewhere on the continent. From 136 specimens of _B. polyosoma_ (56 juveniles, 5 subadults, and 75 adults) examined in the British Museum Tring, eight of the juveniles were in dark brown plumage, while ten adults specimens were in phase 4 and 5 (one in phase 4, and nine in phase 5). All eighteen dark brown or dark grey specimens originated from the Falkland Islands and Patagonia (for details see Table 19). Vaurie (1962) has seen specimens in these colour phases from other regions as well, but in smaller numbers (referring to adults only, his data concern 13 specimens of phase A and E against 57 of phase B, C, and D for the Falkland Islands, Patagonia and Tierra del Fuego; and for other regions of the South American continent 7 against 51 for the dark and lighter phases, respectively). Little is known about the selective value of these colour phases, and Reynolds (1935) seems to have been the only author to comment on it: "From personal observation of breeding adults in their respective breeding localities south of Magellan's Strait it would seem that environment has an extraordinary effect on the plumage of _Buteo p. polyosoma_. From northern Tierra del Fuego south to Cape Horn the climate varies progressively from moderately to exceedingly wet. The _Buteo_ accordingly are white-breasted as far south as the Beagle Channel, where the light phase meets the greyer variety of the dark phase.

Farther south at Cape Horn the extreme dark brown form is, if not unique, certainly the common bird". This observation suggests that in this species the occurrence of a dark brown plumage is related to conditions of high humidity.

Ad. 2. The "red-tailed" buzzards (B.jamaicensis, B. ventralis) cannot conveniently be separated from the "brown-tailed" buzzards (B. swainsoni, B. solitarius, B. galapagoensis) since both types occur in adult birds of the same species. B. jamaicensis harlani has not a red but rather a greyish brown tail. The "white-tailed" buzzards (B. polyosoma, B. poecilochrous, B. albicaudatus) form a distinct group in this respect.

Ad. 3. The reddish brown colour on the back is more pronounced in the female than in the male of B. polyosoma (the same is probably true for B. poecilochrous), whereas reddish brown patches on the shoulders of B. albicaudatus are equally represented in both sexes.

Ad. 4. Varying degrees of albinism are not uncommon in B. jamaicensis, and is usual in the prairie race B.j. kriderі.
Nonetheless, B. jamaicensis in general, has been classified under 4b.

Ad. 5. Bent (1937) commented already on the downy young of B. albicaudatus as being "an odd-looking chick, quite different from other young hawks"; this now is documented by Stevenson & Meitzen(1946) with a photograph of a 14 days old young (Aransas Refuge, Texas; 25 April 1941).
They describe the downy young as "covered with a dirty-gray, or brownish, down" and "a black mask on the face". Whether this is true for the whole of the rather disrupted breeding range (see Voous 1968) is unknown. Photographs taken in Curaçao, Netherlands Antilles, of young of about ten days and younger suggest a rather homogeneous white down (Voous, pers. comm.). Concerning the colour of the downy plumage in other American buzzard species there is no common opinion either.
To quote Marchant (1960), referring to B. polyosoma :
"Down of nestling is said to be yellowish-white (Housse), but for my birds it was always salmon-pink", the last again is not supported by Perreyra (1937) indicating the down to be yellowish white with somewhat greyer wings (al nacer y hasta los 12 dias era su plumón de color blanco crema algo más obscuro sobre las alas; p. 227). Fitch et al (1946) state for B. jamaicensis : "The downy plumage of the nestlings is white" (documented with photographs), whereas other authors phrase it as "buffy white to grayish white" or "pale smoky gray" (Friedmann 1950), and "first down greyish or buffy-white; later replaced with a woollier white down" (Brown & Amadon 1968). Not all inconsistencies can be explained by different authors referring to either the first or the second downy plumage, although this may be the case with B. polyosoma. There may be some individual and geographic variation in this respect.
The downy chicks of B. poecilochrous, B. ventralis, and B. solitarius have not yet been described.

Ad. 6. The actual length of the wing is evidently considerably influenced by the shape and length of the wing tip, and although generally used as an indication of a bird's body size, it is often inadequate for a more detailed comparison. Therefore an attempt has been made to look for another, less variable, unit which was found in the wing depth.
The wing depth was calculated by subtracting the length of the wing tip from the wing length. The length of the wing tip is the distance from the edge of primary 1 to the edge of the longest primary (in this case primaries 6, 7, or 8; counting the innermost primary as no. 1).

The term wing depth was used to avoid confusion with not well defined but nonetheless often used terms such as wing breadth, wing width, and wing base. In Figure 11. wing depth is given in relation to length of the wing tip; species are arranged in a sequence from large to small wing depth. The wing depths in females of B. albicaudatus, B. polyosoma, B. galapagoensis, and B. swainsoni are practically the same, whereas males of B. albicaudatus have a greater wing depth than the other males, which means that B. albicaudatus shows less sexual dimorphism in this respect.

Ad. 7. B. swainsoni, B. albicaudatus, and B. galapagoensis have the longest wing tip. This is not wholly in agreement with a general rule that, given closely related birds, migrants are longer-winged than resident birds (Kipp 1959) although here too the two migratory buzzards have the outer primaries slightly longer than those of the sedentary Galapagos Hawk. The wing tip is certainly also shaped by hunting method and flight caracteristics (a soaring or a flapping flight), which was already recognized by Bent (1937) for B. swainsoni : "The wings are narrower and slightly more pointed than the redtails [B. jamaicensis]; the wing beats are somewhat quicker and more frequent..."

The relation between wing tip and wing depth for thespecies is given in Table 20, and has been discussed in connection with the tail length in Ad. 10.

Ad. 8. The shape of the wing tip or wing formula was constructed from the distance of the tip of primary 1 to that of 2, 2 to 3, etc.

These distances were calculated in percentages, based on the wing depth as hundred per cent. The wing formulae for eight American buzzards are given in Figure 20. For ease of comparison three auxiliary lines are drawn : line a through the top of primaries 7 and 8, line b through 6 and 9, and line c through 6 and 8. Three types of wing have been recognized :

Type A : primary 8 is longer than p. 6, and slightly shorter than p.7: B. polyosoma and B. galapagoensis.

Type B : primary 8 is much longer than p. 6, and slightly longer than p.7 : B. albicaudatus and B. swainsoni.

Type C : primaries 6 or 7 are longest : B. poecilochrous, B. jamaicensis, B. ventralis, and B. solitarius.

It is interesting to note that in B. galapagoensis the length of the wing tip of adult males differs significantly $(0.05>p>0.01)$ from that of adult females, but not from juveniles. A comparison between galapagoensis and polyosoma has been made in Figure 13.

Ad. 9. Amadon (1965), in discussing the taxonomic value of the shape of the primaries, concludes : "One is led to suggest that the number of notched primaries may not be a very good clue to relationship. ... This is not to say that the character is of no use; it is one of the features showing the Craxirex group to be a monophyletic unit".

Apparently the evidence is not very strong.

Ad. 10. B. galapagoensis has relatively the longest tail (87-88 per cent of wing depth), whereas B. albicaudatus has the shortest (67-68 per cent; see Table 20). A relatively longer tail makes a hawk better manoeuvrable in the air. There is no difference among the sexes of the species examined. Sexes differ, however, in the relative length of the wing tip : the males of B. galapagoensis and B. swainsoni have relatively longer wing tips than their females, whereas the opposite is true in B. poecilochrous.

Those species showing the greatest wing depth (i.e. B. poecilochrous, B. jamaicensis) also have a relatively long tail, but those with a long wing tip may have either a relatively short tail (B. albicaudatus) or a long tail (B. galapagoensis, B. swainsoni). Only detailed studies on hunting behaviour will be able to reveal the aerodynamic significance of these differences in structure.

Ad. 11. B. swainsoni has on an average the smallest claws (21.9 and 22.9 mm for inner and hind claws, respectively), B. ventralis the largest (35.5 and 35.4 mm, respectively). B. polyosoma has been placed in the smaller category although females average over 25 mm in claw length; particularly on the Falkland Islands and Juan Fernandez the females had longer claws than those on the continent. But the average length of the claws of males of B. polyosoma range under 25 mm, a reason to place this species in this category.

Ad. 12. The relation between the lengths of bill and inner claw and between inner claw and hind claw is shown in Figure 14. B. albicaudatus has a relatively large bill, whereas the opposite is true for B. ventralis. Of all species B. polyosoma has the widest range. With respect to claw lengths the ranges of the males of B. polyosoma, B. albicaudatus, B. swainsoni, and B. solitarius overlap at various degrees. B. poecilochrous forms a link of this group with B. jamaicensis and B. galapagoensis is outstanding in showing less overlap in claw and bill length with other females than the male does with the males of the other species.

I have seen no specimens of B. jamaicensis socorrensis from Socorro Island, Mexico; according to Brown & Amadon (1968), this island race has very powerful legs and feet, but they give no measurements.

Ad. 13. Insect capturing raptors such as tropical kites, have short tarsi. Buzzards are versatile predators but even the two species known to be most insectivorous (e.g. B. solitarius, B. swainsoni) have the shortest tarsi of the buzzard species here considered.

Ad. 14. Bird capturing raptors, such as falcons, have relatively longer toes than snake capturing hawks. These conditions are adaptations to the special prey species. This kind of adaptation is not apparent in the length of the middle toe of the buzzards here considered and both prey classes are regularly taken by several of them. The relation between middle toe and tarsus is shown in Table 21. B. swainsoni, B. ventralis, and B. galapagoensis have the greatest index. For B. galapagoensis this may result from the relatively large middle toe, reflecting large, heavy prey taken, rather than from a shorter tarsus; the last named condition is present in B. swainsoni, probably as an adaption to insect capturing.

Ad. 15. Although buzzards have several distinct calls, only from few species detailed descriptions have been given. The classification into two categories is based on differences of the alarm call and/or attention call.

Voous (1955) versed the voice of B. albicaudatus as "kjü-kjü-kjü", which agrees with the description of Brown & Amadon (1968) "a high pitched cackling, like the syllable 'ke' repeated", while they add "It has a tinkling sound that has been compared to the bleating of a goat or the call of the Laughing Gull". Lehmann (1945) states that the call of B. poecilochrous is very similar to that of B. albicaudatus and the laughing of a Grey Eagle Buzzard (Su grito es muy semejante al de albicaudatus y recuerda también la carcajada de Geranoaetus; p. 114).

Calls of B. ventralis have not yet been described. Data on the voice of other buzzards species has been taken from sonagrams available at the Zoological Department of the Free University of Amsterdam (pers. comm. Tj. van Dijk).

Ad. 16. No typical food specialists occur in the species of buzzards here considered, but the distinction of three categories may be valid. B. solitarius and B. swainsoni appear to be mainly insect eating, in addition to feeding on small birds and small rodents. B. ventralis feeds, as far as known, mainly on medium-sized rodents. The remaining buzzards species have a noteworthily broad food spectrum.

The result of the comparison of all the characters presented above is summerized in Table 22.

Two groups of species become apparent : the polyosoma-albicaudatus group (with B. polyosoma, B. albicaudatus, B. galapagoensis, B. poecilochrous, and B. swainsoni) and the jamaicensis-ventralis group (with B. jamaicensis, B. ventralis, and B. solitarius). B. solitărius, although included in the latter group, remains difficult to place. Mayr (1943) related this hawk to B. swainsoni.

Nevertheless a clear-cut separation of the two groups is obscured through a high score of characters shared by poecilochrous and galapagoensis with jamaicensis and ventralis. These four species are similar in structure and strength of feet and claws, while poecilochrous resembles jamaicensis and ventralis in the structures of wing and tail; the colouration of the adult plumage of galapagoensis resembles that in jamaicensis and ventralis. Claws and feet, as well as wings and tail are very adaptable features in birds of prey and therefore seem less suitable to indicate relationship (e.g. B. polyosoma and B. poecilochrous though apparently close relatives, differ considerably in those respects).

7.3 Systematic position of Buteo galapagoensis

By the absence of any fossil evidence, the geographical origin and the systematic relationship of the Galapagos Hawk have to be decuded from a comparison of the characters of the present living American buzzard species.

The small and long-winged North American long-distance migrant B. swainsoni does not seem to be the closest living relative of the Galapagos Hawk. It would only be too speculative to suppose that an early colonization by this species would have changed it into what is now the Galapagos Hawk.

Another North American wide-spread species, B. jamaicensis, has a similar prey apparatus (bill and claws) as the Galapagos Hawk, but other more relevant features, such as the voice and the colour of natal down differ to such an extent that this species has to be placed in another group.

The South and Central American species B. albicaudatus has almost as many features in common with the Galapagos Hawk as B. polyosoma, but B. albicaudatus shows differences in the bill-claw and tail-wing ratios to such an extent as to make it unlikely to consider this species as the closest of the living relatives of the Galapagos Hawk.

In the previous section evidence was given to consider the Galapagos Hawk most similar and therefore most closely allied to B. polyosoma. The variation in plumage of B. polyosoma (5 phases in the adult plumage) does not seem to be an unsurmountable objection, since the dark brown plumage seems to predominate in its southermost range, while in the island form of Juan Fernandez, B. polyosoma exsul only one or two colour phases are known to occur. As regards the Galapagos Hawk, one must accept that the reduction of colour phases has gone as far as the loss of even the white in the tail, present in all phases of the adult, but not the juvenile plumage of B. polyosoma. In addition the Galapagos Hawk has developed a noteworthily heavy bill and claws.

COMPARISONS WITH BUZZARDS ON OTHER OCEANIC ISLANDS

Buzzards on oceanic islands in the Pacific and Atlantic - such as the Hawaiian Islands, Juan Fernandez Islands, Cape Verde Islands, Canary Islands, Madeira and The Azores - differ in many ways from continental species, on account of both the degree and duration of isolation and the subsequent adaption to a characteristically poorly diversified environment. These islands are volcanic in origin, having arisen form the ocean floor; they are considered never to have had any continental land connection. As a result of this isolation, land mammals, reptiles and amphibians are either poorly-represented or absent, and the buzzard's prey has come to consist mainly of insects, birds and carrion. It was as a consequence of human settlement that rats and mice (and many other, less important, prey species) became an additional source of food, changing the original food spectrum which in many cases will remain unknown. The Hawaiian and Canary Islands had a native human settlement; the other islands here considered were first colonized by man in post-Columbian time.

The Hawaiian and the Juan Fernandez Islands are geologically younger than the Galapagos Islands. The islands in the Atlantic Ocean are of late or midden Tertiary origin.

In the following sections Buteo solitarius, Buteo polyosoma exsul, and Buteo buteo subspecies will be considered. Some adaptations will be discussed in relation to available prey species and to other predators.

8.1 Hawaiian Islands and Juan Fernandez Islands.

The Hawaiian Islands are remote from any continent, about 2500 miles from north America and 5000 miles from the Philippines. The archipelago comprises eight main islands and many islets forming altogether a chain sixteen hundred miles in length. The major island, Hawaii, situated at latitude 20° North, has an area of over 10.000 square kilometres.

The climate is subtropical to temperate , temperatures varying greatly according to altitude. The summit area (4206 metres in altitude) of the island of Hawaii may bear snow in winter.

Most of the surface areas visible in the Hawaiian Islands today - except on Hawaii itself -date from the Pliocene, between one and five million years ago. The island of Hawaii has lava flows mostly less than a million years old and is thus an island of the pleistocene Ice Ages (Carlquist 1970).

Land mammals (except one species of bat), reptiles, and amphibians are not native to the island. Lizards, Black Rats Rattus rattus, Norway Rats Rattus norvegicus, Polynesian Rats Rattus exulans, House Mice Mus musculus, rabbits, goats, and Small Indian Mongoose Herpestes auropunctatus, cats, and dogs have been introduced by man (Tomich 1969).

The Hawaiian Hawk Buteo solitarius is only known from the Island of Hawaii. Insects and very likely birds have been in early days its main prey, but only few actual data exist (Hawaii Audubon Society 1967, Carlquist 1970).

Originally, only two other predatory birds, the Short-eared Owl Asio *flammeus sandwichensis* and the Hawaiian Crow *Corvus tropicus*, may have competed for food with the buzzard. The crow is also restricted to the island of Hawaii; the owl on the other hand has been recorded on all main islands. Nothing seems to be known of the prey originally taken by these predators. It is feasible that the presence of the Short-eared Owl prevented the Hawaiian Hawk from colonizing the smaller islands of the archipelago.

The Hawaiian Hawk has suffered greatly from human persecution and introduction of land predators. It is now very rare; estimated numbers are not known, but there are apparently less than 200 birds (I.U.C.N. Red Data Book, 1966).

The Barn Owl has been recently introduced on two islands (Hawaii, Kauai). The Osprey, Marsh Hawk *Circus cyaneus* and Peregrine Falcon are recorded as migrants.

The Juan Fernandez Islands are situated over 300 miles from the Chilean coast at latitude 33° South. The archipelago comprises two islands and some islets. The island of Masafuera (Alexander Selkirk) lies 400 miles from the coast and has an area of 64 square kilometres; 90 miles to the east lies the slightly larger Masatierra (Robinson Crusoe).

The climate is moderately cool with considerable variation in rainfall from year to year. Dense fogs frequently cover the mountains. Snow is reported as settling on the summit of Masafuera (1650 m).

The islands are considerd to be of late Tertiary or Pleistocene age. Land mammals, reptiles, and amphibians are not native to the islands. Black Rats, House Mice and goats have been introduced by man.

The Red-backed Buzzard *Buteo polyosoma exsul* is a resident of Masafuera only. Lönnberg (1940), quoting K. Bäckström, gives the foodlist of this buzzard as follows: "I have seen them attack young kids (of goats) left behind and catch petrels, thrushes and Lophortyx (quails)". Johnson (1965) states: "They subsist principally on rats and mice but are reported to have harried the shearwaters (*Pterodroma*) to such an extent as to force them to enter their burrows at night whereas on Masatierra the same species continues to come and go during daylight hours". This statement regarding *Pterodroma* (gadfly petrels) has to be viewed with caution as several species are involved: on Masatierra, *Pterodroma cooki defilippiana* and *P. neglecta* leave the colony in broad daylight; while on Masafuera, *P. externa externa*, and also probably *P. leucoptera masafuerae*, is normally away from land during the day. Therefore the difference in daily rhythm among these petrels has to be attributed more to interspecific competition for food rather than to hawk predation.

On Masatierra, where the Short-eared Owl *Asio flammeus suinda* and the Kestrel *Falco sparverius fernandensis* are residents, the buzzard is only a casual visitor. Lönnberg (1940) states for the Kestrel: "It feeds almost exclusevely on the very numerous spiders. Its absence from Masafuera is probably due to lack of food there, i.e. the scarcity of large spiders and the almost complete absence of grasshoppers, which constitute its main food on Masatierra". The Short-eared Owl (for which I have found no foodlist) and the Kestrel exploit the potential preys present on Masatierra, which apparently have been insufficient for the buzzard. Only detailed studies can reveal the inter-specific differences and their effect on the present distribution of these predators. It is said that about 50 pairs of buzzards still occur on Masafuera.

Swainson's Hawk *Buteo swainsoni*, Long-winged Harrier *Circus buffoni* and Black Vulture *Coragyps atratus* have been recorded as accidental visitors (Lönnberg 1940).

8.2 Cape Verde Islands, Canary Islands, Madeira, Azores

In addition to the Pacific islands, these Atlantic islands have been included for comparison as the geographic origin of buzzards living in these latter archipelagoes is known. Differences between continental and island forms may reveal trends of adaptation of a predator in relation to its prey. A short description of predators and prey species is here given; details of flora and fauna can be found in Allorge et al. (1946), Volsøe (1951, 1955), and Bannerman (1963, 1965, 1966, 1968).

The Cape Verde Islands, situated at latitude 16° North, about 45 km (280 miles) from the west coast of Africa, comprise ten islands and some islets with a total area of 4033 square kilometres.

The archipelago is considered to be of middle Tertiary origin (Bannerman & Bannerman 1968). This is still disputable, some islands have probably emerged more recently, since volcanic strata have been found covered with sedimentary rock of pleistocene origin (On les avait attribuées (les couches sedimentaires calcaires) au Tertiaire en raison des fossiles de mollusques qui, *en Europe*, habitaient en effet les eaux chaudes du Miocène; mais ces mêmes mollusques se retrouvent de nos jours dans les mers de la zone intertropicale. ... L'ile (Sal) présente donc ce contraste de cônes volcaniques relativement anciens (?) et d'un socle géologiquement récent...; de Naurois & Bonnaffoux 1969).

The climate is subtropical to temperate and dry; scarce and irregular rains are typical (Bannerman & Bannerman 1968).

There are no native land mammals (apart from a species of bat), and no amphibians. Native reptiles (a skink, lizards and geckos) do occur. Amongst others, Black Rats, House Mice, and goats have been introduced by man.

Buteo buteo bannermani has been recorded from five islands (Santo Antao, São Vicente, Boavista, São Tiago, and Fogo). Almost all that is known about this buzzard has been summarized in a few lines by de Naurois (in Bannerman 1968): "In former days *Buteo buteo bannermani* was well known on Santiago and was thought to have disappeared from Sao Vicente and Boa Vista, on which last two islands we certainly did not find it. The buzzard population of Santiago is down to a dangerous low level, perhaps less than twenty pairs. No one had previously made observations on the breeding of this buzzard. After a long search on Santiago, we found one nest in rocks on a steep slope. Unfortunately the bird was sitting on an intertile and abnormally small egg. We can only suggest that eggs are laid in autumn or at the beginning of winter" (p. 278). According to Moreau (1966) the buzzard nests only in the higher parts of the islands (p. 317: "It is interesting that of the species shared with both Europe and tropical Africa two that are widespread in the latter area breed there only at high altitudes connoting cool climates, namely the quail *C. coturnix* and the buzzard *B. buteo*; so that these also are most likely to have established themselves in the Cape Verdes during a glaciation"). De Naurois (1969) states: "En 1968, toujours sur Santiago, nous pûmes identifier 5 aires comprises dans un rectangle de 4 km de longueur sur 1 km de largeur (entre les altitudes de 500 et 900 m)...". In a footnote he adds: "R.E. Moreau (1966, p. 317) fait remarquer que cette espèce paléarctique occupe au cap Vert les régions de haute altitude. Ceci n'est pas tout à fait exact. Nous avons observé la Buse en vol à 300 m, au nid à 500 m". The highest point of Santiago is 1392 metres; whatever one considers 'high altitudes', the buzzard is apparently absent from the hot and arid lowlands.

The relatively large numbers (8 species) of other resident avian predators has limited the range of niches this buzzard might otherwise have occupied. On the five islands where the buzzard is (or was) a resident, it lives alongside the Osprey Pandion haliaetus, Black Kite Milvus migrans and/or Red Kite Milvus milvus fasciicauda, Kestrel Falco tinnunculus (ssp. neglectus or ssp. alexandri), Egyptian Vulture Neophron percnopterus, and the Brown-necked Raven Corvus ruficollis; the Barn Owl Tyto alba detorta has been recorded on four of these islands (de Naurois 1969). The Peregrine Falcon Falco peregrinus madens has been found breeding on two islands, on both of which buzzards are absent.

Virtually nothing is known of the food of the buzzard. In stomachs of kites remains of goat, rodents, small birds, and lizards have been found (de Naurois 1969); offal and young poultry also form part of the food of kites. Kestrels feed on small birds, mice, lizards, cockroaches, grasshoppers, and beetles (Bannerman & Bannerman 1968). Vultures and ravens are scavengers, their numbers probably having increased as a consequence of human settlement; they have been seen hunting grasshoppers. The Barn Owl feeds on rats, mice, small birds (petrels and passeriformes), geckos, and insects (de Naurois 1969).

Only further field studies can evaluate the degree of inter-specific competition and the manner of coexistence of so many different species of birds of prey in this archipelago. The coexistence of buzzard, kites, kestrel, and vulture is of particular interest as all these species seem to depend to some extent on the same food source.

In addition to the resident raptors only the European Kestrel Falco tinnunculus tinnunculus has been recorded as a migrant; there is one doubtful (sight) record for the Montagu's Harrier Circus pygargus (Bannerman & Bannerman 1968).

The Canary Islands, situated at latitude 28° North, about 100 km (some 60 miles) from the west coast of Africa, comprise seven islands and some islets, with a total area of 7580 square kilometres.

The archipelago is considered to be of late Tertiary (Pliocene) origin, arisen from the ocean floor. Yet Bravo (1953) believes that during the Miocene, fracturation and submersion of the continental platform occurred, and during this process the islands were formed. Sauer & Rothe (1972) have given further evidence to consider at least the eastern islands of continental origin in discovering ostrich eggshell fragments on Lanzarote.

The climate is subtropical to temperate, according to altitude. The Peak of Tenerife (3718 m) is snow-covered in winter.

There are no native land mammals (except bats) and no native amphibians, but native reptiles (lizards, geckos) do occur. Black Rats, House Mice, rabbits, goats, and frogs have been introduced by man.

Buteo buteo insularum has been recorded as breeding on practically all the islands. Heavily persecuted by man it is now very are on the eastern islands (Lanzarote, Fuerteventura) and its numbers have diminished considerably at former strongholds on Gran Canaria and Tenerife. Lizards, grasshoppers, beetles, and rats have been reported as its prey (Lack and Southern 1949, Bannerman 1963).

There are 15 different avian predators resident in the archipelago. The coexistence of so many birds of prey can only be understood against the background of differing habitats and available prey species. Attempting a detailed analysis is beyond the scope of this paper, but some brief information is given in Table 23. It is likely that kites and kestrels compete with the buzzard for food, as on all islands where they occur they live alongside each other.

In addition to the resident species the following bird of prey species have been recorded as migrants: Honey Buzzard Pernis apivorus, White-tailed Eagle Haliaeetus albicilla, Black Kite Milvus migrans (one sight record), Marsh Harrier Circus aeruginosus, Montagu's Harrier Circus pygargus, European Kestrel Falco tinnunculus tinnunculus (probable, no specimen collected), Red-footed Falcon Falco vespertinus, Hobby Falco subbuteo, Peregrine Falcon Falco peregrinus (likely, but not identified to race), Tawny Owl Strix aluco, and Short-eared Owl Asio flammeus, but apparently none of these plays a significant role in the islands' ecology. Their occurrence further underlines the relatively unisolated position of the archipelago.

Madeira, with a few small satellite islands, is situated at latitude 33° North, about 800 km (some 500 miles) from the west of Africa; it has a total area of 720 square kilometres. The island is of volcanic origin and probably dates back to Eocene times. (Upwelling of volcanic materials began from a depth of 4000 metres on the ocean floor.)

The climate is temperate to subtropical and strongly influenced by trade winds. Winds from the Sahara bring drought, sometimes sand, and even swarms of desert locusts. There are neither native land mammals nor amphibians; native reptiles (lizards, geckos) do occur. Madeira ("island of the wood") has suffered sweeping changes as a result of fires caused by man; Black Rats, House Mice, and frogs have been introduced.

Buteo buteo harterti is still common on Madeira (Bannerman & Bannerman 1965, Schindler 1965), where it occurs from the sea cliffs to the island's summit (1861 m). Small birds, insects, and reptiles are mentioned as its prey, but no further detail is given by Bannerman (1965). It is of interest to note that the buzzards on Madeira exhibits a greater sexual size dimorphism than buzzards on the other Atlantic islands (based on comparison of wing lengths). There are only three other resident predators, the Kestrel Falco tinnuculus canariensis (recorded prey : lizards, grasshoppers, crickets, mice, small birds), Sparrow Hawk Accipiter nisus granti (prey : pigeons), and Barn Owl Tyto alba schmitzi (analysis of 32 pellets : 21 rats, 50 mice, 1 petrel, 1 blackbird, 1 canary, and 23 grasshoppers).

The following predatory birds have been mentioned (Bannerman & Bannerman 1965) as regular migrants or accidental visitors : Osprey (rare), Marsh Harrier (one specimen), Montagu's Harrier (one specimen), Hobby (rare), Peregrine Falcon (apparently no confirmed record), European Kestrel (probably regularly, but few definite records), Short-eared Owl (common), Scops Owl Otus scops (common in certain years), Egyptian Vulture (rare), and Raven (rare).

The Azores situated at latitude 38° North, about 1400 km (880 miles) from Portugal and about 1700 km (1080 miles) from the nearest coast of America (Newfoundland), comprise nine islands and some islets with a total area of about 2300 square kilometres. The southernmost island Santa Maria lies 750 km (some 460 miles) from Madeira. The climate is temperate to subtropical and much influenced by anticyclonic conditions present on the eastern side of the subtropical North Atlantic. Subtropical weather, with winds from the northeast to southeast, prevails in the summer; western gales are typical of the winter. Rainfall is abundant and well distributed throughout the year. The mountain of Pico (2320 m) has snow for a few days in the year only. The archipelago is considered to be of Tertiary (Miocene) origin.

There are no native land mammals (except one species of bat), no native amphibians, nor reptiles. Frogs, lizards, rats (Rattus rattus, R. norvegicus), mice, rabbits, goats, Weasels Mustela nivalis, Ferrets M. putorius furo have been introduced by man (Ulfstrand 1961).

Buteo buteo rotschildi has been recorded from seven islands (it is not represented on the westernmost islands, Corvo and Flores). Surprisingly little is known about this bird. At one time it was very abundant; the archipelago probably owes its name to this buzzard (açor meaning goshawk or any large bird of prey). Its food consists of rats, poultry, and carrion (Bannerman & Bannerman 1966); originally insects and small birds were most likely the principal prey.

The only other resident predatory bird is the Long-eared Owl Asio otus otus, so far recorded from four islands. Starlings are on the foodlist of this nocturnal species. It is considered to be a rather recent colonist from Europe.

The Azores, although further away from the continent than the other Atlantic islands considered, apparently are regularly reached by various migrants, probably as a result of meteorological conditions. The following predatory birds have been recorded : Osprey (rare), European Kestrel (rare), Lesser Kestrel Falco naumanni naumanni (one specimen), Barn Owl (one doubtful record), Short-eared Owl (two records), Snowy Owl Nyctea scandiaca (one specimen), Egyptian Vulture (one specimen), Carrion Crow Corvus corone (uncommon), Rook Corvus frugilegus (occasionally in flocks), Jackdaw Corvus monedula (one specimen), the Golden Eagle Aquila chrysaetos, Peregrine Falcon, and Tawny Owl Strix aluco are given as unconfirmed single records (Bannerman & Bannerman 1966).

The paucity of resident avian predators is thus unlikely to be caused by the isolated position of the archipelago as individuals of many species have arrived in the islands, but for some reason (e.g. the lack of diversity of prey species) have been incapable of successful colonization.

8.3 Seven Islands of Izu, Bonin Islands

The Seven Islands of Izu and the Bonin Islands are situated in the Western Pacific Ocean. They lie about 140° longitude East (position of Tokyo) and form a long chain, almost in a straight line from north to south, of some 1000 km (Izu's 35° - 32° and Bonin's 28° - 26° latitude North).

The buzzard Buteo buteo toyoshimai is not uncommon in the Bonin Islands, but nothing has been reported of its feeding habits (Dr. Yamashina, in litt.). Wing measurements given by Yamashina are 356-386 mm for 14 adult females, and 335-350 mm for 5 adult males. Bill lengths of male and female appear to have considerable overlap : 22.0 - 28.0 mm (14 females) and 22.5 - 25.5 mm (4 males). Therefore the differentiation in size and structure between males and females of this insular buzzard is still incompletely known. Further studies are required, both of prey species and other predators present, to enable an adequate comparison with situations on other islands.

DISCUSSION AND CONCLUSIONS

Quite a number of land birds have broader niches or feeding stations on islands than they have on the mainland (see Lack 1969). Islands have less diversified ecological conditions and one generalised species may occupy niches filled by several species on the mainland. Birds of prey appear not to be an exception to this rule; in fact, very few specialists have been able to colonize islands. It cannot be without significance that such a versatile predator as a buzzard is the sole diurnal resident bird of prey on various oceanic islands, e.g. Galapagos, Hawaii, Azores. The Canary Islands are the only islands which have a notable specialist, in the presence of Eleonora's Falcon (in addition to other predators including kite, sparrowhawk, kestrel, peregrine, vulture). The relative abundance of species of birds of prey on the Canaries in comparison with the Azores can be explained by the size of the archipelagos (the Canaries are three times the area of the Azores) and the diversity of the flora and fauna : flowering plants 1531 versus 610 species, land and freshwater birds 53 versus 22 species (Lack 1969).

The Galapagos are about three times the size of the Azores and have 553 species of flowering plants (Wiggins & Porter 1971) and 35 species of land and freshwater birds. Madeira, one tenth the size of the Galapagos, has more species of flowering plants and less species of land and freshwater birds (690 and 37 species; Lack 1969) than the Galapagos; yet, Madeira has three species of resident diurnal birds of prey. What do these figures mean in terms of resident predators and their prey? I am convinced that they are no more than a reflection of the diversity of the flora and partly of the fauna, and may be used as an indication of the diversity of prey species, but not of the actual numbers of available prey. Whereas the absence of a variety of diurnal resident birds of prey on the Azores is evidently caused by ecological factors (the lack of diversity of prey species) the presence of but one species of buzzard in the Galapagos (as well as Hawaii) is likely to be caused principally by the isolated position of the islands which make them difficult to reach. Lack's general conclusion that the small numbers of resident bird species on islands are due, not to difficulties of dispersal, but to ecological limitations, holds true for birds of prey on the Azores, but not on the Galapagos and Hawaii. In fact one could well argue that by the absence of other diurnal birds of prey the Galapagos Hawk has been able to develop such a high degree of sexual size dimorphism, that male and female occupy different food niches and in this respect act as two species.

I am therefore inclined to ascribe the presence of only one resident diurnal species of bird of prey in the Galapagos to ecological limitations, combined with a lack of dispersal capacities of other South American birds of prey. Had the kestrel (in this case : Falco sparverius)been able to reach the Galapagos before the buzzard , it would have occupied the 'kestrel niche' - at present taken over by the buzzard and partly by the nocturnal Barn Owl combined. The questions are, whether there ever existed a 'kestrel niche' in the Galapagos Islands and whether under present Galapagos Island conditions buzzard and kestrel could live alongside each other. Significant in this context is the situation in the Juan Fernandez archipelago where both buzzard and kestrel occur, but on two different islands. The fact that the buzzards on the Atlantic islands differ only slightly from the nominate form may indicate that (1) they are recent colonists (made possible by recent faunal turn-overs during the pleistocene Ice Ages), which have not yet had time to differentiate; or (2) they have been resident already for a long time but gene-flow through new arrivals has limited differentiation; or (3) ecological conditions have been so much the same as those in continental Europe that no differentiation did occur. Insular races of Buteo buteo, described by various authors, have not been recognized by recent authorities (Vaurie 1961, Brown & Amadon 1968). Vaurie (op. cit.) states that he is "unable to find any constant character to warrant the recognition of any insular race". He gives measurements for wing lengths which indicate that the Madeira buzzard has a greater sexual dimorphism than the other island forms, but they fall well within the limits of continental buzzards.

	males	females
Cape Verdes	-	185+ (1)
Canaries	363.7 (4)	374.4 (3)
Madeira	380.6 (5)	420.6 (3)
Azores	351.9 (13)	368.7 (10)

+ almost certainly misprint for 385

The figures given by Brown & Amadon for the nominate form range from 350-400 mm (males) and 375-425 mm(females).

Sexual dimorphism in colour of the plumage in island buzzards is very much reduced (Juan Fernandez) or completely lacking (Galapagos).

Sexual size dimorphism appears to be most pronounced on islands with few resident species of birds of prey (Galapagos, Hawaii). Probably this is also the case among buzzards on Juan Fernandez and Madeira, but exact data are too scanty.

Reynolds (1972), referring to the genus *Accipiter*, attributes the smaller size of the male to the birds' hunting habit; the male is the major food provider and foraging efficiency increases with reduction in body size; for there is a greater variety and abundance of prey among smaller species. The larger female takes the larger, mostly less agile, and the same time less numerous prey. The dominance of the female in this pair relation is in Reynolds' opinion the consequence, and not the cause, of this type of sexual size dimorphism. This hypothesis gives no clear explanation to the fact that the female is invariably the larger of the sexes, unless one assumes that in all habitats, at all seasons, an avian predator is better off when catching the smaller prey - be it birds or rodents. This may be the case in the Galapagos Hawk, in which the female during the breeding period takes the larger marine and land iguanas (if available), carrion (if available), and rats, and such small hidden prey as centipedes; whereas the male deals with those species, which are numerous in the breeding season, such as doves, rats, finches, and lizards.

As a matter of fact I have no record of a female buzzard catching a Darwin's finch. Outside the breeding period the greater size of the female allows her to exploit the larger prey without competing with the male - the latter having to suffice with the now less numerous smaller prey. However, I have seen a pair of hawks (outside the breeding period) in their territory jointly eating from a land iguana (which had most likely been killed by the female). Whereas the female rarely hunts during the breeding period (when her main task is to incubate the eggs and guard the young)and is fed by the male, outside the breeding period she may make kills from which the male, in his turn, profits. Although the difference in prey species caught by male and female might be correlated with differences in body size and structure of the birds and thus in hunting methods, the difference in the food caught by two males in the same territory and brought to the same nest was more difficult to interprete. These males did not seem to divide the available territory, but the difference in preys caught seemed to indicate individual difference in hunting skill or in 'searching image'. This latter concept means that birds are thought to follow imprinted images obtained by previous hunting successes and that they subsequently catch types of prey more frequently, leaving other potential preys unharmed (see Tinbergen 1960). Rats, the hawk's staple food, however, were caught by both males to the same degree.

In some instances more black finches (adult males of ground finches) than brownish grey finches (juveniles, females and some males of ground finches) were caught than corresponded with the ratio of black and brown individuals present in the area. Unless this high ratio black birds is associated with some aspect of the behaviour of the adult males (which seems unlikely), it can only be related to the colour of the plumage. This fits in with Pielowski's (1961) conclusion that Goshawks *Accipiter gentilis* primarily select those pigeons as prey which differ from the colour of most other birds of the group. (In his study area Goshawks took more white from a flock of mainly dark individuals than would be expected from the ratio white/dark pigeons present, and vice versa). No satisfactory explanation has been given as to why adult male Galapagos ground finches are black (with various intermediate, partly black and brown, colour forms). In this connection it is of interest that Lack (1947) could not detect anything in the courtship behaviour to suggest that the black colouration was significant in the display of these finches. The colour, therefore or colour-pattern, of these ground finches may have some cryptic significance. Bowman (1961) supports this in stating : "Natural selection has regulated the population make-up in such a way that during the most critical time of the year (the end of the dry season) there is for each species and for each sex of the species an optimal proportion of the most advantageous plumage morphs. Hence in an environment where there are pronounced contrasts in background coloration, it is significant, I believe, that equally pronounced contrasts in plumage coloration also exist" (p. 197-198). Black ground finches feeding among dry grasses and the reddish brown cinders of Sant Fe are most conspicuous- at least to a human observer. The absence of black lava fields on this island renders these birds at a disadvantage in terms of hawk predation. However, if Bowman's opinion gives the correct and complete picture of the situation, then it is not clear why black birds still exist on Santa Fe.

The Galapagos Hawk is the only bird of prey known to be polyandric to the extent that two males may copulate with a female, incubate the eggs, and bring prey to the female and young. This 'tri-bond' may continue for several breeding periods. A case has been reported in the Bateleur Terathopius ecaudatus, an African snake hawk, in which a third adult bird, identified as a male, frequently associated with a breeding pair throughout the breeding period;but in this instance the second male was not observed to take part in incubation or the rearing of the young (Brown & Amadon 1968).

Surprisingly few detailed ecological studies of buzzards have been undertaken. This cannot be because buzzards are uncommon. The migration of Buteo swainsoni has been called "the most impressive avian gatherings in North America since the demise of the Passenger Pigeon" (Brown & Amadon 1968), yet, to my knowledge, no ecological study has been undertaken, and Bent (1937) is still the best author to consult for general information on most of the North American buzzards. Published data on South American buzzards, however, are too inadequate in practically every aspect to allow comparisons to be made with the Galapagos Hawk. Food data are given in general terms, as for example Buteo polyosoma : "cavies and other small mammels" (Hudson 1920); "small mammels and birds, reptiles and snails, among which rats and various kinds of mice are by far the most numerous" (Johnson 1965); and "chiefly mammals" also doubtless birds when obtainable, and probably snakes. Known to eat lizards, frogs, grasshoppers and other orthoptera" (Brown & Amadon 1968). For Buteo poecilochrous Lehmann (1945) mentions rats, doves, lizards, and beetles; and de Macedo (1964) found rodents and tinamous as prey remains at a nest of this buzzard. For Buteo albicaudatus in Texas (U.S.A.) Stevenson& Meitzen (1946) record a variety of preys, but a quantitative food study was not undertaken : eight species of mammals (mainly rabbits and pocket gophers), ten species of birds (mainly Bob-white Quail and Meadowlark), six species of reptiles (various snakes), and insects. No information was given on the duration of incubation; one young left the nest after 47 days.

Since a comparison with South American buzzards is not feasible with this dearth of published information, data on the Galapagos Hawk will be collated mainly with those derived from publications on the Red-tailed Hawk Buteo jamaicensis and the Common Buzzard Buteo buteo, with a few remarks on Swainson's Hawk B. swainsoni and the Red-shouldered Hawk B.lineatus.

At times sea birds do form part of the food spectrum of the Common Buzzard (although not mentioned in Glutz von Blotzheim et al.1971); in this respect the Galapagos Hawk is thus not exeptional in the genus. According to Davis & Saunders (1965), Common Buzzards on Skomer Island (one mile off the southwest coast of Wales, Great Britain) feed predominantly on rabbits and Puffins Fratercula arctica, but apparently not on the numerous shearwaters present.

Craighead & Craihead (1956) present data on food items of B.jamaicensis, B. swainsoni, and B. lineatus, and have made estimates of food requirements for various raptors (e.g. B. jamaicensis : 136 grs 117 grs per day in fall/winter for female and male, respectively; 73 grs per day in spring/summer for the male).

Fitch et al. (1946) comment on "the slightly more rapid cadence of wingbeats" of the male Red-tailed Hawk in comparison with the female, a difference also known in B. buteo. When members of a pair of either B. buteo or B. jamaicensis are seen together, the larger size and more robust build of the female are easily recognizable characters. During the period of nest building these buzzards are extremely wary in avoiding dectection; their behaviour agrees with that of the Galapagos Hawk of which I have rarely been able to observe actual nest building. Towards the end of the fledging period adults remove unused food less consistently, and the nest becomes littered with portions of old carcasses; this was not observed in the Galapagos Wawk, which continued to keep the nest clean. Red-tailed Hawks studied by Fitch et al. (l.c.) were aggressive and usually swooped at their investigators when climbing to the nest, a habit I often painfully experienced myself in similar encounters with the Galapagos Hawk. The diversity of prey species taken by the Red-tailed Hawk in California is well demonstrated by the fact that among 625 prey items (comprising a three years' record of fourteen different nests) there were represented no less than 23 species. However ground squirrels (380), pocket gophers (79), and rabbits (62) formed the bulk of the prey (91.6 per cent of biomass), and only 22 preys (7 species) were birds, eleven of which were quail. Luttich et al. (1970) have studied a migratory population of Red-tailed Hawks in Canada. During a four years' period 2553 prey items (at 54 nests), brought to tethered young, comprised fifty species. Mammals, mainly ground squirrels and hares, accounted for 66.3 per cent of the prey biomass (although mice provided 31 per cent of total prey occurrence, they made up only 4 per cent of total biomass of prey taken) and 33.7 per cent were birds (31 species), mainly ducks and coots. The average quantity of food brought to 44 nests was 547 grs per day. This is considerably higher than my calculations (358 grs; average of 10 nests) for the Galapagos Hawk. The mean initial brood size of 1.9 nestlings per breeding pair with young (versus 1.6 for the Galapagos Hawk) probably does not account for all the extra food brought to the nests of the Red-tailed Hawk. This appears unlikely as according to Luttich "there was no tendency for more food to be brought to those nests having greater numbers of young". The ultimate success of the Red-tailed Hawk was higher than that of the Galapagos Hawk, but this was influenced by other factors as well (see later).

The reproduction and survival rates of four species of Buteo are presented in Tabel 24. The mean clutch size of the Galapagos Hawk was slightly smaller (as compared with the Red-tailed Hawk; Luttich et al. 1971) while hatching success and nestling mortality were both considerably lower and first year mortality was probably higher. The relative higher nestling mortality in the Red-tailed Hawk resulted from predation by Great Horned Owl Bubo virginianus (Luttich et al. 1971) and from attacks of blood-sucking flies Eusimulium clarum (Fitch et al. 1946), whereas most of the first year mortality had to be attributed to birds being shot by man. None of these factors plays a role in the life of the Galapagos Hawk. The high breeding success of the Broad-winged Hawk, and to a lesser extent that of the Common Buzzard, resulted from a combination of high clutch size, high hatching percentage, and relatively low nestling mortality.

In view of the above considerations and comparisons, my conclusion regarding the regulation of numbers in the Galapagos Hawk is, that the extremely low hatching success and high death rate in the first year are the prime factors asserting control over the population. The high death rate of first years is not caused by predation but rather by food shortage.

Incubation and fledging periods are longer in the Galapagos Hawk than in other buzzards so far studied. The most thorough study on this point undertaken on the Common Buzzard indicated an incubation period of 33-35 days and a fledging period of 42-49 days (Mebs 1964). In the Red-tailed Hawk the incubation period is about 28-32 days, usually 30 days (Brown & Amadon 1968), whereas the fledging period is given as 45-46 days (Fitch et al. 1946) and as 44 days (Luttich et al. 1971). For the Galapagos Hawk I found incubation and fledging periods to be 37-38 days and 50-60 days respectively. The Galapagos Hawk reached breeding-age later than currently recorded for the Red-tailed Hawk and the Common Buzzard. Mebs (1964) states for the Common Buzzard that "maturity is probably reached only with two years on the average". Luttich et al. (1971) mention that the "reddish rectrices of the adult plumage do not normally appear before the second summer of life, and thus at the start of the breeding season red-tailed birds are at least 2 years of age". I found it exceptional for the Galapagos Hawk to be breeding by the age of two years. The postponing of maturity, then, is a further factor limiting the population-size, but the reasons for this delay in maturity are at present unknown. Only further investigation of ringed birds will reveal if the average life span of adult buzzards in the Galapagos Islands is longer than that of buzzards elsewhere.

The conclusions on the taxonomy of eigth American *Buteo* species, based on the comparison of a series of characters, subsequently raise the question whether the number of shared characters is in fact a reliable indication for the degree of relationship at all. Particularly since one may expect that closely related, sympatric species usually have less characters in common than equally closely related allopatric species. This may indeed be the case in the sympatric pair of *B. polyosoma* and *B. poecilochrous* in comparison with the allopatric *B. albicaudatus*, the last named two species have 8 and 13 characters, respectively, in common with the first. These three species were already recognized by Stresemann (1925) to be closely allied, mainly based on the similarity of the colour of the adult plumage, whereas *polyosoma* and *poecilochrous* were separated on different wing formulae. Vaurie (1962), studying *polyosoma* and *poecilochrous* came to the same conclusion, giving evidence to consider them as distinct species. The Galapagos Hawk is considered to be most closely allied to *B. polyosoma*. This conclusion is mainly based on similarity of the call-notes and the colour of the downy chick. Both species have the same wing formula, but since this is a very adaptable feature, it cannot be considered a conclusive character. Furthermore, *B. polyosoma* is widespread in western and southern South America : west of the Andes from the tropical to the parámo zone in Colombia, Ecuador, Peru and Chile; in Argentina particularly in the Patagonia pampas; further in Tierra del Fuego, and the Falkland and Juan Fernandez Islands (de Schauensee 1971). The widely distributed occurrence of this species is an indication that it could have been within the possibilitie to colonize the Galapagos Islands in past times, but it must be admitted that it is not supported by present evidence of stragglers in this part of the Pacific.

SUMMARY

A total of some 120-150 pairs of Galapagos Hawk *Buteo galapagoensis*, endemic to the Galapagos Archipelago, Ecuador, survive on the following islands : Pinta, Marchena, Fernandina, Isabela, Santiago, Santa Cruz, Pinzón, Santa Fe, and Española. It has been exterminated by human persecution on San Cristóbal, Floreana, Baltra, Seymour, and Daphne, and is on the verge of extinction on Santa Cruz. Although numbers have decreased considerably during the last fifty years, especially on inhabited islands, e.g. on Santa Cruz where they have dwindled from several hundreds to not more than two pairs, the species does not seem to be in immediate danger of extinction. It is one of the tamest *Buteo* species in the world; a human visitor can approach and feed a wild bird from the hand.

Adult birds are from dark to sooty brown; juveniles are buffy white, streaked with dark brown. The male can be distinguished by its smaller size and slender build : wing length of the male is 91 per cent that of the female; in weight the proportion is 73 per cent; in hind claw (as a measure of killing power) it is 81 per cent.

Individuals of the species hold the same territory for many years, and probably normally mate for life. The average area for seventeen territories on Santa Fe was 117 ha.

Nesting took place in the arid regions - never in the humid highlands. Breeding was recorded in all months, but in years with heavy rainfall in the hot season (January - April) a peak of breeding activity was observed in June/July, with a second clutch of some pairs in October/November. Consequently, the breeding cycle is irregular in not following a distinct annual pattern.

Polyandry, with two or three males forming a bond and freely mating with one female, occurred not infrequently. The males assisted with incubation and in dyandric pairs both males provided prey for the young. The food brought to the nest has been calculated at 358 grs per day for female and young together. The incubation period was recorded as 37-38 days and the fledging 50-60 days; both periods appear to be longer than those known for other *Buteo* species. Maturity is probably reached at three, or more, years. The Galapagos Hawk is a versatile predator. Indigenous rats (*Oryzomys* spp.) and ground doves (*Nesopelia galapagoensis*) formed the main prey; lava lizards (*Tropidurus* spp.), Darwin's finches (*Geospiza* spp.) and centipedes (*Scolopendra galapagoensis*) were also taken, but at places where these did not occur the Galapagos Hawk reared its young on marine iguanas (*Amblyrchynchus cristatus*), shearwaters (*Puffinus lherminieri*) and the placentae of sea lion (*Zalophus californianus wollebaeki*). Snakes (*Dromicus* spp.) were very rarely taken. It was a common scavenger on dead goats and other carcasses, sometimes flocks of up to forty birds gathering together at these feeding places.

Considerable differences were noticed between preys brought to different nests in the same breeding season and also by the same pairs in different breeding periods. Differences in prey, although in many cases reflecting availability at the time, could not always be explained by birds taking the most numerous or the most easily obtainable prey. Males and females generally took different preys during the breeding period, but as the female at that time is mainly concerned with guarding the young, the data obtained are mainly those of the hunting success of males; they do not therefore provide a reliable indication of differences in hunting efficiency between the sexes. Females took large prey, like land- and marine iguanas, easily available carrion and the placentae of sea lion, the usually well concealed contipedes, and to a lesser extent rats, doves, and lizards. Males, on the other hand, took smaller prey, such as doves, rats, finches, lizards, the placentae of sea lion and other carrion, and sometimes small marine iguanas and centipedes. I was fortunate enough to observe how two males of a diandric pair consistently brought different prey species to

the young; these males must have had different *searching images* (Tinbergen).

Unluckily, few records have been obtained of prey caught outside the breeding period. Although it could be expected that the male and the female normally take different prey outside the breeding period, this could not be proved; the fact, however, that considerably more adult females than adult males were found at carrion suggested that females had greater difficulties than males in catching prey.

The Galapagos Hawk is considered to be most closely related to the Red-backed Hawk *Buteo polyosoma*. Both species have similar call-notes, colour of downy chicks, and wing formulae. *B. polyosoma* is very variable in length of claws and bill; the Galapagos Hawk, beyond this range, has a heavier preying-apparatus. In contrast to *B. galapagoensis*, *B. polyosoma* has a polymorphic adult plumage with five distinct colour phases. The adult plumage of the Galapagos Hawk is dark brown; this type (apart from tail colouration) occurs in *B. polyosoma* as well, and is most frequent in the southern part of its wide range in South America.

Buteo species are the sole diurnal raptors in a few other oceanic islands, e.g. Hawaii, Azores, indicating that buzzards are well suited to colonize remote islands. There is a tendency to increased sexual dimorphism in size in buzzards occurring on islands where few other predators are present. This differentiation between the sexes appears to be related to ecological factors (occupation of different niches), rather than to social factors (dominance of females over males).

RESUMEN

El *Buteo galapagoensis*, gavilán endémico al Archipiélago de Galápagos, Ecuador, sobrevive en número aproximado de 120 a 150 parejas en las islas Pinta, Marchena, Fernandina, Isabela, Santiago, Santa Cruz, Pinzón, Santa Fe y Española. Ha desaparecido por la persecución humana de San Cristobal, Floreana, Baltra, Seymour y Daphne, mientras que en Santa Cruz está en vía de extinción. Aunque el número ha declinado considerablemente durante los últimos cincuenta años, especialmente en islas habitadas como Santa Cruz, donde ha disminuido de algunos centenaras a no más de dos parejas, la especie no parece estar en inmediato peligro de extinción. Con certeza, este gavilán es todavía uno de los más mansos *Buteo* en el mundo, siendo posible a una persona acercarse al ave y alimentarla en la mano. Los adultos son café oscuro a negro fuliginoso, mientras los jóvenes de color crema bordado de café oscuro. Si se ven ambos sexos juntos, el macho puede ser distinguido por su menor tamaño y delicada construcción. Cuando se toma la longitud de las alas como medida para expresar la diferencia en tamaño, el macho es el 91 por ciento de la hembra; en peso la proporción es el 73 por ciento, y en la garra posterior (como medida del poder matar) es de 81 por cienta.

Un ave sedentaria, en posesión del mismo territorio por muchos años, es probablemente normal que copule por vida. El área promedio de ocupación en diecisiete territorios en Santa Fe fue de 117 hectáreas.

Los terrenos para anidación están en las regiones áridas y nunca en las húmedas altitudes. Se registró reproducción durante todos los meses, pero en años con fuerte lluvia durante la estación calurosa (enero-abril) se observó un máximo de actividad en junio/julio, con una segunda postura de algunas parejas en octubre/noviembre. Consequentemente, el ciclo de reproducción es irregular y no sigue un patrón anual preciso. Parejas poliándricas, con dos o tres machos formando un grupo y copulando libremente con una hembra, ocurrió con cierta frecuencia. A veces los machos incuban los huevos y alimentan los pichones por turno. El alimento traído al nido ha sido calculado en 358 grames por día para la hembra y pichones juntos. El período de incubación fue de 37 a 38 días y el de emplume alcanzó a 50 y 60 días; ambos períodos parecen ser más prolongados que los conocidos para otras especies de *Buteo*. La madurez es alcanzada probablemente a los tres años o más.

El Gavilán Galapagueño es un predador versátil, capturando cualquier presa sobre la que puedo arrojarse. Ratas indígenas (*Oryzomys* spp.) y palomas tierreras (*Nesopelia galapagoensis*)fueron las principales presas, y en adición capturaron lagartijas (*Tropidurus* spp.), pinzones de Darwin (*Geospiza* spp.)y ciempies (*Scolopendra galapagoensis*), pero en lugares donde éstos no habían el gavilán crió a sus pichones con iguanas marinas (*Amblyrhynchus cristatus*), rasantes (*Puffinus lherminieri*) y la placenta de león marino (*Zalophus californianus wollebaeki*); culebras (*Dromicus* spp.) fueron muy raremente cogidas. Fue bien connocido como consumidor de cabras muertas y otras carroñas; grupos de más de cuarenta gavilanes se contaron en esos lugares de alimentación.

Se notó considerable diferencia entre presas traídas a los nidos por distintas parejas en la misma estación reproductora y por las mismas parejas en differentes períodos de reproducción. Las diferencias en las presas capturadas, aunque en la mayoría de casos reflejando la disponibilidad de especies al tiempo en el territorio, no siempre pudieron ser explicadas porque las aves atrapen las presas más numerosas o más fáciles de obtener. Machos y hembras tomaron diferentes presas durante el período de reproducción, pero como la principal tarea de la hembra durante ese tiempo consiste en hacer guardia y proteger a los pichones, los datos obtenidos corresponden principalemente a la cacería de los machos y no ofrecen una clara indicación de las diferencias en la eficiencia de cacería entre los sexos. Las hembras atraparon grandes presas, como iguanas de mar y tierra, carroña de fácil obtención y placenta de león marino; en menor escale ratas, palomas y lagartijas, pero también el normalmente bien oculto ciempies. Contrariamente, los machos capturaron presas más pequensas : palomas, ratas, pinzones y lagartijas; placenta de león marino, otra carroña y a veces pequeñas iguanas marinas y ciempies. Tuve la fortuna suficiente para observar cómo los dos machos de una familia diándrica trajeron constantemente presas diferentes a los pichones. Esos machos deben haber tenido distinto *poder escudriñador* (Tinbergen).

Desafortunadamente, sólo unas pocas observaciones se obtuvieron de presas cogidas fuera del período de reproducción. Sin embargo podría esperarse que tanto el macho como la hembra capturen como término medio presas diferentes también fuera del tiempo de reproduccion; esto no se pudo probar, pero el hecho de que más hembras adultas hayan sido encontradas alimentándose de carroña podría ser indicativo de que las hembras tienen más dificultad para coger las presas que los machos.

El Gavilán Galapagueño aquí es considerado más cercanamente emparentado al Aguilucho Común *Buteo polyosoma* (en el Ecuador se llama guarro). Ambas especies tienen voz similar, color del felpudo pichón y fórmula de ala. *B. polyosoma* es muy variable en longitud de garras y pico; el Gavilán Galapagueño tiene patas, garras y pico todavía más largos.

En contraste a *B. galapagoensis*, *B. polyosoma* tiene plumaje adulto polimórfico con cinco distintas feses de coloración. El plumaje adulto del Gavilán Galapagueño es café oscuro sencillo, y este tipo (exepto por ser coliblanco envés de colicafé) ocurre también en *B. polyosoma* siendo más frecuente en la parte sureña de su amplia distribución en Sur América.

Especies de *Buteo* son las únicas rapaces diurnas en otras islas océanicas, como Hawaii, Azores, indicando que estos gavilanes están bien adaptados para colonizar islas remotas. Hay una tendencia a aumentar el dimorfismo sexual en el tamaño de gavilanes presentes en islas donde pocos predadores existen. Esta diferenciación entre los sexos parece estar relacionada a factores ecológicos (ocupación de diferentes nichos) más que a factores sociales (dominación de hembras sobre machos).

SAMENVATTING

De voor de Galapagos Eilanden (Ecuador) endemische Galapagos Buizerd Buteo galapagoensis handhaaft zich met 120-150 broedparen op de volgende eilanden : Pinta, Marchena, Fernandina, Isabela, Santiago, Santa Cruz, Pinzón, Santa Fe en Española. Ten tijde van de eerste kolonisaties van de mens werden buizerds in grote aantallen doodgeknuppeld en zijn daardoor uitgeroeid op San Cristóbal, Floreana, Baltra,Seymour en Daphne. Alhoewel gedurende deze eeuw de aantallen sterk zijn terug gelopen, met name op de door de mens bewoonde eilanden (bijv. Santa Cruz waar de aantallen zijn verminderd van enige honderden tot twee broedparen), wordt de buizerd niet met uitsterven bedreigd daar hij geen direct gevaar loopt op onbewoonde eilanden. De soort is beschermd bij de Ecuarodiaanse wet. Hij is een van de tamste buizerdsoorten ter wereld; in het vrije veld op de mens afkomend, pakt hij aangeboden prooi uit de hand. En waar elders kan men een buizerd vangen in een vlindernet?

De volwassen vogels zijn donkerbruin, soms bijna zwartbruin; het jeugdkleed heeft een isabellakleurige tot bijna witte ondergrond met donkerbruine vlekken en strepen. Waar men mannelijke en vrouwelijke exemplaren bijeen ziet, kunnen mannetjes onderscheiden worden aan hun geringer formaat en slankere bouw. Als men het verschil in afmeting uitdrukt in de vleugellengte is de grootte van het mannetje 91 procent van die van het wijfje. in gewicht bedraagt deze verhouding 73 procent, terwijl deze 81 procent is bij de grootte van de nagel van de achterteen (een maat voor de predatiekracht).

De Galapagos Buizerd is een standvogel, die jaren achtereen hetzelfde territorium bezet en vermoedelijk gewoonlijk voor het leven paart.

De gemiddelde grootte van zeventien territoria op Santa Fe bedroeg 117 ha. Het broedterrein lag in de droge streken, nooit in het vochtige hoogland. In alle maanden werden broedgevallen vastgesteld, maar in de jaren met zware regenval in het hete seizoen (januari-april) vertoonde de broedactiviteit een piek in juni/juli, waarbij sommige paren een tweede legsel in october/november hadden. Vaak bleven de hevige regens achterwege, tengevolge hiervan was de broedcyclus onregelmatig en niet aan een vast, jaarlijks patroon gebonden. Veelmannerij (polyandrie) kwam regelmatig voor. In zulke situaties, waarbij twee of meer mannetjes binnen eenzelfde territorium met een vrouwtje samenleefden, copuleerden de mannetjes met dit vrouwtje, bebroedden de eieren en brachten prooidieren voor het vrouwtje en de jongen. Het naar het nest aangevoerde voedsel werd berekend op 358 gram per dag. De broedduur bedroeg 37-38 dagen, waarna de jongen uitvlogen na 50-60 dagen. Geslachtsrijpheid werd vermoedelijk op zijn vroegst in het derde levensjaar bereikt.

De Galapagos Buizerd heeft een breed voedselspectrum; hij pakt elke beschikbare prooi. Endemische ratten (Oryzomys spp.) en grondduiven (Nesopelia galapagoensis) waren de voornaamste prooi, daarnaast werden lavahagedissen (Tropidurus spp.), Darwin vinken (Geospiza spp.) en duizendpoten (Scolopendra galapagoensis) geslagen. Waar deze prooidieren niet voorkwamen brachten de buizerden hun jongen groot met zeeleguanen (Amblyrhynchus cristatus), pijlstormvogels (Puffinus lherminieri) en placenta's van zeeleeuwen (Zalophus californianus wollebaeki). Slangen (Dromicus spp.) werden zelden als prooi aangevoerd. De buizerd is als aaseter een bekende verschijning bij kadavers van geiten en andere dieren; bij zulke gelegenheden werden soms wel veertig vogels aangetroffen. Er bleken aanzienlijke verschillen te bestaan tussen de prooien die in hetzelfde broedseizoen door verschillende paren op de nesten werden aangevoerd, alsmede tussen prooien van eenzelfde paar in verschillende broedseizoenen. Meestal weerspiegelen de verschillen in prooi de beschikbaarheid van de talrijke of gemakkelijkst te vangen soorten in het territorium; niet alle verschillen konden echter op deze wijze verklaard worden. In de broedtijd namen mannetjes en wijfjes gemiddeld verschillende prooien.

De wijfjes houden zich in deze tijd voornamelijk bezig met het bewaken en beschaduwen van de jongen, zodat de gegevens aanwijzingen geven over het jachtsucces van de mannetjes en niet over verschillende in doeltreffendheid van jacht methoden tussen mannetjes en wijfjes.
De wijfjes sloegen de grotere prooidieren zoals land- en zeeleguanen, gemakkelijk verkrijgbaar aas en placenta's van zeeleeuwen, zeer verborgen levende duizendpoten en tevens ratten, duiven en hagedissen.
De mannetjes namen daarentegen veel kleinere prooidieren, zoals duiven, ratten, vinken en hagedissen, maar ook placenta's van zeeleeuwen en ander aas en soms kleine zeeleguanen en duizendpoten. Ik had het geluk waar te kunnen nemen hoe de twee mannetjes van een diandrisch paar verschillende prooidier-soorten aanvoerden. De mannetjes moeten vrijwel zeker verschillende *zoekbeelden* (Tinbergen) hebben gehad. Helaas werden weinig waarnemingen gedaan aan prooien die buiten het broedseizoen gegeten werden. Het valt te verwachten dat ook buiten de broedtijd mannetjes en wijfjes hoofdzakelijk verschillende prooidier-soorten nemen, hoewel dit niet bewezen kan worden. Uit het feit dat men op aas aanzienlijk meer volwassen wijfjes dan volwassen mannetjes ziet fourageren zou men echter af kunnen leiden dat de wijfjes meer moeite hebben met het vangen van prooidieren dan de mannetjes.

De Roodrug Buizerd *Buteo polyosoma* wordt hier beschouwd als de nauwste verwant van de Galapagos Buizerd. Beide soorten vertonen grote overeenkomst in geluid, kleur van de donsjongen en vleugelformule.
De Galapagos Buizerd heeft zwaardere poten, klauwen en snavel.
In tegenstelling tot *B. galapagoensis* heeft *B. polyosoma* een polymorf adult kleed, met vijf duidelijke kleurfasen. Het verenkleed van de volwassen Galapagos Buizerd is donkerbruin. Dit kleurtype (zij het met een ander kleurpatroon van de staart) komt ook bij *B. polyosoma* voor, en wel het talrijkst in het zuidelijk deel van zijn uitgestrekt areaal in Zuid Amerika.

Op een aantal andere oceanische eilanden, zoals Hawaii en de Azoren, komen *Buteo* soorten ook voor als de enige dagroofvogels, waaruit men af zou kunnen leiden dat buizerden geschikt zijn om geïsoleerde eilanden te koloniseren. Op eilanden waar weinig andere predatoren zijn (zoals b.v. op Galapagos, Hawaii, Juan Fernandez, Madeira), bestaat de tendens naar een toenemende sexuele dimorphie in lichaamsgrootte (c.q. klauwgrootte) bij buizerden. Deze differentiatie tussen mannetjes en wijfjes blijkt eerder samen te hangen met oecologische faktoren (bezetting van verschillende niches), dan met sociale faktoren (dominantie van wijfjes over mannetjes).

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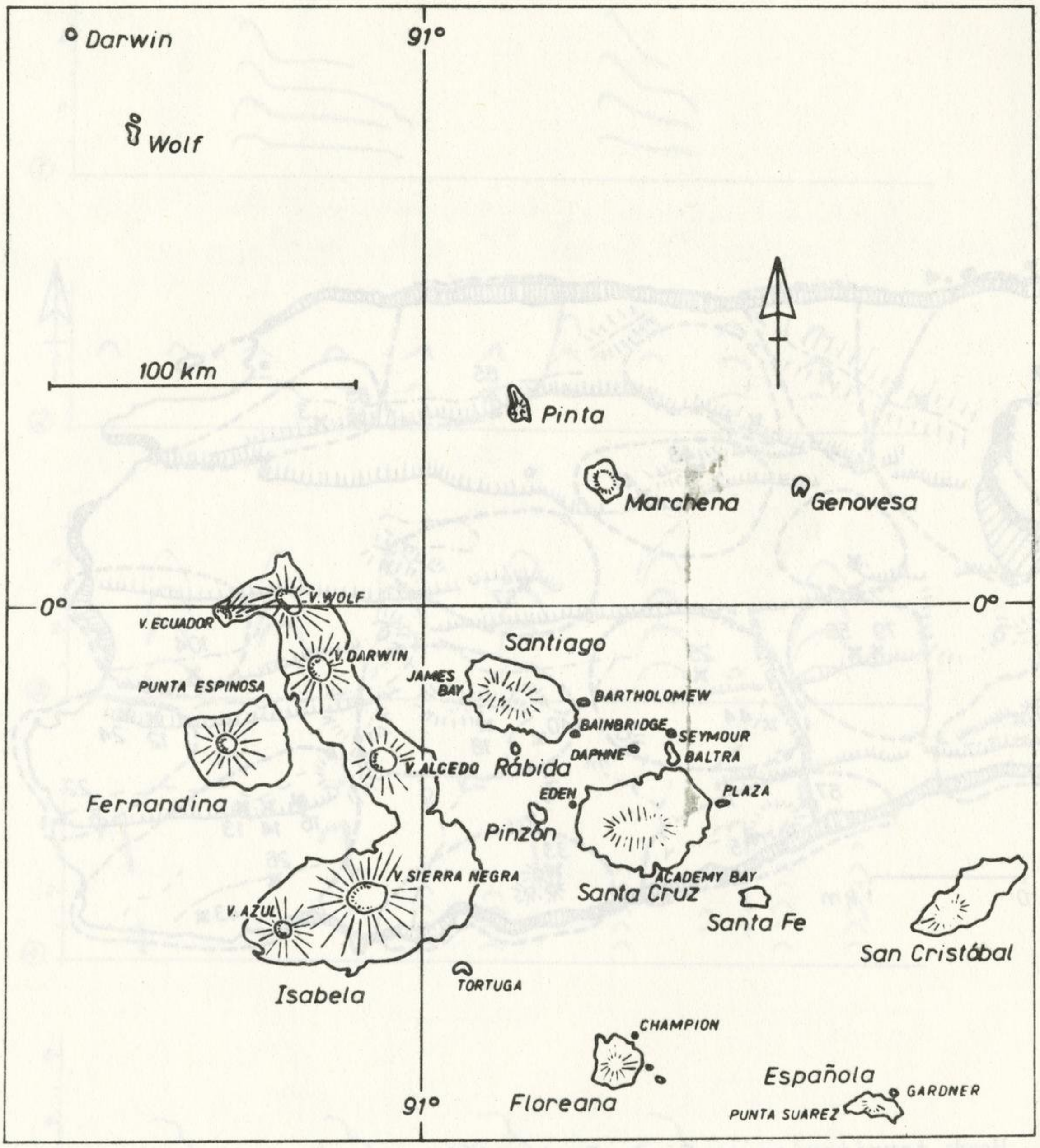


Fig. 1. The Galapagos Islands

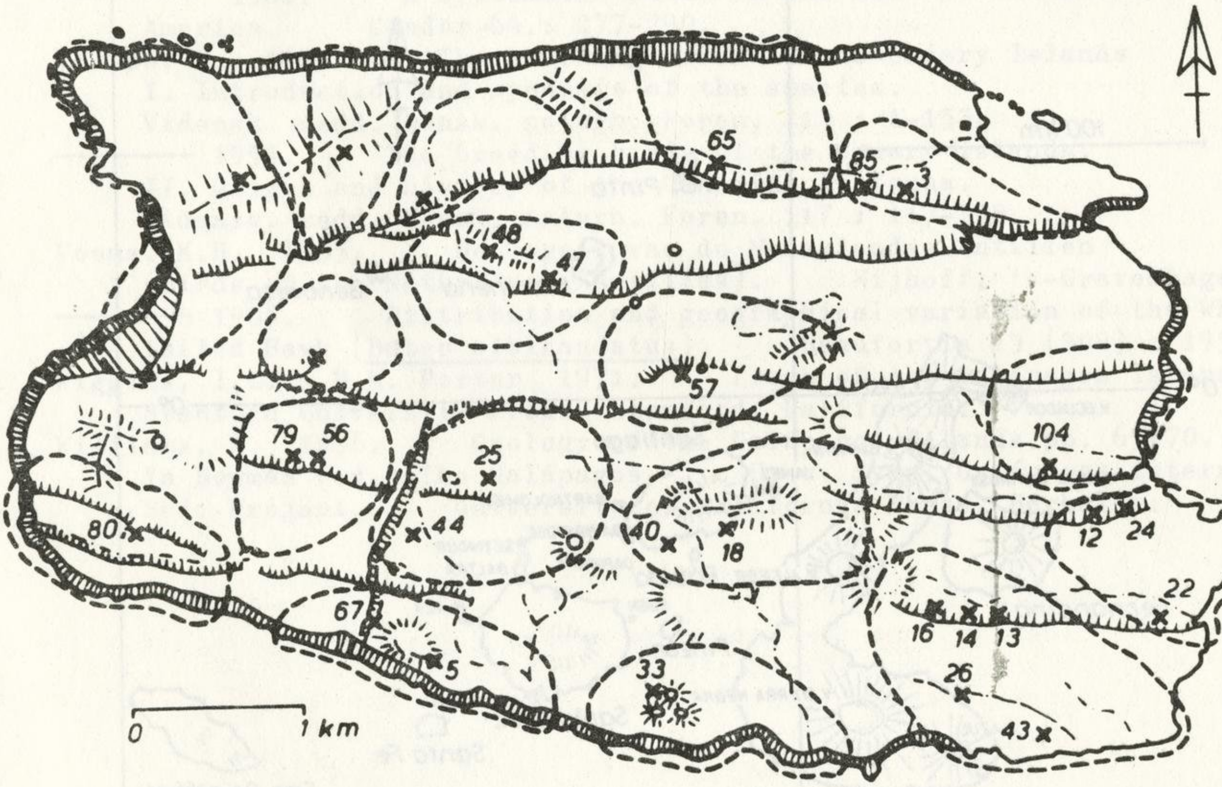


Fig. 2. Hawk territories on Santa Fe in 1969; x = nest with nest number

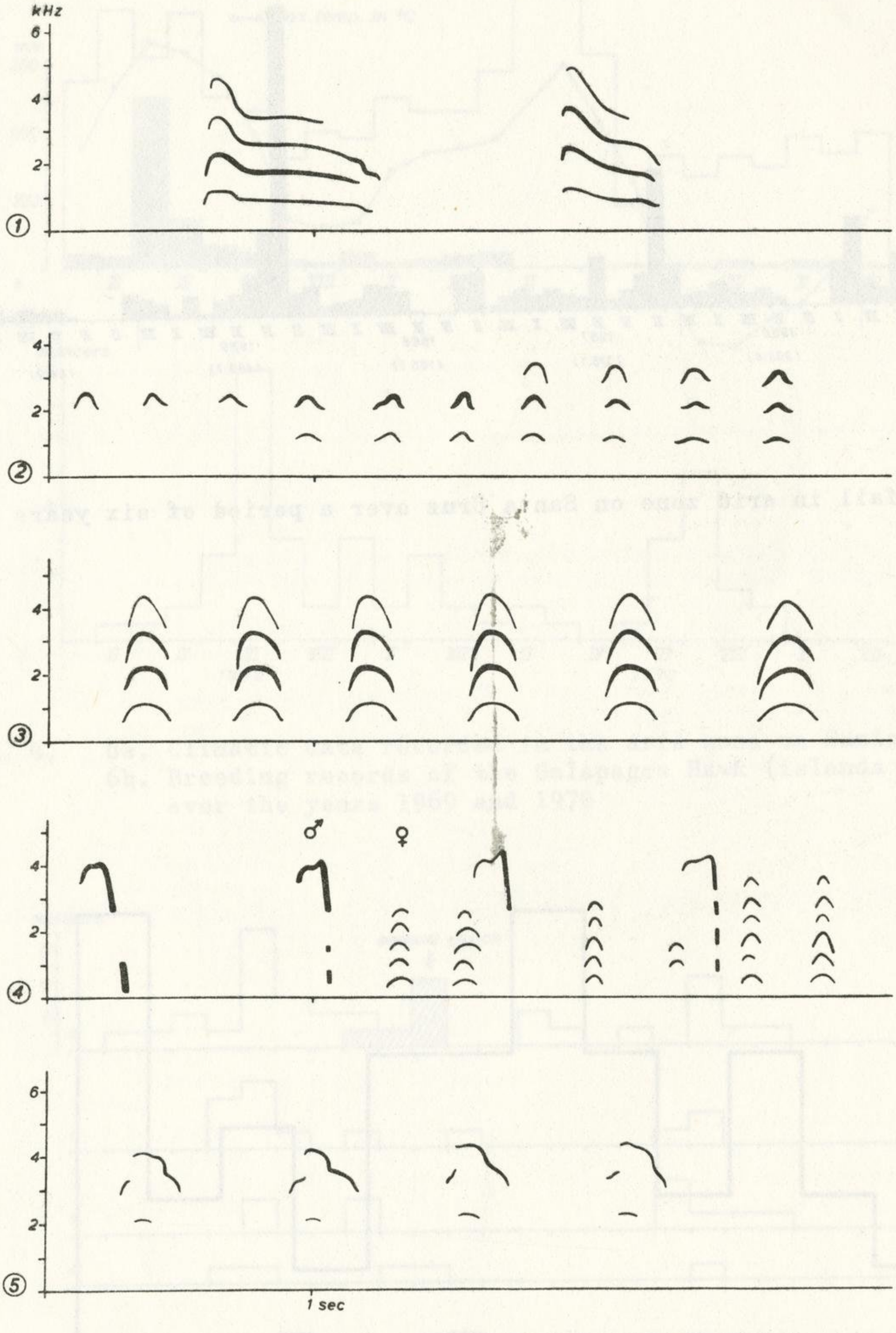


Fig. 3. Call-notes of the Galapagos Hawk

1. attention-call; 2. exciting-call; 3. begging-call;
4. copulation-call; 5. hunger-call.

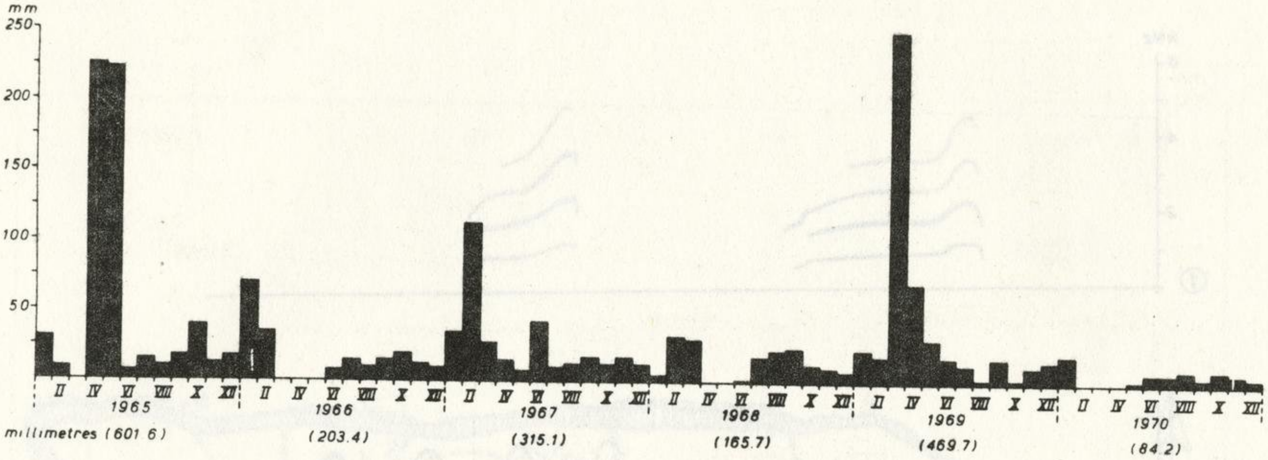


Fig. 4. Rainfall in arid zone on Santa Cruz over a period of six years

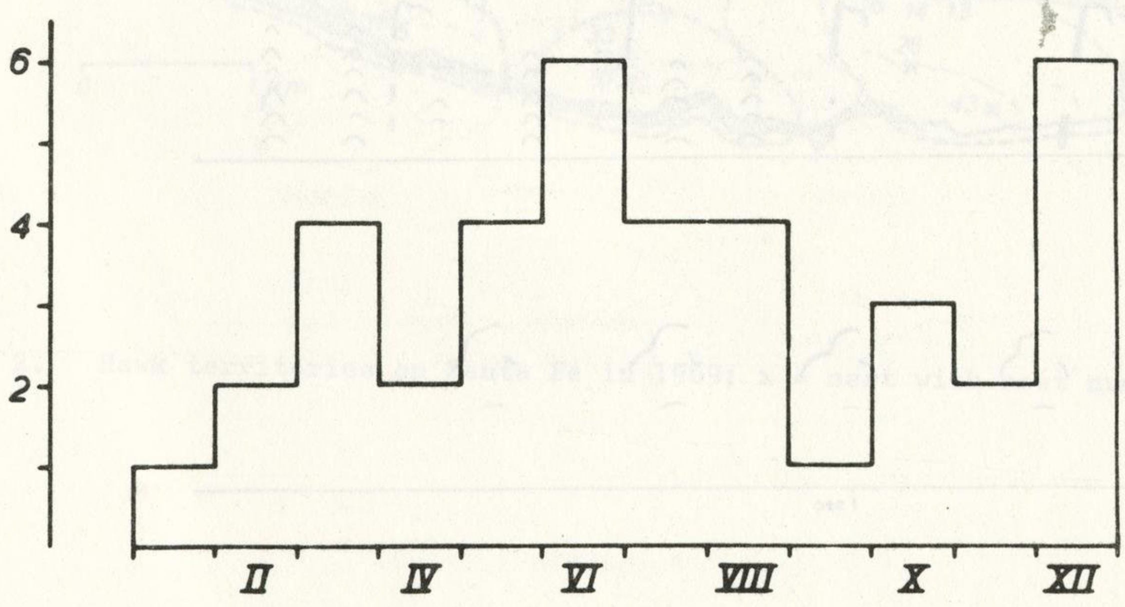


Fig. 5. Breeding records over a period of three years (1966-1968); numbers per month

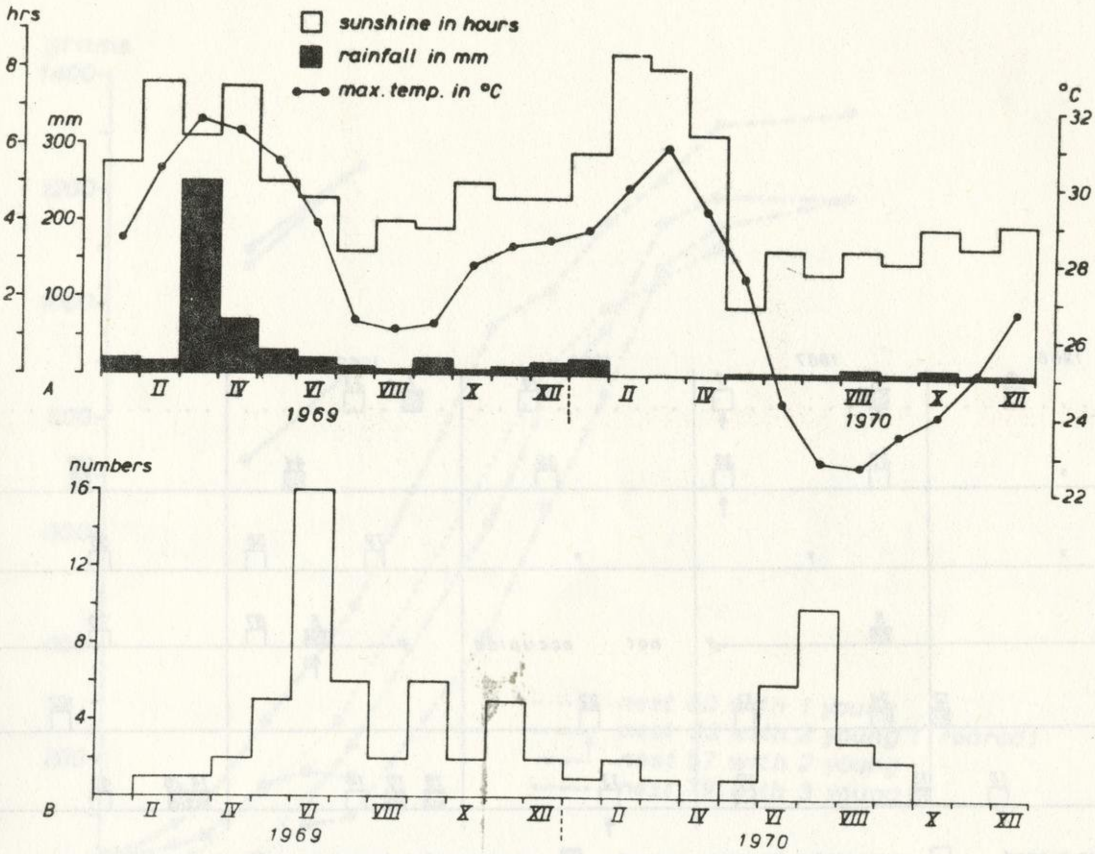


Fig. 6. 6a. Climatic data recorded in the arid zone on Santa Cruz
6b. Breeding records of the Galapagos Hawk (islands combined) over the years 1969 and 1970

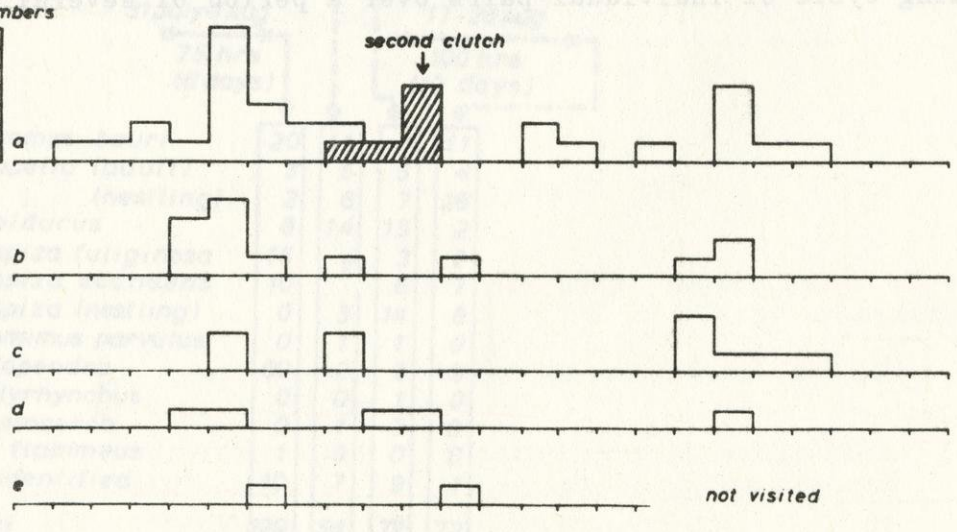


Fig. 7. Breeding records separated by islands

a-g : Santa Fe, Santiago, Española, Pinzón, Santa Cruz, Isabela, and Fernandina, respectively

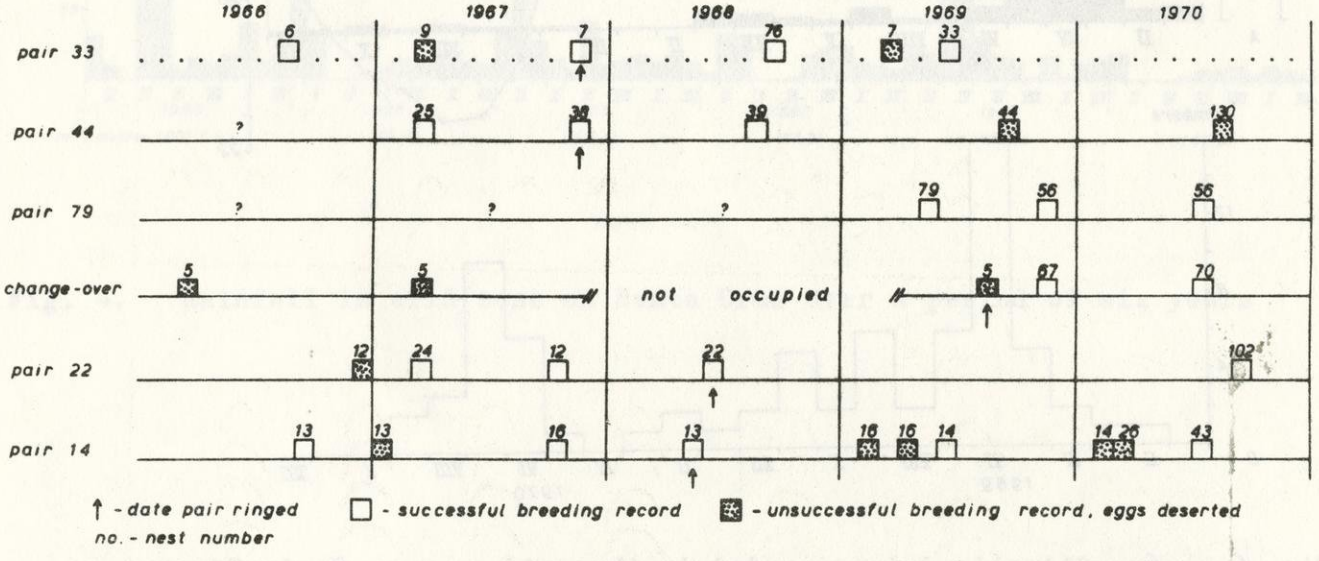
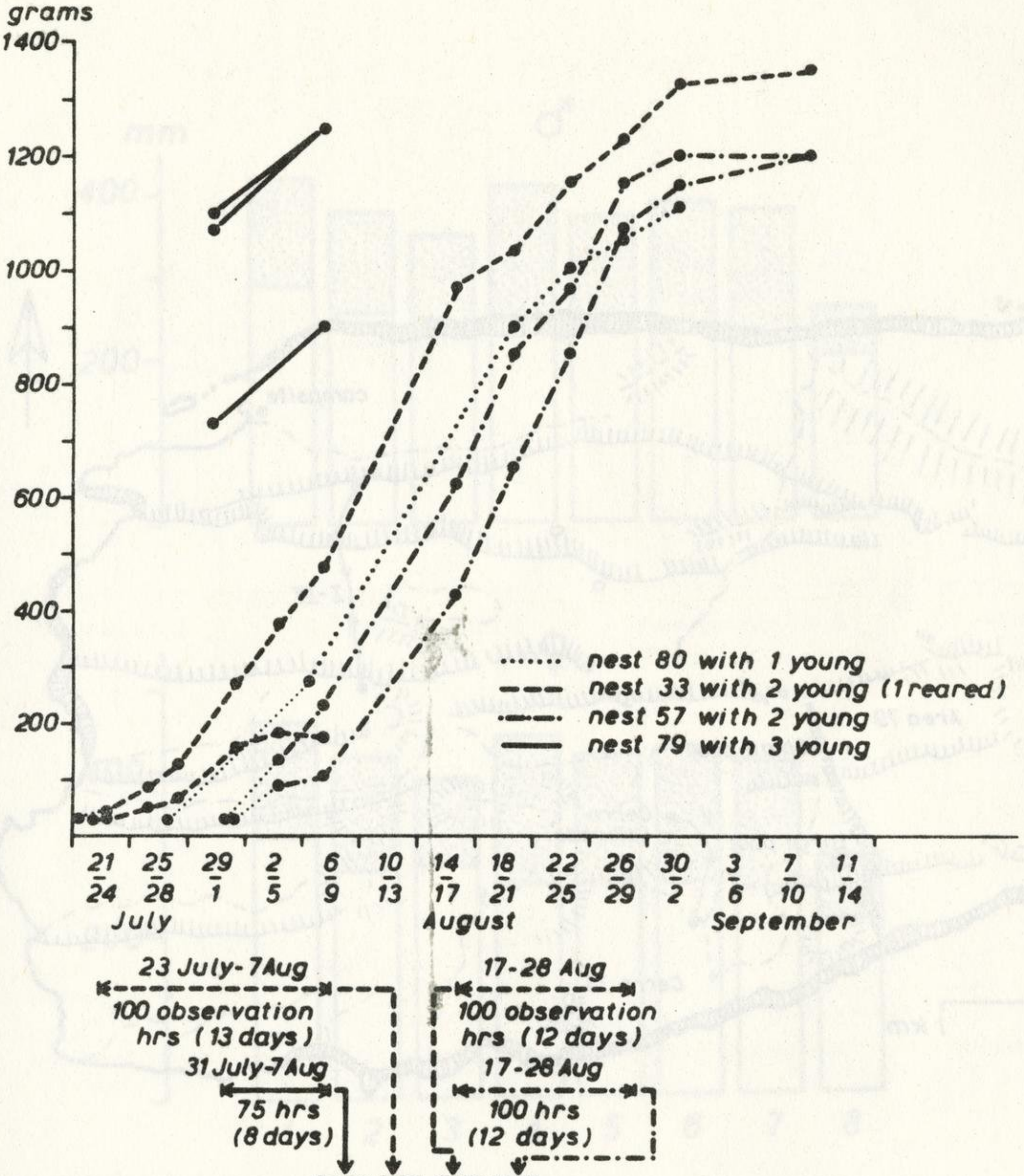


Fig. 8. Breeding cycle of individual pairs over a period of several years



Oryzomys bauri	20	11	8	11
Nesopelia (adult)	3	6	5	4
(nestling)	2	6	7	28
Tropidurus	8	14	15	2
Geospiza fuliginosa	15	3	3	2
Geospiza scandens	10		6	7
Geospiza (nestling)	0	3	14	8
Nesomimus parvulus	0	1	1	0
Scolopendra	60	2	3	9
Amblyrhynchus	0	0	1	0
Schistocerca	0	1	0	0
Asio flammeus	1	0	0	0
not identified	10	7	9	1
Total	129	54	72	72

Fig. 9. Growth curves of young and prey brought to nests on Santa Fe in July - September 1969

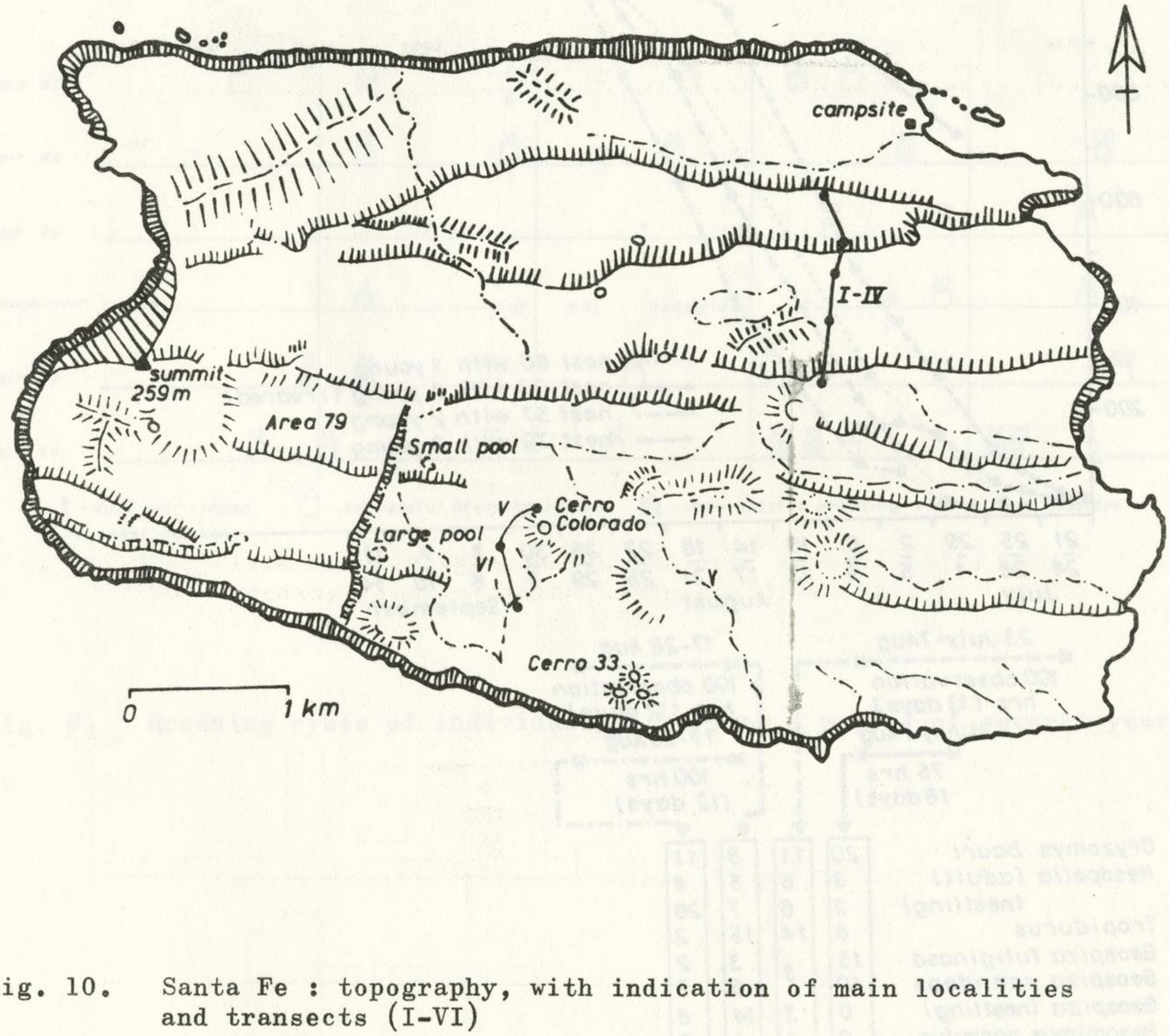


Fig. 10. Santa Fe : topography, with indication of main localities and transects (I-VI)

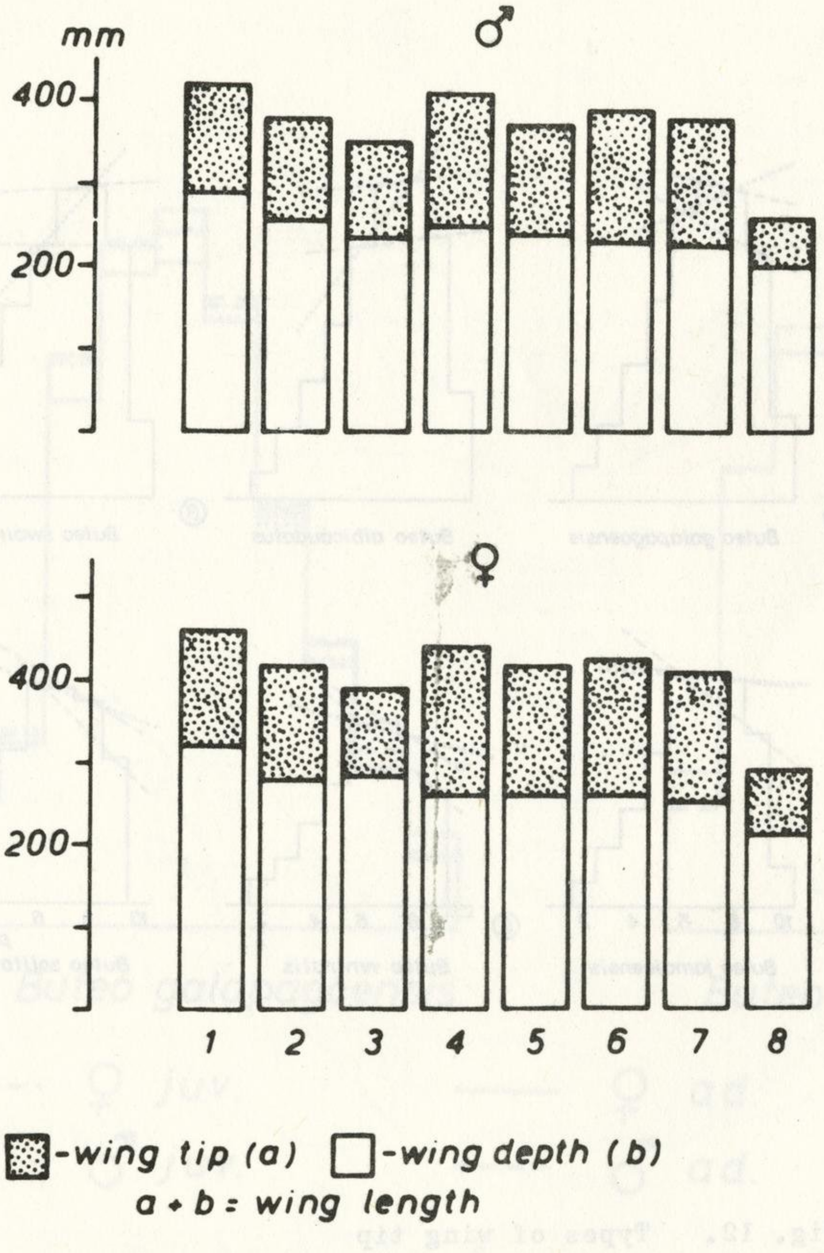


Fig. 11. Wing lengths, wing depths and wing tips in eight American buzzards

1. poecilochrous; 2. jamaicensis; 3. ventralis; 4. albicaudatus; 5. polyosoma; 6. galapagoensis; 7. swainsoni; 8. solitarius

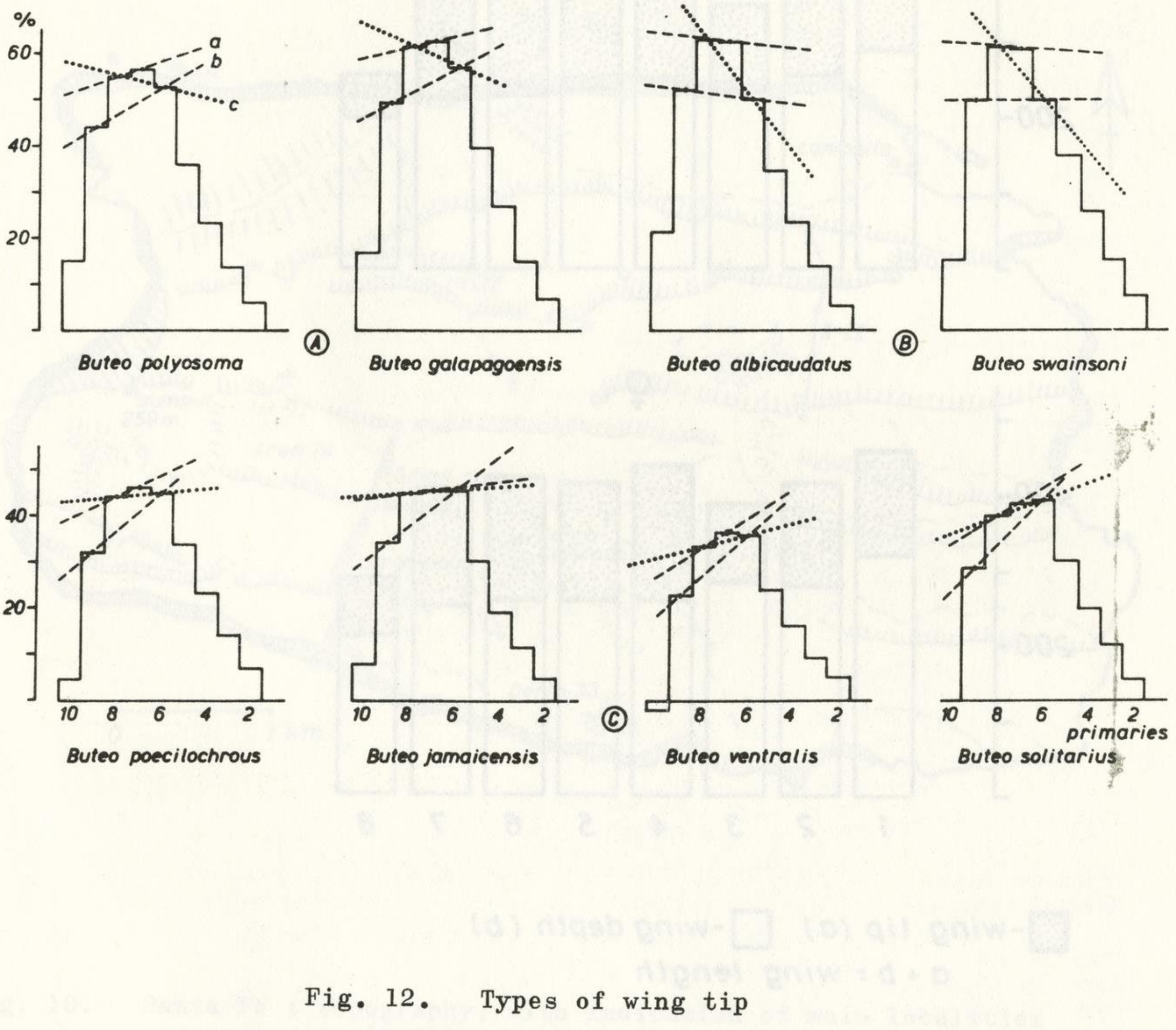


Fig. 12. Types of wing tip

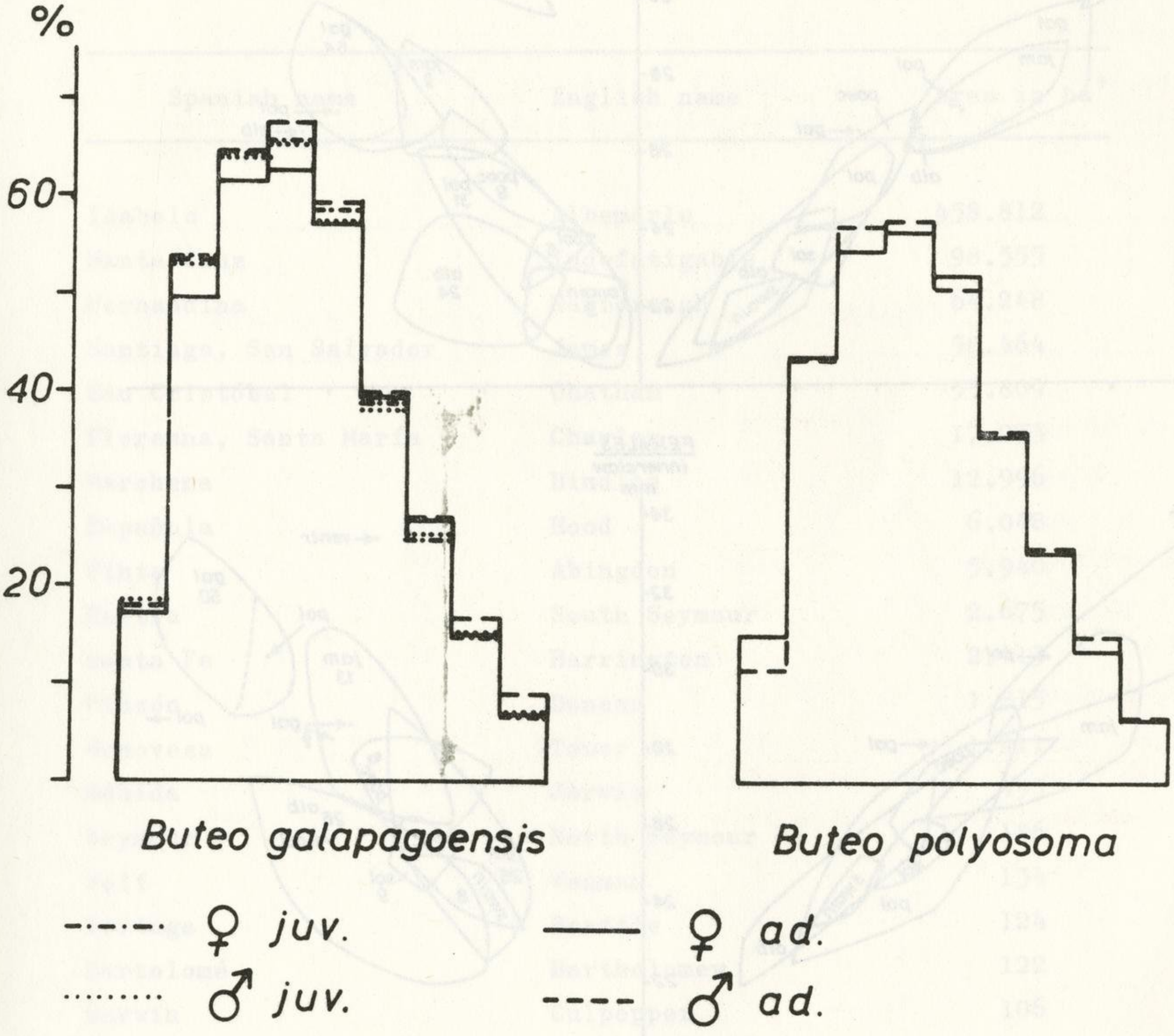


Fig. 13. Sexual dimorphy in wing tips of <u>B. galapagoensis</u> and <u>B. polyosoma</u>

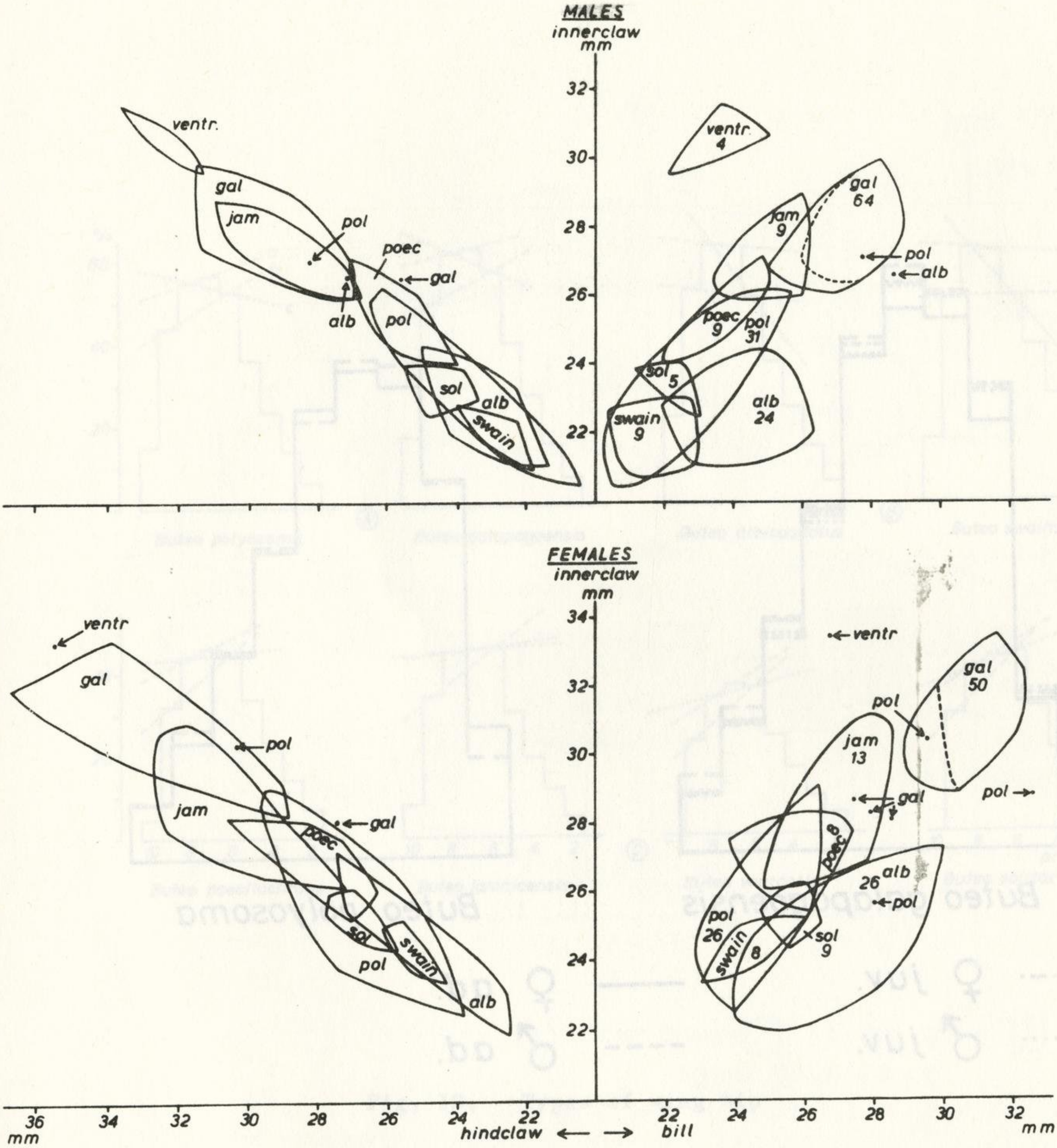


Fig. 14. Relation between bill and claws in eight American buzzards

Figures under abbreviated species names indicate number of records on which the outline of cluster of points has been composed. For galapagoensis adults and juveniles have been separated (left of dotted line juveniles only). Points of polyosoma, which are indicated with an arrow, refer to specimens of the Falkland Islands.

Table 1. List of islands

Spanish name	English name	Area in ha[+]
Isabela	Albemarle	458.812
Santa Cruz	Indefatigable	98.555
Fernandina	Narborough	64.248
Santiago, San Salvador	James	58.464
San Cristóbal	Chatham	55.809
Floreana, Santa María	Charles	17.253
Marchena	Bindloe	12.996
Española	Hood	6.048
Pinta	Abingdon	5.940
Baltra	South Seymour	2.675
Santa Fe	Barrington	2.413
Pinzón	Duncan	1.815
Genovesa	Tower	1.411
Rábida	Jervis	495
Seymour	North Seymour	186
Wolf	Wenman	134
Tortuga	Brattle	124
Bartolomé	Bartholomew	122
Darwin	Culpepper	106
Gardner	Gardner near Hood	55
Daphne	Daphne	32
Sombrero Chino		22
Eden	Eden	20
Roca Flamenca	Bainbridge Rocks (one islet of the group)	18
Plaza Sur	Plaza	13

[+] from J. Black & D. Weber, unpublished

Table 2. Santa Fe : breeding results in 1969 and 1970

	1969			1970		
	Jan-Apr	May-Sept	Sept-Dec	Jan-Apr	May-Sept	Sept-Dec
Clutch 1 egg	1	3	2	1	2	0
2 eggs	3	8	2	2	5	0
3 eggs	0	3	2	0	0	0
Total of clutches	4	14	6	3	7	0
Total of eggs	7	28	12	5	12	0
Mean clutch size	1.7	2.0	2.0	1.7	1.7	-
Young reared	0	14	4	0	7	0
Fledging success	-	50 %	33 %	-	58 %	-

Table 3. Distribution of main prey species

Prey species	Santa Fe	Española	Pinzón	Santiago	Fernandina
Oryzomys	x	-	-	-	x
Rattus rattus	-	-	x	x	-
Zalophus	!	x	!	!	x
Sus	-	-	-	x	-
Capra	x	x	-	x	-
Diomedea	-	x	-	-	-
Puffinus	!	x	x	!	!
Creagrus	!	x	!	!	!
Nesopelia	x	x	+	x	+
Myiarchus	+	x	x	x	x
Pyrocephalus	-	-	x	x	+
Nesomimus	x	x	-	x	x
Dendroica	+	x	x	x	x
Geospiza spp.	x	x	x	x	+
Camarhynchus spp.	+	-	+	x	+
Certhidea	+	x	x	x	+
Amblyrhynchus	!	x	!	!	x
Conolophus	x	-	-	-	!
Tropidurus	x	x	x	x	x
Dromicus	x	x	x	x	x
Scolopendra	x	x	x	x	x
Total of species groups present	9	15	10	14	9

x = present
+ = rare
! = distribution very local
- = not present

Table 4. Santa Fe : density-activity pattern of rice rats (<u>Oryzomys</u>)
Average number of rats trapped per night per 10 square metres (rats released)

Locality	Aug 1969	Jan 1970	Apr 1970	July 1970	Nov 1970
Large Pool Area	23	-	-	-	5
Cerro 33	10	9	10	10	4
Area 79	-	9	-	-	-
Cerro Colorado	-	9	-	-	-

\- = no information

Table 5. Santa Fe : bird census in four hawk territories (each census area = 2 ha)
August - September 1969

Hawk territory	Geospiza fuliginosa			Geospiza scandens			Geospiza spp.	Nesopelia galapagoensis				Nesomimus parvulus		
	occupied nest	pair	juv	occupied nest	pair	juv	deserted nest	occupied nest	ad	juv	deserted nest	occupied nest	ad+juv	deserted nest
57	7	12	9	3	8	7	53	3	5	2	4	0	8	1
79	2	2	6^+	1	0	4^+	30	0	2	1	1	0	2	0
33	1	1	4	0	0	1	14	0	0	0	0!	0	3	15!
14	0	1	1	0	1	1	9	1	1	0	0	0	2	0

+ = G. fuliginosa and G. scandens occurred in mixed flocks

! = Nesopelia sometimes breeds in an abandoned nest of Nesomimus

Table 6. Santa Fe : finch census in hawk territory 57 (census area 2 ha)

Date		Geospiza fuliginosa occupied nest			Geospiza scandens occupied nest		
			pair	juv		pair	juv
30 August	1969	7	12	9	3	8	7
3 October	1969	2	12	23	0	6	9
1 April	1970	0	3	20	0	2	4
26 July	1970	0	14	40	0	6	8
14 October	1970	0	5	12	0	2	3

Table 7. Santa Fe : density-activity pattern of lava lizards (<u>Tropidurus</u>)

Numbers counted per transect of 500 m length and 3 m width

	Transects I-IV combined (total length 2 km)					Transect V			
date	male	female	juvenile	total	date	male	female	juvenile	total
13 Aug 1968	6	19	11	36	15 Aug 1968	12	26	2	40
15 Aug	5	3	1	9	12 Sept	8	14	0	22
12 Sept	15	19	2	36	13 Sept	13	14	0	27
13 Sept	14	18	2	34	16 Sept	11	9	0	20
19 Jan 1969	15	13	1	29	15 Apr 1969	8	10	0	18
9 Apr	8	9	6	23	5 June	10	30	8	48
10 Apr	8	7	4	19	8 June	11	31	4	46
11 Apr	10	4	3	17	30 July	15	24	11	50
12 Apr	11	9	6	26	4 Aug	20	22	7	49
15 Apr	8	10	7	25	20 Nov	9	26	10	45
31 May	7	5	2	14	14 Oct 1970	4	13	2	19
22 July	10	9	16	35	2 Nov	5	5	0	10
23 July	8	13	11	32	28 Dec	4	11	2	17
24 July	4	8	14	26					
30 July	3	4	5	12					
19 Nov	8	4	16	28					
20 Nov	4	6	22	32			Transect VI		
2 Apr 1970	3	0	5	8					
23 July	0	0	0	0	8 June 1969	3	2	8	13
24 July	1	5	5	11	30 July	6	5	0	11
28 Dec	4	3	12	19	28 Dec 970	4	8	2	14

Table 8. Pinzón : density-activity pattern of Black Rats (Rattus rattus)
Number of rats trapped in a linear series of
10 traps placed 10 metres apart (rats killed)

date		coastal	inland
31 Aug-3 Sept	1966	6	
28-30 Dec	1966	7	
1-4 March	1967	4	0
10-13 Aug	1967	7	4
24-27 Jan	1968	9	4
1-4 July	1969	11	1

Table 9. Santiago : density-activity pattern of lava lizards (<u>Tropidurus</u>) along the beach of Buccaneer Cove
Numbers counted per transect of 250 m length and 3 m width

date	male	female	juvenile	total
9 June 1966				30
6 Apr 1968	2	5	8	15
9 July 1969	7	26	5	38
10 July 1969 a)	10	28	12	50
10 July 1969 b)	10	32	8	50
6 Dec 1969	4	21	40	65
14 July 1970	8	12	36	56
15 July 1970	7	13	38	58

a) at 8.30 a.m.; b) at 9.30 a.m.

Table 10. Santa Fe : sexual diversity in food brought to nests in five different territories

Nest no.	Date	Hours of observation	Sex	Oryozomys	Nesopelia adult	Nesopelia nestling	Geospiza adult	Geospiza nestling	Tropidurus	Scolopendra	Zalophus (placenta)	Amblyrhynchus	Conolophus	Nesomimus	Asio flammeus	Schistocerca	Not identified
39	13-16 Sept 1968	23	♂ (white)	-	-	-	4	-	3	-	-	-	-	-	-	-	-
			♂ (yellow)	-	-	-	-	-	5	-	-	-	-	-	-	-	-
			♀	2	1	-	-	-	-	1	-	-	-	-	-	-	-
			unknown	-	-	-	-	-	-	1	-	-	-	-	-	-	-
79	30 July-7 Aug 1969	75	♂	16	2	2	25	-	6	5	-	-	-	-	1	-	8
			♀	3	1	-	-	-	2	55	-	-	-	-	-	-	2
56	6-16 Jan 1970	100	♂	11	6	-	3	-	1	4	-	-	-	-	1	-	-
			♀	2	-	-	-	-	-	2	-	-	-	-	-	-	-
56	7-15 Oct 1970	75	♂	2	15	-	19	-	2	-	-	-	-	-	-	-	-
			♀	-	-	-	-	-	2	2	-	-	-	-	-	-	-
33	23 July-7 Aug, and 17-28 Aug 1969	200	♂	18	11	13	12	17	27	2	-	-	-	2	-	1	16
			♀	1	-	-	-	-	2	3	-	1	-	-	-	-	-
57	17-28 Aug 1969	100	♂	10	3	27	9	8	2	9	-	-	-	-	-	-	1
			♀	1	1	1	-	-	-	-	-	-	-	-	-	-	-
14	25 Aug-3 Oct 1969	267	♂ (orange)	16	2	4	13	5	2	35	-	-	-	-	-	-	4
			♂ (blue-white)	17	5	15	7	4	3	4	-	8	-	-	-	-	4
			♀	1	-	-	-	-	-	1	-	1	-	-	-	-	-
			unknown	-	1	3	1	-	-	-	-	-	-	-	-	-	1
43	1-12 Oct 1970	100	♂ (orange)	-	-	-	15	-	-	1	25	1	-	-	-	-	-
			♀	-	-	-	-	-	-	1	15	3	1	-	-	-	-
			unknown	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Total males	519	:	90	44	61	107	34	51	60	25	9	0	2	2	1	33
	Total females	108	:	10	3	1	0	0	6	65	15	5	1	0	0	0	2
	Grand total	635	:	101	48	65	108	34	57	126	40	14	1	2	2	1	36

Table 11. Santa Fe : prey brought to various nests calculated for periods of 100 hours of observation with the percentage of weight per prey species

Prey species	Nest 79* Aug 1969		Nest 56 Jan 1970		Nest 56* Oct 1970		Nest 33 July 1969		Nest 33 Aug 1969		Nest 57 Aug 1969		Nest 14 Aug 1969		Nest 14 Sept 1969		Nest 43 Oct 1970	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
Oryzomys bauri	27	41.8	13	44.5	3	7.4	11	37.7	8	27.2	11	28.5	9	31.5	20	55.0	1	2.1
Nesopelia adult + juv.	4	8.8	6	29.4	20	70.0	6	29.4	5	24.2	4	14.8	3	15.0	5	19.5	0	-
Nesopelia nestling	3	2.6	0	-	0	-	6	11.8	7	13.6	28	41.4	9	18.0	6	9.4	0	-
Geospiza fuliginosa	20				11				3		2		3		2		10	
Geospiza scandens	13				15				6		7		2		4		5	
Geospiza spp. combined		13.8	3	2.9		19.0	3	2.9		9.4		7.6	2	6.8		4.9		8.4
Geospiza nestling	0	-	0	-	0	-	3	1.5	14	6.8	8	2.9	4	2.0	2	0.7	0	-
Tropidurus	11	3.6	1	0.7	5	2.6	14	10.3	15	10.9	2	1.1	1	0.7	0	-	0	-
Scolopendra	80	17.7	6	2.9	3	1.0	2	1.0	3	1.5	9	3.3	10	5.0	12	4.7	2	0.6
Zalophus(placenta)	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	40	49.1
Amblyrhynchus	0	-	0	-	0	-	0	-	0	-	0	-	8	20.0	3	5.8	4	24.5
Conolophus	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	1	15.3
Nesomimus	0	-	0	-	0	-	1	2.0	1	1.9	0	-	0	-	0	-	0	-
Asio flammeus	1	8.8	1	19.6	0	-	0	-	0	-	0	-	0	-	0	-	0	-
Schistocerca	0	-	0	-	0	-	1	-	0	-	0	-	0	-	0	-	0	-
Not identified	13	2.9	0	-	0	-	7	3.4	9	4.5	1	0.4	2	1.0	0	-	0	-
Total preys	172		30		57		54		72		72		53		54		63	
Biomass in grs		4520		2045		2855		2041		2060		2705		2000		2560		3265

* extrapolated to a period of 100 hours of observation

Table 12. Española : prey brought to nests

Prey species	Nest 10		Nest 2	
	10-14 Aug 1969		9-20 Aug 1970	
	number	%	number	%
Nesopelia (adult + juv.)	-	-	40	86.5
Geospiza conirostris	1	1.2	-	-
Tropidurus	12	34.4	5	6.5
Scolopendra	3	1.4	3	0.6
Zalophus (placenta)	28	53.5	-	-
Amblyrhynchus	1	9.5	-	-
Nesomimus	-	-	2	2.6
Diomedea	-	-	3	2.2
Oceanodroma	-	-	1	0.7
Unidentified	-	-	4	0.9
Total preys	45		58	
Hours of observation	50		100	
Number of preys/hour	0.90		0.58	
Biomass in grs	2095		4625	

Table 13. Pinzón : prey brought to nests

Prey species	Nest 1 11-14 Apr 1966	Nest 4 2-6 July 1969
Rattus rattus	-	1
Nesopelia (adult)	1	-
Tropidurus	4	7
Scolopendra	-	2
Puffinus lherminieri	1	-
Myiarchus magnirostris	2	-
Pyrocephalus rubinus	1	-
Schistocerca	1	-
Unidentified	1	2
Total preys	11	12
Hours of observation	32	15
Number of preys/hour	0.34	0.80

Table 14. Pinzón : list of pellets and other prey remains

Nest	Date	Pellets		Other remains
		no.	contents	
1	10 Aug 1967	5	Rattus (5x)1) Scolopendra (1x)2) G. fuliginosa (1x)	1 Nesopelia 1 Amblyrhynchus
2	30 Aug 1966	8	Rattus (8x) Scolopendra (4x)	1 Coccyzus
	1 Nov 1966	6	Rattus (6x) Scolopendra (2x)	7 Rattus (skulls) 2 Puffinus 2 Amblyrhynchus
7	5 Feb 1966	20	Rattus (20x)3) Scolopendra (13x)	1 Nesopelia
	1 Sept 1966	22	Rattus (22x) Scolopendra (17x)	1 Nesopelia 1 Amblyrhynchus
	1 Nov 1966	5	Rattus (5x) Scolopendra (4x)	2 Rattus (skulls) 1 Amblyrhynchus
8	1 Sept 1966	18	Rattus (18x) Scolopendra (4x) Schistocerca (6x)	1 Coccyzus
	11 Aug 1967	18	Rattus (13x) Scolopendra (7x) Schistocerca (4x)	

1) which means that remains of *Rattus* have been found in each of 5 pellets examined

2) which means that remains of *Scolopendra* have been found in one of 5 pellets examined. Etc.

3) incl. 8 skulls

Table 15. Santiago : prey brought to nests

Prey species	Nest 1 Cape Trenton 3-11 Feb 1966	Nest 2 Buccaneer Bay 6-9 June 1966	Nest 3 Buccaneer Bay 15-23 Jan 1967	Nest 4 James Bay 3-6 Feb 1970
Rattus rattus	-	-	-	2
Nesopelia adult	-	-	-	1
Tropidurus	-	9	11	5
Scolopendra	-	-	-	3
Amblyrhynchus	3	-	-	-
Puffinus lherminieri	6	-	1	-
Pyrocephalus rubinus	-	1	-	-
Geospiza spp.	-	-	1	1
Unidentified	-	2	1	-
Total preys	9	12	14	12
Hours of observation	100	30	58	32
Number of preys/hour	0.09	0.40	0.24	0.37
Biomass in grs	1950	125 (412)	315 (535)	400 (1200)

() = biomass extrapolated to periods of 100 hours of observation

Table 16. Total of prey brought to 17 nests in various islands over a period of 1357 hours of observation

Prey species	Number	Percentage of total prey weight
Nesopelia	90 ad. + 64 nestl.	34.5
Oryzomys bauri	102	21.4
Zalophus (pieces of placenta)	68	8.2
Amblyrhynchus	19	7.3
Tropidurus	110	7.0
Geospiza spp.	112 ad. + 34 nestl.	6.9
Puffinus lherminieri	8	4.3
Scolopendra	137	4.1
Asio flammeus	2	2.4
Conolophus	1	1.5
Rattus rattus	3	0.9
Diomedea irrorata (chick)	3	0.9
Nesomimus	4	0.6
Pyrocephalus rubinus	2	-
Myiarchus magnirostris	2	-
Oceanodroma castro	1	-
Schistocerca	2	-
Total preys	764	100
Biomass in grs	33.517	

Table 17. Percentage of prey weight per animal class

Mammals :	land mammals	22.3	
	placentae of sea lion	8.2	30.5
Birds :	land birds	44.4	
	sea birds	5.2	49.6
Reptiles			15.8
Arthropods			4.1
Total			100

Table 18. Mean weight (grs) and measurements (mm) of eight American species of *Buteo*1)

Species	weight	wing length	wing depth	tail	tarsus	middle toe	inner claw	hind claw	bill
Adult males									
polyosoma (excl. Falkland)		371	239	179	75	38	22.8	23.2	22.5
polyosoma (Falkland Islands)		371		181	84	38	22.8	23.9	22.2
polyosoma exsul		384		213	78	41	23.7	23.6	21.5
poecilochrous		421	289	208	86	42	25.4	25.5	23.8
galapagoensis	1000	388	232	205	74	45	27.9	28.9	27.5
albicaudatus		409	250	170	79	41	22.9	23.1	24.6
swainsoni	908[a]	379	226	184	62	39	21.9	22.9	21.8
jamaicensis	1028[a]	383	257	213	79	44	27.2	28.7	25.4
ventralis		353	235	203	76	47	30.5	32.1	23.6
solitarius		260	198	143	69	37	23.2	24.5	22.3
Adult females									
polyosoma (excl. Falkland)		415	261	203	79	39	25.1	26.3	24.9
polyosoma (Falkland Islands)		399		193	85	43	26.5	27.5	24.9
polyosoma exsul		429		206	81	47	28.2	29.6	26.7
poecilochrous		458	314	221	91	46	26.8	27.6	25.9
galapagoensis	1366	425	261	228	80	51	31.6	32.6	31.3
albicaudatus		442	263	177	85	43	24.1	24.5	26.9
swainsoni	1069[a]	409	253	205	67	42	24.2	25.2	24.4
jamaicensis	1224[a]	414	280	232	84	47	28.4	30.5	27.1
ventralis	1135[a]	389	285	206	86	54	33.3	35.4	26.8
solitarius		291	210	163	70	41	25.3	26.8	25.5

1) for statistical details see Appendix

a) from Brown & Amadon (1968)

Table 19. Relative abundance of colour phases in <u>Buteo polyosoma</u>

				Colour phases						
				adult 1		adult 2		adult 3	adult 4	adult 5
juv. 1	juv. 2	juv. 3	subadult	a	b	a	b			
33	15	8	5	37	15	9	1	3	1	9

juvenile 1	Head, neck, back and mantle dark brown mottled with buff; breast buffy-brown with dark brown streaks; abdomen buffy-brown with dark brown (double anchor-shaped) striped pattern; thighs banded reddish brown; tail dark brown to greyish brown with 15-18 black-brown bands.
juvenile 2	As juv. 1 but breast and throat with more white, and back with more reddish brown; tail dark brown to greyish brown with 10-15 black-brown bands.
juvenile 3	Plumage completely dark brown; tail dark brown to greyish brown with 15-18 black-brown bands.
subadult	Head, neck, and mantle dark brown slightly mottled with buff; back and nape reddish brown; throat and breast white; abdomen white with tiny grey bands and a few reddish brown feathers; thighs white with reddish brown to grey bands; tail with one or more white feathers with 10-11 tiny grey bands and black subterminal band and with one or more greyish brown feathers with 10-12 black-brown bands.
adult 1a	Head, neck, and mantle dark brown, greyish brown or dark grey; back and nape reddish brown; breast and throat white; abdomen and thighs white with greyish bands; tail white with 10 narrow grey bands and one broad subterminal black band (phase B of Vaurie).
adult 1b	Head, neck and mantle grey; back grey with reddish brown or completely grey; further as 1a (phase D of Vaurie).
adult 2a	Breast and abdomen pure white; back grey; further as 1b (phase D of Vaurie).
adult 2b	Back and nape reddish brown; further as 2a (phase B of Vaurie).
adult 3	Plumage completely dark grey; back slightly reddish brown in some individuals; tail as 1 (phase C of Vaurie).
adult 4	Plumage completely dark brown; tail as 1 (not included by Vaurie).
adult 5	Head, neck, and mantle dark brown, greyish brown or dark grey; back and nape reddish brown; throat, breast and abdomen reddish brown or throat and breast dark grey with a variable degree of reddish brown; thighs black-brown or banded reddish brown; tail as 1 (phases A and E of Vaurie).

Male plumages : 1b, 2a, 3, and 4
Female plumages : 1a, 2b, and 5
Some males seem to appear in the plumages 1a and 5 too.

Table 20. Wing tip and tail in relation to wing depth

Species	wing tip/wing depth index males	wing tip/wing depth index females	tail/wing depth index males	tail/wing depth index females
B. galapagoensis	0.67	0.63	0.88	0.87
B. swainsoni	0.67	0.61	0.81	0.81
B. albicaudatus	0.61	0.63	0.68	0.67
B. polyosoma	0.58	0.56	0.75	0.78
B. ventralis	0.50	0.38$^{1)}$	0.86$^{2)}$	0.72$^{1)}$
B. jamaicensis	0.48	0.48	0.79	0.79
B. poecilochrous	0.42	0.47	0.72	0.70
B. solitarius	0.38	0.43$^{1)}$	0.72	0.77$^{1)}$

1) one specimen only
2) juveniles

Table 21. Middle toe in relation to tarsus by several American buzzards

Species	middle toe/tarsus index	
	males	females
B. swainsoni	0.63	0.63
B. ventralis	0.62	0.63
B. galapagoensis	0.61	0.64
B. jamaicensis	0.56	0.56
B. solitarius	0.54	0.55
B. albicaudatus	0.52	0.51
B. polyosoma	0.51	0.49
B. poecilochrous	0.49	0.50

Table 22. Common characters in eight American buzzards

Species	polyosoma	poecilochrous	albicaudatus	galapagoensis	swainsoni	jamaicensis	ventralis	solitarius
polyosoma	5c	2b3a4a10b 12b13b15a 16b	1a2b3a4a 5a6a7b9a 11a13b 14a15a 16b	1a5a6a7b 8a9a12b 13b15a 16b	1a5a6a7b 9a11a 12b14a	1a10b12b 13b16b	1a10b13b	1a10b11a 12b14a
poecilochrous	8	1b	2b3a4a10b 13b14b15a 16b	11b12b13b 14b15a16b	12b	6b7a8c 10b11b 12b13b 14b	6b7a8c 10b11b 13b14b	7a8c10b 12b
albicaudatus	13	8	10a12c	1a5a6a7b 9a13b14b 15a16b	1a5a6a7b 8b9a11a 14a	1a5b13b 14b16b	1a13b 14b	1a11a 14a
galapagoensis	10	6	9		1a2a3a4b 5a6a7b9a 10c12b	1a2a3a4b 11b12b13b 14b16b	1a2a3a4b 11b13b14b	1a2a3a4b 12b
swainsoni	8	1	8	10		1a2a3a4b 12b15b	1a2a3a4b	1a2a3a4b 11a12b13a 14a15b16a
jamaicensis	5	8	5	9	6		1a2a3a4b 6b7a8c9b 10b11b13b 14b	1a2a3a4b 7a8c9b10b 12b15b
ventralis	3	7	3	7	4	12	12a16c	1a2a3a4b 7a8c9b10b
solitarius	5	4	3	5	10	10	8	6c

types of characters

total number of shared characters

Table 23. Resident predatory birds on the Canary Islands

Species	Number of islands on which present	Number of islands on which coexisting with buzzard	Food recorded
Osprey *Pandion haliaetus*	8	5	Fish
Red Kite *Milvus milvus milvus*	4	4	Carrion, offal, rats, mice, rabbits, poultry, grasshoppers
Sparrow Hawk *Accipiter nisus granti*	5	5	Rock Pigeon, quail, small birds, bats
Canarian Buzzard *Buteo buteo insularum*	8		Lizards, grasshoppers, beetles, rats
Western Canarian Kestrel *Falco tinnunculus canariensis*	5	5	Lizards, grasshoppers, crickets, beetles, ants, frogs, rats, mice
Fuerteventuran Kestrel *Falco tinnunculus dacotiae*	3	3	Lizards, grasshoppers, beetles, ants, mice
Eleonora's Falcon *Falco eleonorae*	4	2	Small birds, mainly passing migrants
Barbary Falcon *Falco peregrinus pelegrinoides*	5	4	Pigeons, sandgrouse, partridges, sparrows
Barn Owl *Tyto alba gracilirostris*	3	3	Mice
Tyto alba alba	3	3	Mice, rats, lizards, small birds
Canarian Long-eared Owl *Asio otus canariensis*	3	3	Mice, crickets
Egyptian Vulture *Neophron percnopterus*	5	5	Carrion, offal, grasshoppers, beetles
Raven *Corvus corax tingitanus*	8	8	Carrion, offal, grasshoppers, beetles mice, lizards, bird-eggs, fruit, corn
Red-billed Chough *Pyrrhocorax pyrrhocorax barbarus*	1	1	Insects, titmice, fruit, corn
Great Grey Shrike *Lanius excubitor koenigi*	4	4	Lizards, geckos, grasshoppers, crickets, beetles

Table 24. Reproduction and survival rate

Species		No. of nests	Mean clutch size	Hatching success (%)	Nestling mortality (%)	Breeding success (%)	First-year mortality (%)
Galapagos Hawk	a)	34	1.9	45	14	39	66 1)
Red-tailed Hawk	b)	98	2.0	77	27	48	51 2)
Red-tailed Hawk	c)	19	2.0	68	38	42	
Common Buzzard	d)	85	2.5	82	20	62	51 3)
Broad-winged Hawk	e)	5	2.4	100	17	83	

a) this study; calculated from two year period on Santa Fe
b) from Luttich et al. (1971)
c) from Fitch et al. (1946)
d) from Mebs (1964)
e) from Rusch & Doerr (1972)

1) from field observations
2) calculated for a stable population; 62 per cent according to ringing results
3) calculated from ringing results

APPENDIX

Statistical details of data presented in Table 18

		n	observed range	mean	st. dev.
WING					
B. polyosoma (1)	♂	24	352-390	371.8	10.60
	♀	18	400-447	415.1	11.55
B. polyosoma (2)	♂	3	363-378	370.6	
	♀	6	389-410	399.0	7.77
B. polyosoma (3)	♂	3	382-386	384.3	
	♀	2	426-432	429.0	
B. poecilochrous	♂	6	408-435	420.8	9.04
	♀	5	452-465	457.6	5.32
B. galapagoensis					
juv.	♂	40	375-407	386.9	8.21
ad.	♂	31	373-403	387.8	7.87
juv.	♀	34	398-444	425.5	10.56
ad.	♀	21	408-437	425.3	8.89
B. albicaudatus	♂	13	394-435	409.0	11.68
	♀	17	412-482	441.8	17.71
B. swainsoni	♂	8	355-399	378.9	13.51
	♀	8	389-420	408.6	9.23
B. jamaicensis	♂	7	377-395	382.7	9.09
	♀	12	397-434	414.5	11.34
B. ventralis	♂	4	345-363	353.0	
	♀	1		389	
B. solitarius	♂	4	251-265	259.7	
	♀	8	284-300	291.1	6.24

Adults, except stated otherwise

(1) excluding Falkland Islands and Juan Fernandez Islands
(2) Falkland Islands
(3) Juan Fernandez Islands; sex indication hypothetical, except for one female with wing 432

		n	observed range	mean	st. dev.
TAIL					
B. polyosoma (1)	♂	24	161-199	178.7	6.94
	♀	18	191-217	203.2	7.58
B. polyosoma (2)	♂	3	175-190	181.0	
	♀	6	182-202	193.2	7.25
B. polyosoma (3)	♂	3	195-223	213.3	
	♀	2	192-221	206.5	
B. poecilochrous	♂	6	197-227	208.3	11.57
	♀	5	211-227	221.2	6.10
B. galapagoensis					
juv.	♂	40	197-225	213.0	7.06
ad.	♂	31	190-218	205.0	6.60
juv.	♀	34	217-250	236.4	9.17
ad.	♀	21	214-243	227.6	7.45
B. albicaudatus	♂	13	152-199	170.1	14.46
	♀	17	160-202	176.9	12.55
B. swainsoni	♂	8	181-192	184.5	4.50
	♀	8	194-213	205.5	6.91
B. jamaicensis	♂	7	202-243	213.0	14.42
	♀	12	217-258	231.7	13.01
B. ventralis	♂	4	195-210	203.5	
	♀	1		206	
B. solitarius	♂	4	140-147	143.0	
	♀	8	152-177	163.0	8.55
BILL					
B. polyosoma (1)	♂	24	20.2-26.6	22.5	1.58
	♀	17	22.9-28.1	24.9	1.24
B. polyosoma (2)	♂	3	21.3-23.2	22.2	
	♀	6	22.8-26.1	24.9	1.27
B. polyosoma (3)	♂	2	20.5-22.5	21.5	
	♀	2	26.6-26.9	26.7	
B. poecilochrous	♂	6	22.3-25.1	23.8	1.11
	♀	5	24.8-27.2	25.9	1.02
B. galapagoensis					
juv.	♂	39	25.8-28.2	26.8	0.67
ad.	♂	31	24.9-29.0	27.5	0.87
juv.	♀	33	27.5-31.4	30.1	0.97
ad.	♀	21	30.0-32.5	31.3	0.78
B. albicaudatus	♂	13	22.0-28.7	24.6	1.73
	♀	17	24.0-30.0	26.9	1.57
B. swainsoni	♂	8	20.5-22.9	21.8	1.00
	♀	8	23.5-26.1	24.4	0.96
B. jamaicensis	♂	7	24.2-27.0	25.4	1.00
	♀	12	25.4-28.5	27.1	0.96
B. ventralis	♂	4	22.2-25.0	23.6	
	♀	1		26.8	
B. solitarius	♂	4	21.7-23.0	22.3	
	♀	8	24.8-26.5	25.5	0.53

		n	observed range	mean	st. dev.
INNER CLAW					
B. polyosoma (1)	♂	24	20.4-26.0	22.8	1.38
	♀	18	22.5-26.7	25.1	1.04
B. polyosoma (2)	♂	3	20.8-24.0	22.8	
	♀	7	24.5-27.7	26.5	1.08
B. polyosoma (3)	♂	3	23.4-24.2	23.7	
	♀	2	28.0-28.5	28.2	
B. poecilochrous	♂	6	24.2-27.0	25.4	1.20
	♀	5	25.3-28.2	26.8	1.28
B. galapagoensis					
juv.	♂	40	26.0-29.0	27.4	0.83
ad.	♂	31	26.3-29.8	27.9	0.85
juv.	♀	33	28.2-31.7	30.1	0.86
ad.	♀	21	30.0-33.4	31.6	0.83
B. albicaudatus	♂	13	21.0-26.5	22.9	1.44
	♀	16	21.9-27.2	24.1	1.49
B. swainsoni	♂	8	20.9-22.7	21.9	0.68
	♀	8	23.4-25.2	24.2	0.73
B. jamaicensis	♂	7	26.0-28.8	27.2	1.14
	♀	12	26.4-31.0	28.4	1.47
B. ventralis	♂	4	29.6-31.5	30.5	
	♀	1		33.3	
B. solitarius	♂	4	22.4-24.0	23.2	
	♀	8	24.4-26.2	25.3	0.64
HIND CLAW					
B. polyosoma (1)	♂	24	20.5-26.6	23.3	1.53
	♀	18	23.8-27.5	26.4	1.08
B. polyosoma (2)	♂	3	21.5-25.6	23.9	
	♀	6	25.0-28.6	27.5	1.34
B. polyosoma (3)	♂	3	23.2-24.0	23.6	
	♀	2	29.4-29.9	29.6	
B. poecilochrous	♂	6	24.6-27.0	25.5	0.84
	♀	5	26.3-30.3	27.6	1.69
B. galapagoensis					
juv.	♂	40	25.6-30.0	28.1	0.97
ad.	♂	31	27.2-31.4	28.9	0.97
juv.	♀	34	27.4-32.0	31.0	1.11
ad.	♀	21	30.8-36.7	32.6	1.42
B. albicaudatus	♂	13	21.4-27.0	23.1	1.39
	♀	16	22.5-27.4	24.5	1.43
B. swainsoni	♂	8	21.8-24.0	22.9	0.73
	♀	8	24.3-26.1	25.2	0.64
B. jamaicensis	♂	7	27.1-30.9	28.7	1.52
	♀	12	28.3-32.5	30.5	1.52
B. ventralis	♂	4	31.3-33.5	32.1	
	♀	1		35.4	
B. solitarius	♂	4	23.4-25.5	24.5	
	♀	8	25.7-27.8	26.8	0.72

		n	observed range	mean	st. dev.
TARSUS					
B. polyosoma (1)	♂	13	70-88	75.5	5.30
	♀	11	73-89	79.4	5.18
B. polyosoma (2)	♂	3	82-86	83.7	
	♀	5	81-91	85.0	3.74
B. polyosoma (3)	♂	3	75-79	77.7	
	♀	2	76-87	81.5	
B. poecilochrous	♂	6	82-88	86.0	2.19
	♀	5	89-95	91.4	2.30
B. galapagoensis					
juv.	♂	40	65-79	72.6	2.84
ad.	♂	31	70-80	74.2	2.81
juv.	♀	34	69-88	78.7	4.51
ad.	♀	21	74-89	80.4	4.15
B. albicaudatus	♂	11	72-89	79.4	5.63
	♀	13	80-89	84.6	2.72
B. swainsoni	♂	8	58-72	62.5	4.34
	♀	8	63-72	66.6	3.50
B. jamaicensis	♂	7	71-90	79.4	7.41
	♀	12	75-94	84.0	6.35
B. ventralis	♂	4	68-80	76.5	
	♀	1		86	
B. solitarius	♂	4	69-73	69.2	
	♀	8	69-73	70.3	1.30
MIDDLE TOE					
B. polyosoma (1)	♂	10	35-40	37.7	2.00
	♀	11	37-41	39.2	1.25
B. polyosoma (2)	♂	3	36-41	38.3	
	♀	6	40-45	42.8	2.32
B. polyosoma (3)	♂	3	39-42	41.0	
	♀	2	46-48	47.0	
B. poecilochrous	♂	6	39-44	42.5	2.07
	♀	5	43-49	45.6	2.61
B. galapagoensis					
juv.	♂	40	41-47	43.8	1.59
ad.	♂	31	41-50	45.4	2.39
juv.	♀	34	45-55	49.4	2.73
ad.	♀	21	45-57	51.0	2.90
B. albicaudatus	♂	11	39-48	41.3	2.65
	♀	14	39-51	43.4	3.61
B. swainsoni	♂	8	35-41	39.0	1.93
	♀	8	40-44	42.0	1.31
B. jamaicensis	♂	7	41-46	43.6	1.81
	♀	12	45-51	47.5	1.68
B. ventralis	♂	4	46-48	47.2	
	♀	1		54	
B. solitarius	♂	4	37-38	37.5	
	♀	8	39-42	40.6	1.06

Measurements are also given for juvenile Galapagos Hawks; 7 juvenile females (Santa Cruz (5), Fernandina (1), Isabela (1)) with wing lengths varying from 380-397 mm, and 2 males (Santa Fe (1), San Cristóbal (1)) with wings of 416-442 mm, have been excluded. I considered these birds to have been incorrectly determinated to sex.

The available museum specimens of the Galapagos Hawk were not sufficient to divide the material regarding to different islands, but in relation with the figures given for Santiago, those of Española are of interest, particularly as Swarth (1931) commented on island forms : "If these hawks are as sedentary as might be implied from their absence from some of the islands, it is not surprising that slight variations should appear in parts of their habitat, variations such as the larger measurements of Hood Island specimens seem to be" (pp. 49-50).

Española (specimens)

males (ad.+juv.)	n	observed range	mean	st. dev.
wing	5	402 -422	415.0	8.43
bill	5	28.8- 29.4	29.2	0.51
inner claw	5	28.1- 30.0	28.8	0.74
hind claw	5	28.1- 30.7	29.2	0.95
females (ad.+juv.)				
wing	2	442 -460	451.0	
bill	1	32.4		
males (probably wrongly sexed)				
wing	2	446 -447	446.5	
bill	2	31.8- 33.5	32.6	

The following measurements taken in the field support the slightly larger size of the Española buzzard, but warrant no subspecific denomination.

		weight	bill	inner cl.	hind cl.	wing
nest 2	male 'red T'	1150	28.6	29.6	29.9	
	male 'red V'	1100	29.4	29.6	29.5	
	female	1500	31.7	33.7	34.8	461
nest 10	male	1110		25.1	28.7	
	female	1460		33.5	33.3	

Measurements and weights of seventy-one captured Galapagos Hawks, determinated to sex on mensural differences. Weights in grs, other data in mm.

Santiago, 16 - 18 December 1970

	n	observed range	mean	st.dev.
Presumed males (juveniles)				
bill	26	26.2-28.4	27.3	0.60
inner claw	26	26.3-28.7	27.8	0.67
hind claw	26	27.0-29.9	28.5	0.78
weight	26	750-1110	923	91.13
Presumed males (adult)				
bill	5	26.9-28.1	27.5	0.55
inner claw	5	27.3-29.2	28.2	0.86
hind claw	5	27.1-29.4	28.4	0.96
weight	5	800-1000	896	79.56
Presumed females (juveniles)				
bill	18	29.6-32.3	31.0	0.67
inner claw	18	29.4-32.8	30.8	0.93
hind claw	18	30.1-33.1	31.3	0.89
weight	18	1200-1450	1330	72.56
Presumed females (adult)				
bill	22	30.0-33.3	31.4	0.68
inner claw	22	29.3-32.2	30.7	0.84
hind claw	22	29.7-33.9	31.8	1.16
weight	22	1200-1540	1357	96.86