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BREEDING ECOLOGY OF THE SWALLOW-TAILED GULL, *CREAGRUS FURCATUS*[1]

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THE Galápagos Swallow-tailed Gull, *Creagrus furcatus*—referred to as *Creagrus* throughout this paper—was little known until a series of papers by Moynihan (1962), Hailman (1964a, 1964b, 1965), Snow and Snow (1967, 1968), and Nelson (1968a) showed it to be one of the most aberrant and interesting species of gulls. Hailman (1964b) showed that the species breeds throughout the year but that natural groupings of nests have their breeding synchronized, probably by social stimulation. Snow and Snow (1967), working on South Plaza Island, found that individual pairs of gulls lay, on average, every 10 months if successful in raising a young, and rather more frequently if unsuccessful. Between cycles the molting adults are absent from the colonies for an average of about 4.5 months. With the exception of the Snows, who made fortnightly observations between February 1963 and April 1964, observers of the species had spent little time in Galápagos and a further long-term study on the species was obviously needed.

Between November 1965 and July 1967 my wife and I were resident at the Charles Darwin Research Station in the Galápagos and were able to make regular visits to Plaza and scattered observations at most other seabird colonies in the archipelago. We spent at least 10 days a month on Plaza, with a single exception, usually divided into a stay of a week or more with several day visits timed so that never more than 10 days elapsed without a visit. In all we spent 208 days on the island.

The systematic position of the species is obscure, but in view of its specialized biology and behavior I have considered it best left in the monotypic genus and have not followed Moynihan (1959) in lumping all the gulls into a single genus *Larus*. Moynihan (1959) tentatively placed *Creagrus* alongside the much smaller Sabine's Gull (*Xema sabini*) because

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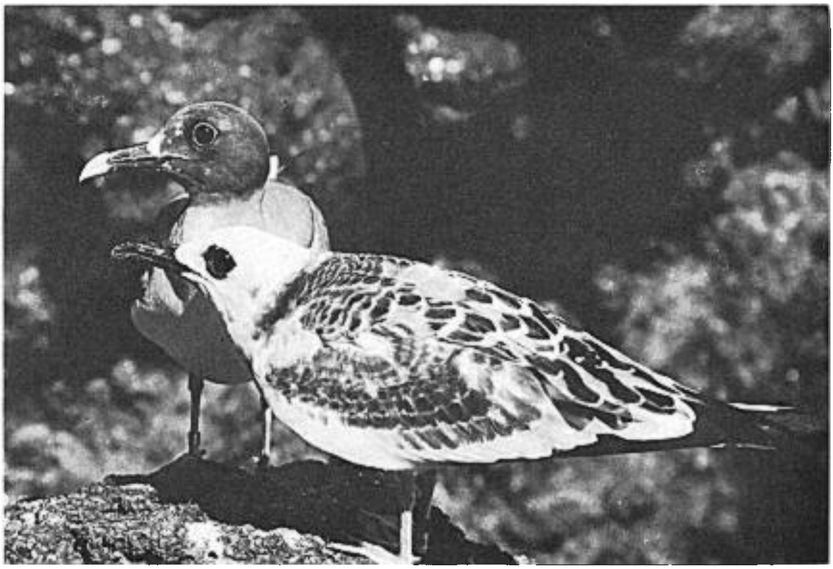

Figure 1. Juvenile *Creagrus furcatus* begging food from adult that shows some molt of the head feathers. Note the very large eyes.

of superficial morphological similarities, but I agree with Brown et al. (1967) that there is little reason to consider them closely related. I know of no evidence to support the contention of Nelson (1968b:202) in supposing a close relationship with the Andean Gull (*L. serranus*).

MORPHOLOGY

Creagrus is a medium-sized gull. During the breeding season its plumage is a striking white with very dark gray head and neck; it has a bill with pale tip, a white forehead, red legs, gray mantle, and large white wing patches. In nonbreeding plumage the hood is lost except for an ill-defined dark area around the eye and a slight collar. Two individual birds (one twice) returned to Plaza at the start of a breeding season while still in nonbreeding plumage but attained the full breeding dress before actually commencing breeding. Most birds started the molt of the head and hood when feeding young.

The juvenile plumage is brownish-black and white (Figure 1) and presumably the young molt soon after leaving the colony as the plumage is by then often worn. The intermediate immature plumage, if any, has not been described but must be passed at sea as even nonbreeding birds at the colonies are in fully adult plumage. I did see three breeding birds with black marks on normally all-white feathers, two with marks on the

TABLE 1
WEIGHTS OF BREEDING *CREAGRUS FURCATUS*

	Number	Average (g)	Range	SD
Males	6	713	630–780	59
Females	11	673	610–720	40
Birds with eggs	23	685	580–775	51
Birds with small young	42	679	600–810	54
Birds with medium young	12	652	530–735	56
Birds with large young	11	658	600–830	69

alula and one on the secondaries, a third with black tips to the outer (longest) pair of rectrices.

Snow and Snow (1967) show that, as in most gulls, the males are noticeably larger than the females. I obtained measurements of bill length and depth for 74 sexed birds, and although males did have longer and heavier bills than females, the differences were far less than in some European species (Harris, 1964, Barth, 1966). Males also tended to be heavier than females (Table 1) and birds with eggs or small young heavier than those with large young but the differences were not significant ($P > 0.05$). The average difference in the weighings of 13 birds that were weighed more than once was 35 g, the maximum being 80 g.

FEEDING

Although gulls are widespread in many habitats, *Creagrus* appears to be the only species to feed entirely by night. This behavior was hinted at by Gifford (1913), and Moynihan (1962) thought that the relatively enormous eyes and the diet of squid suggested nocturnal feeding. Hailman (1964b) discussed the species' adaptations to a nocturnal existence and noted that 17 birds regurgitated squid on being caught on Tower; once he saw a fish fed to a young on Plaza. Snow and Snow (1967) found that food consisted entirely of clupeoid fishes (37 remains) and squids (12). Several fish were referred to *Sardinops* sp. and the squids to *Symplectoteuthis oualaniensis*.

Regurgitated food I collected on Plaza consisted of 96 fish and 36 squid and on Tower of 5 squid and a single fish. This difference between the colonies is probably valid as only a handful of the hundred pellets regurgitated by the gulls on Tower contained fish bones. On Plaza the proportion of squid in the diet varied considerably (Table 2) and presumably reflected the availability of prey. Snow and Snow (1967) noted similar changes but recorded most squid in November, whereas I found them commonest in January and February.

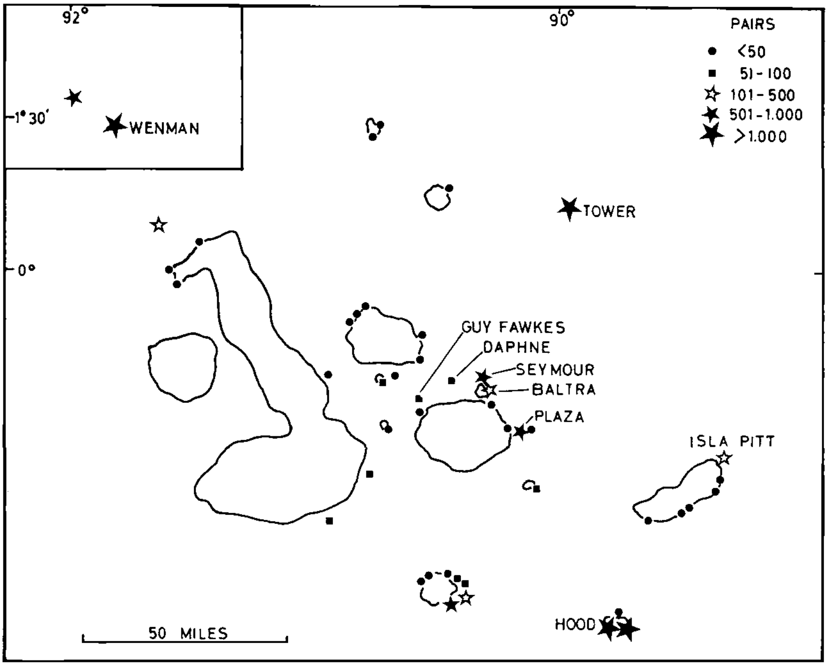

Figure 2. Distribution and estimated sizes of colonies of *Creagrus furcatus* in Galápagos.

M. R. Clarke has kindly identified some of the squid remains and has estimated the weights of the prey (Table 3). A surprising feature was the large size of some of the squids. That all these squids were taken as carrion is unlikely with so many other scavengers present, so presumably the gulls killed them and ate them piecemeal. The majority of the fish were clupeoids up to 200 mm long, but flying fish, including a flying garfish, were also recorded.

As first noted by Streets (1912), the species is pelagic outside the breeding season, but my little evidence on the feeding of young (below) suggests that the breeding adults feed near the colonies. Figure 2 shows the distribution and approximate sizes of the Galápagos *Creagrus* colonies. I suspect the total population is probably in the region of 10,000 pairs, a figure reached independently by Lévêque (1964). Although the birds avoid the colder, and richer, waters in the west of the archipelago, the colonies are widely spread among the islands and are reasonably small except where nesting areas are scarce in relation to potential feeding areas, that is on the fringes of the archipelago. Possibly each of the colonies

TABLE 2
PREY REGURGITATED BY ADULT AND YOUNG *CREAGRUS FURCATUS*

Month		Plaza Fish	Plaza Squid	Tower Fish	Tower Squid
1965	November	1			
	December	2	6		
1966	January		7		
	February	5	9		1
	March	5			
	April	9	1		
	May	17			
	June	5			
	July	3			1[1]
	August	6	1	1	1
	September	5	1		
	October	3	6		
	November	11			
	December	7	2		
1967	January	5	2		2[1]
	February	6			
	March	4			
	May		1		
	June	2			
TOTAL		96	36	1	5

[1] Indicates many pellets examined and almost entirely squid remains.

has its own feeding range. In the Galápagos a similar spacing out occurs among the inshore-feeding Blue-footed Booby (*Sula nebouxii*) and to a lesser extent the midwater-feeding Masked Booby (*S. dactylatra*), whereas the distant-water species, the Red-footed Booby (*S. sula*), is found in only a few, generally larger, colonies (for discussion see Nelson 1968b).

SELECTIVE ADVANTAGES OF NOCTURNAL HABITS

Among seabirds there are remarkably few purely nocturnal feeders like *Creagrus* and also the Galápagos Storm-petrel (*Oceanodroma tethys*) (Harris, 1969), although many other species are crepuscular or may feed at night during a full moon, for instance Sooty Tern (*Sterna fuscata*), Wedge-tailed Shearwater (*P. pacificus*) (Gould, 1967), the White Noddy (*Gygis alba*) (Ashmole and Ashmole, 1967), and *S. sula* (Murphy, 1936: 869). This holds although it is usually assumed, and rarely proved, that fish and squid are far commoner near the surface by night than by day.

Hailman (1963, 1964a) suggests that predation by frigate-birds (*Fregata minor* and *magnificens*) is responsible for the nocturnal habits of *Creagrus* and cleptoparasitism by frigates again is responsible for the dusky color of the other endemic Galápagos gull, the Lava Gull (*L. fuliginosus*). Snow and Snow (1968) support this view and note that gulls and frigate-birds

TABLE 3
IDENTIFICATIONS AND ESTIMATED BODY WEIGHTS OF CEPHALOPOD REMAINS FROM STOMACH AND PELLETS OF *CREAGRUS FURCATUS*[1]

Place	Data	Type	Identification	Estimated weights (g)
Academy Bay	24.12.65	Stomach	Ommastrephid Histioteuthid	80 37, 25
Plaza	13.12.65	Regurgitated	*Symplectoteuthis oualaniensis*	150 (fresh)
Plaza	13.12.65	Regurgitated	?	70 (fresh)
Tower	18.4.66	Stomach	Ommastrephid Ommastrephid(?) Histioteuthid	300 120 23
Tower	20.4.66	Pellets	*S. oualaniensis*	200, ?
Tower	17.7.66	Pellets	Ommastrephids	1,000, 900, 650, 160, 120, 130, 100, also six others possibly of this group

[1] All ommastrephids are probably *S. oualaniensis* and all histioteuthids probably *Calliteuthis* sp. Identifications and estimated body weights by M. R. Clarke.

rarely coexist. Certainly during the hours following dawn any adult *Creagrus* that left the shelter of the cliffs was mercilessly chased by frigates, which also tried to dislodge fledged young from the cliffs, whereas during the late afternoon and evenings, when the adults frequently roosted on the flat top or on the sea, they were not molested. Even at night the gulls were not entirely safe, as frigates were seen occasionally patrolling the cliffs at full moon.

Another possibility is that the nocturnal habits evolved in response to interspecific competition for food, as the Red-billed Tropic-bird (*Phaethon aethereus*), which feeds by day, appears to take fish and squids very similar to those eaten by the gulls, though probably from farther afield. The tropic-birds would seem better adapted for diurnal pelagic feeding as plunge-diving enables them to catch prey well below the surface of the sea, whereas gulls are restricted to prey very close to the surface.

BREEDING BIOLOGY

The Plaza Islands are two islets of basaltic lava about 400 yards off the eastern tip of Santa Cruz (= Indefatigable). Both have numbers of seabirds, but, apart from regular checks on North Plaza, all observations were made on the southern island, which is called Plaza throughout this paper. South Plaza is about 800 yards long by an average of 150 yards wide with the long axis running approximately east-west. On the very sheltered northern shore the island slopes gently into the sea; the southern edge, exposed to the prevailing wind and swell, has cliffs mainly 30–60 feet high, decreasing to 10 feet at the ends of the island. All but a few gulls nested

TABLE 4
INTERVAL BETWEEN SUCCESSIVE LAYINGS IN MARKED ADULT *CREAGRUS FURCATUS*

Next laying followed after	Pairs that Fledged young	Lost young	Lost egg
191–200 days		1	3
201–210	2	4	2
211–220	2	3	1
221–230	2		1
231–240	6	4	2
241–250	5	5	5
251–260	7	9	1
261–270	10	3	4
271–280	6	2	2
281–290	9		2
291–300	6		1
301–310	3	1	
311–320	3		
321–330	1		1
331–340			
341–350			
351–360			
361–370	1		
Average interval in days	268	244	247

either on the cliffs or among the considerable quantities of boulders at the cliff-bases. In other colonies *Creagrus* nests in a wide variety of habitats, on coral beaches and among mangroves and low *Cryptocarpus* bushes (Tower), among dense thorn scrub (North Plaza), and among *Opuntia* cacti more than 800 feet up on the top of Wenman. It is far from restricted to cliff-nesting (see below).

Except for a few in the first 3 months, all nests found were given a number painted on the rock or on a stake alongside and the positions marked on a map. Data on nest site, situation, and exposure to sea and aerial predators were recorded; all accessible eggs were measured and a series of chicks was weighed every month. Adults were marked with numbered monel rings and some with individual plastic colored rings. In all we marked 167 adults and caught 53 birds that R. Lévêque and the Snows had marked previously.

THE BREEDING CYCLE

It has been known for some time (Murphy, 1936) that *Creagrus* nests in all months of the year, suggesting that conditions are equally favorable or unpredictable for breeding at all times, but only recently have Snow and Snow (1967) demonstrated that successful pairs attempt to breed every 10 months while unsuccessful birds try even more frequently.

In the present study dates of laying were known for 120 successive layings by ringed birds (Table 4). Successful birds nested again an average of 9 months later, unsuccessful pairs after about 8 months. These figures are significantly ($P < 0.05$) lower than those Snow and Snow (1967) found for successful birds, a mean of 268 days as compared to 298 days.

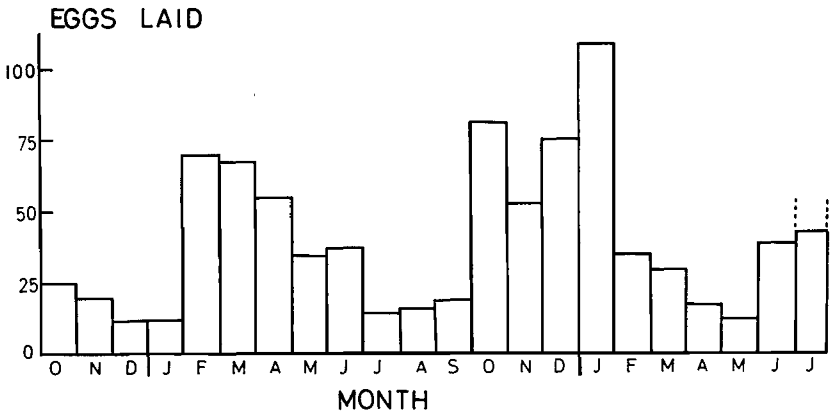

Figure 3. Distribution of laying dates of *Creagrus furcatus* on Plaza 1965–67. The second peak being higher than the first is probably due to more time being available for nest finding.

BREEDING SYNCHRONY

Any discussion on breeding synchrony is closely tied to the definition of a colony. Here Plaza is treated as one colony because young birds reared there return to breed, but the birds within each of several well-defined subcolonies on the islet have their breeding synchronized to a considerable degree (Hailman, 1964b).

Treating Plaza as a unit shows considerable peaks and troughs of egg-laying (Figure 3), but even within one of these troughs some subcolonies

TABLE 5

LAYING PEAKS OF *CREAGRUS FURCATUS* IN DIFFERENT GALÁPAGOS COLONIES[1]

	Peaks of laying				Troughs of laying		
	1965	1966	1967	1968	1965	1966	1967
Plaza		Feb.–Apr.	Jan.	Mar.	Dec.	July–Aug.	Apr.–May
		Oct.–Dec.	July				
Hood	Aug.		Feb.	Feb.		May–Dec.	July
Isla Pitt		Apr.	May		Dec.		
Tower (beach)		Dec.		June		July	May–June
Tower (cliffs)		Apr.				June	Apr.–June
		July–Aug.		Apr.			
Baltra		Oct.					
Seymour			Mar.				
Guy Fawkes							May
Daphne							May
Wenman		May					

[1] The months are only approximate as usually only a few visits were made to each colony.

were at peak laying time. These peaks were similar to those Snow and Snow (1967) noted, but were in different months. With the considerable variation (191–361 days) between laying that such a well-marked synchronization occurred is surprising, the more so as breeding birds almost always returned to the same nesting site and were not attracted to areas where birds were already breeding (see Orians, 1961). At any time of year it was possible to find breeding at a peak in some colony (Table 5), so that breeding in Galápagos is not synchronized, but perhaps remains at a reasonably constant level throughout the whole population.

Snow and Snow (1967), noting that on Plaza parts of the gull nesting areas were sometimes subject to much spray and sometimes even waves, suggest that a well-marked peak of laying might break down if it coincides with a period of unfavorable weather. As such weather is to some extent seasonal, they suggest that peaks of laying might possibly be regular for several years until one falls in the roughest time of year (August–November). Then many birds might fail to breed and the normal cyclic pattern would break down. The available data for 1963–68 (Figure 4) suggest a 9-month periodicity of peaks and troughs, probably continuous, over the whole period. Unfortunately no laying peaks were recorded in the roughest time of year, but when my observations ceased in July 1967 such a peak showed every likelihood of materializing. This peak had passed by December and a new peak occurred in March–April 1968 (de Vries, pers. comm.).

There can be little doubt that the varied and noisy displays of the gulls bring about this synchrony, but it is unlikely that this synchrony is just an inevitable concomitant of social nesting (Nelson, 1968a), so presumably it has some definite advantage, possibly against predation or cleptoparasitism by frigate-birds (see below).

Pre-egg Stage

Observations on color-ringed birds indicated adults were away from the colony between breeding cycles an average period of 140 days (65 observations, range 65–225 days). This is not significantly longer ($P > 0.05$) than the average of 129 days Snow and Snow (1967) found. Returning birds were always first seen at the subcolony, and apparently pair formation and copulation occurred there. One male, whose mate died the day after laying, remained at the site and attracted another female that laid about 6 weeks after the first died. There are no gatherings similar to the "clubs" found in other gulls where pre- and nonbreeders gather just outside the colony. The only flocks of *Creagrus* ever seen were when birds were forced off some cliffs by rough weather, or when bathing, or when gathering prior to leaving for fishing in the late evening. Snow and

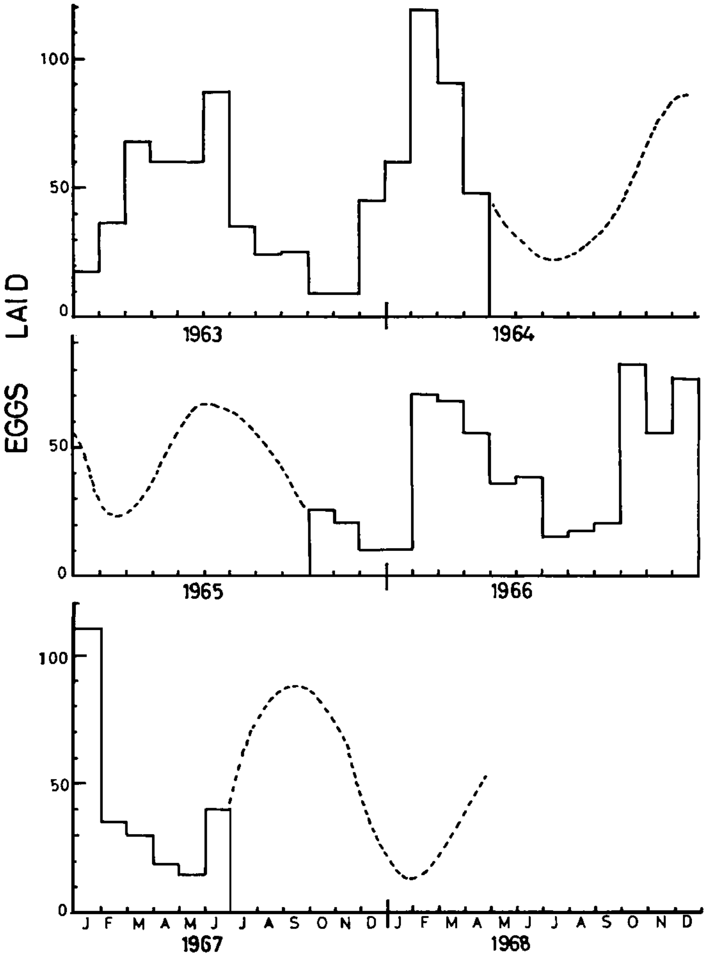

Figure 4. Numbers of eggs of *Creagrus furcatus* laid on Plaza 1963–67 (histogram) and other presumed peaks of laying (indicated by dotted lines). Data for 1963–64 from Snow and Snow (1967).

Snow (1968) noted this predeparture flocking only in May, but I frequently observed it from May to September.

Once a pair take up a territory, they make a rudimentary nest or platform of small pieces of lava, sea urchin spines, white coral, or twigs of *Periloba galapagoensis* (on Isla Pitt), and sometimes decorated with *Ianthina* shells (Figure 5). This nest-building appears to be stereotyped and extremely important in pair formation. Nelson (1968a) thought that the nest was "architecturally functionless" but this form of nest is highly

Figure 5. Egg of *Creagrus furcatus* in nest made of pieces of lava, coral, chiton shells, and bones.

efficient in preventing eggs rolling away (Hailman, 1964a; personal observation). Copulation occurred at any time of day near the nest site but never in bright sun, and most commonly at dusk and dawn.

Egg Stage

Most gull species have, at least in the first laying in a season, a clutch of three eggs; in a few species, such as the Black-billed Gull (*L. bulleri*) (Beer, 1965), and the two kittiwakes (*Rissa tridactyla* and *R. brevirostris*) (Bent, 1921; Cullen, 1957), two is the commonest clutch and in *L. fuliginosus* the few nests found have never contained more than two. *Creagrus* is unique among the gulls in both laying a single egg and having only two brood patches. Among the many thousands of *Creagrus* nests I examined only three had two eggs. In one case a pair had taken over and laid an egg in a scrape already holding an addled and deserted egg, in another an egg had rolled down from a nearby nest, but the third was probably a true instance of a female laying a c/2. This pair, with a nest in a rocky area several yards from the nearest neighbor, had an empty nest one visit and two eggs a week later. As no other bird was ever seen near the nest site and birds jealously guard the nest from long before laying, probably one female laid both eggs. Unfortunately one of the eggs failed to hatch, but another young was added to the nest when the

TABLE 6
FOLLICLE SIZES IN OVARIES OF *CREAGRUS FURCATUS*, *LARUS MARINUS*, AND *L. FUSCUS* IN RELATION TO DATE OF LAYING

Species	Time after laying	Follicle size (mm)							
		a[1]	b	c	d	e	f	g	h
Creagrus furcatus	At laying (0)	–	4	4	4	4	2	2	2
	ca. 12 hours	–	8	5	4	4	3	2	2
	2–3 days	–	4	4	3	2	2	2	2
	ca. 2 months	–	1	1	<1	<1	<1	<1	<1
Larus marinus[2]	0	–	41	34	8	8	6	6	5
	2 days	–	–	30	30	9			
	4 days	–	–	–	10	7	7	6	5
	6 days	–	–	–	14	9	7	5	4
	24 days	–	–	–	7	7	4	4	4
	ca. 4 months	1	1	<1	<1	<1	<1	<1	<1
Larus fuscus	6 days	–	–	–	7	7	4	4	4

[1] a refers to the largest follicle, b to the next, and so on.
[2] In *L. marinus* and *fuscus* time is from the laying of the first egg.

other egg hatched and the pair reared two young. Snow and Snow (pers. comm.) also noted a c/2 laid in one nest; this site was not far from the nest I observed and could refer to the same female. Thus the species seemingly does, extremely rarely, have a two-egg clutch.

In some gulls, such as the Great Black-backed Gull (*L. marinus*), *L. argentatus*, and *L. fuscus*, a few ovarian follicles, often four, enlarge greatly before laying, but only three ovulate, the fourth acting as an insurance against loss of the first egg when it can quickly produce a fourth egg (Paludan, 1951; Harris, 1964). If, starting with the first egg, all eggs are taken as soon as laid, gulls have been known to lay up to 16 eggs (Salomonsen, 1939). In *Creagrus* only a single follicle enlarges and, if the single egg is lost immediately after laying, another egg cannot be produced for about 18 days. Table 6 presents some comparative data on follicle sizes.

The single egg, similar in color and shape to other gull eggs, is usually laid at night though a few are certainly laid during daylight. Eggs showed no significant ($P > 0.05$) monthly differences in measurements (Table 7) or calculated volumes; 78 newly laid eggs averaged 74.3 g (range 63.5–86.0, SD 4.8), or about 11 per cent of the average female's weight. The egg/body weight proportions for five females caught immediately after laying were 10.0, 11.0, 11.6, 11.7, and 13.5 per cent. The egg is therefore only slightly proportionally larger than a single egg in the larger species *L. fuscus* (9.7 per cent of female) and *L. argentatus* (10.3 per cent) (personal data); and slightly smaller than in the smaller *L. ridibundus* (15.2

TABLE 7
MONTHLY MEASUREMENTS OF *CREAGRUS FURCATUS* EGGS LAID ON PLAZA

			Average		SD	
Month		Number	Length (mm)	Breadth (mm)	Length	Breadth
1966	Apr.	6	68.0	46.2	3.8	0.9
	May	13	66.4	46.4	2.5	0.8
	June	21	65.2	46.3	2.4	1.2
	July	5	65.6	46.4	3.0	0.6
	Aug.	14	66.2	45.8	1.9	1.5
	Sep.	6	65.3	45.3	2.4	1.6
	Oct.	72	66.3	45.3	2.8	1.7
	Nov.	38	66.5	46.1	1.9	1.3
	Dec.	49	65.1	46.0	3.3	1.7
1967	Jan.	83	66.0	46.3	2.6	1.3
	Feb.	24	65.2	46.0	2.0	1.3
	Mar.	27	66.4	46.1	2.0	1.0
	Apr.	9	66.7	46.4	2.6	1.2
	May	16	66.2	46.3	2.1	1.2
	June	6	67.4	45.7	2.3	0.9
	July	38	65.3	46.2	2.3	0.9

per cent of adult weight), *R. tridactyla* (14.2 per cent), and *L. canus* (12.8 per cent) (from Lack, 1967) despite the reduced clutch size. Larger eggs of *Creagrus* are no more likely to hatch or produce fledged young than smaller eggs, indeed a young fledged from one of the smallest eggs found (60.0 × 42.0 mm).

Thirty-seven incubation periods known accurately were 29 days (2 cases), 30 (3), 31 (6), 32 (9), 33 (8), 34 (4), 35 (2), 36 (2), and 38 (1), an average of 32.7 days. Previous recorded incubation periods are 33 and 34.5 (Snow and Snow, 1967) and two of 35 days (Nelson, 1968a).

Some birds replaced a lost egg, often but not always in the same nest, but this was not usual. Of 148 lost eggs in nests followed closely, 9 were definitely replaced (as one of the pair were ringed) and 21 probably (in same nest but neither bird of the pair ringed); of 56 pairs losing newly-hatched young, two definitely and one possibly relaid. Thus no more than 20 per cent replaced lost eggs. The average gap between loss of an egg or chick and relaying was 23 days (range 18–30, SD 3.7) for definite replacements and 25 days (11–44, SD 7.3) for possible replacements. Some of the possible cases of relaying were doubtless new pairs, as in five cases nests losing eggs were occupied by another pair soon after, and in one of these cases the gap in laying was only 10 days. In two other nests where young had hatched and were still alive, new pairs laid within a few weeks. This pattern of replacement-laying differs from that noted by Snow and Snow (1967). They found that lost and deserted eggs were

TABLE 8

FEEDING FREQUENCY AND AVERAGE DAILY INCREASE IN WEIGHT OF YOUNG *CREAGRUS FURCATUS*

		Normal young			Experimental twins		
Month		Sample of young weighed	% showing increase	Average daily increase (g)	Sample weighed	% showing increase	Average daily increase (g)
1965	Dec.	11	91	22.8			
1966	Jan.	14	71	35.0	6	67	20.0
	Feb.	11	64	27.9			
	Mar.	58	91	19.0	35	83	25.5
	Apr.	54	78	24.9	18	83	39.0
	May	44	68	20.7	67	66	31.1
	June	10	50	9.0	23	65	38.8
	July	48	27	13.1			
	Aug.	32	53	17.6			
	Sep.	11	55	41.7			
	Oct.	1	100	10.0			
	Nov.	30	73	18.6	16	50	29.1
	Dec.	19	63	20.0	12	83	9.0
1967	Jan.	12	50	28.3	40	60	28.4
	Feb.	23	52	33.3			
	Mar.	4	75	46.6			
	Apr.	11	91	26.0			
	May	45	71	18.9	6	50	5.0
	June	37	65	12.3			
	July	17	67	19.0			

regularly replaced after intervals of usually 30–50 days, but some of their presumed relayings were probably by new pairs.

Little information was obtained on incubation spells, but they appeared usually to be quite short and certainly most birds were able to feed each night. There was no pre- or postlaying exodus of females from the colonies, which might have indicated a strain on the female in producing the egg. One nest had three adults taking turns incubating.

Simple experiments showed that incubating birds with eggs would retrieve eggs placed 6 inches or so outside the nest, usually by rolling them with the ventral edge of the bill, as Tinbergen (1953) describes for *L. argentatus*, but sometimes the bird squatted with the front of the breast over the egg and then moved backward onto the nest. Two separate birds were given the choice of their own egg or a strange egg placed one on either side of the nest; both retrieved both eggs. Similarly a bird given the choice of its own egg or a c/2 brought all three back to the scrape.

CHICK STAGE

On hatching the young was either brooded for several days on the nest, or it left immediately for the cover of a rock. It was impossible to be

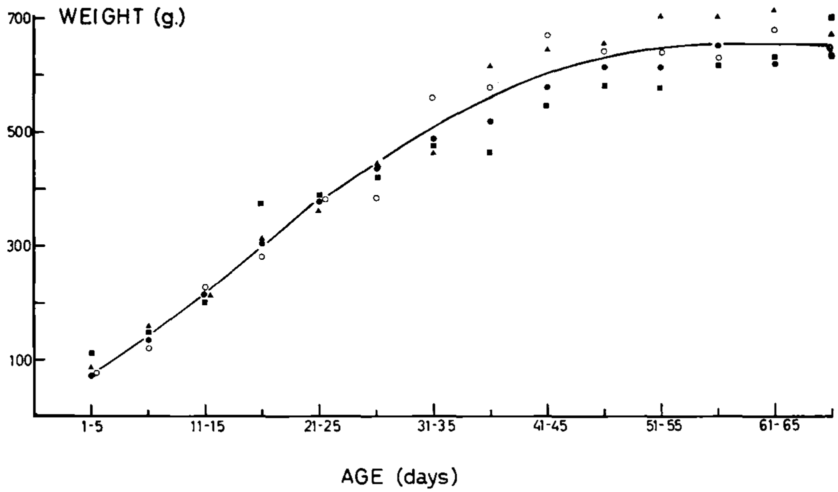

Figure 6. Average growth curve for young *Creagrus furcatus* (solid line) and average weights for young hatched December 1965–April 1966 (22 young, represented by solid circles), May–September 1966 (23 young, open circles), October 1966–February 1967 (25 young, triangles), and March–May 1967 (14 young, squares).

sure if the adult removed the egg shell as the red crab, *Grapsus grapsus,* carried off any left shells, dead young, and even a few living small young.

Unlike *L. argentatus* and *L. fuscus* the adults rarely swooped at or attacked a human intruder, but birds varied considerably, and certain individuals with young repeatedly attacked me sometimes drawing blood from my head. Oher birds would walk up to and peck an observer standing by their nest.

Most young took their first flight when between 60 and 70 days old (extremes of 43 birds being 58 and 84 days), but the adults continued to feed their chick until all three left, possibly together, when the chick was aged about 3 months. The oldest young seen at the colony was 135 days. These records agree with those of Snow and Snow (1967).

Chicks were weighed periodically to obtain growth curves and daily for estimates of feeding frequencies and feed sizes. Chicks were not weighed in the morning as they usually regurgitated, so feeding frequencies and feed sizes are related to daily changes in body weight (Table 8), but the individual prey items were so large that these weighings probably give a reasonable indication of feeding. Young never appeared to be seriously short of food, and the growth curves for young hatched at various times are similar (Figure 6). Though adults and young appeared to leave the colonies at the same time, parental feeding could hardly be prolonged

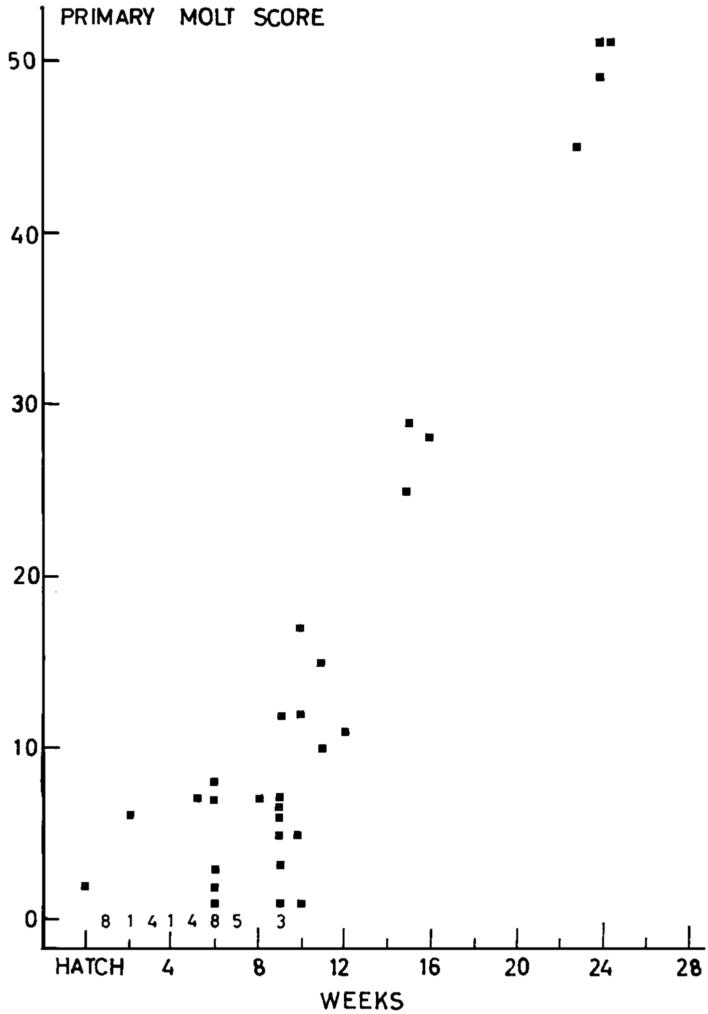

Figure 7. Molt scores for adult *Creagrus furcatus* caught at various dates after their egg had hatched. Numbers opposite the zero indicate numbers of birds handled that showed no primary molt.

after this as the adults have to molt and very soon return to the colonies.

Hungry young pecked both at the pale area at the tip of the adult's bill and also at the white forehead patch, at the same time uttering a begging call not unlike that of other young gulls, before being fed either from the parent's bill or by the parent regurgitating food onto the ground. Frightened young often regurgitated food but, as in *L. argentatus* (personal data) and *L. dominicanus* (Stead, 1932), the adults sometimes reswallowed this and excess food the chicks left uneaten. This was important as any waste food encouraged frigate-birds, which are potential predators on the chicks. Several times when handling the young I witnessed a distraction display in which the adults flew close and regurgitated food, which they held in the bill before reswallowing it. I caught one such adult when it landed and it did not then regurgitate. Perhaps the regurgitated food helps to distract an attacking frigate.

On 29 November 1966 I repeatedly checked from dusk (18:00–18:30) onward the nests of 12 pairs with young in which one of the adults was marked with dye. These checks were made at 18:00, 20:30, 22:00, and 22:45. At six nests feeding birds had returned by 22:45, at five by 22:00 when at least one young had been fed. As none of these feeding birds left before dusk, they must have fed fairly near the colonies.

Molt

The state of primary molt was recorded for all birds caught, using the numerical method detailed by Ashmole (1962). Each feather is assigned a score according to its growth of 0 (old feather), 1 (a missing feather or feather in pin), 2, 3, 4. A new feather scored 5. Each wing can then be given a molt score between 0 (all old feathers) and 55 (all new).

In *Creagrus* the onset of molt varied (Figure 7); a few adults commenced replacement of the innermost primaries as the egg hatched, others caught long after the young fledged still had all the old primaries. Most adults started primary replacement at the time the young fledged. In extreme cases birds completed growing five new primaries on each wing before leaving the colonies. Although breeding and wing molt are often mutually exclusive, this is not always so in the Laridae, as *L. argentatus* and *L. fuscus* in Britain frequently start replacing primaries when feeding young and even, in late nesters, when incubating (pers. data).

As food always appeared to be plentiful in the Galápagos, there seems little reason for the adults to leave the archipelago between breeding attempts. Perhaps with wings and tail in molt they may be at some disadvantage in competing with adults and nonbreeders with intact feathers, and they move to where food might possibly be more abundant off the coasts of Ecuador and Peru.

Adults were difficult to catch before laying started, but four birds handled at this time were still growing the outer primaries. None of these birds commenced breeding until the molt was completed and all birds, including nonbreeders, had a complete molt between successive cycles at the colony.

After hatching the brood patches grow over, which also happens in some birds incubating addled eggs, and a general body molt takes place, which

TABLE 9
NESTING SUCCESS OF *CREAGRUS FURCATUS* IN RELATION TO DATE OF STARTING CLUTCH

Date of laying		Number of nests studied	Percentage hatched	Percentage fledged	Percentage fledged as found by Snow and Snow (1967)
1965	Nov.	9	89	67	
	Dec.	6	83	83	
1966	Jan.	9	89	76	
	Feb.	48	79	64	
	Mar.	35	80	63	28
	Apr.	45	58	50	23
	May	34	79	51	37
	June	30	60	30	30
	July	10	60	36	29
	Aug.	16	44	13	19
	Sep.	13	38	19	14
	Oct.	54	52	38	25
	Nov.	50	68	40	13
	Dec.	68	60	27	33
1967	Jan.	96	67	19	
	Feb.	35	54	10	
	Mar.	29	45	32	
	Apr.	17	53	23	
	May	12	50		

is very noticeable on the head (Figure 1). Only once did I see a bird at the colonies growing rectrices.

NESTING SUCCESS

Nesting success in relation to month of laying, omitting nests involved in experiments, is shown in Table 9. In a few instances it was uncertain whether an egg was lost near hatching or actually hatched and the young was then lost. Birds able to fly freely were considered to have fledged, and very few of these died before leaving the island. Replacement eggs are included, as the success rate was similar to that of normal eggs.

Causes of failure were sometimes difficult to determine but the figures obtained for egg losses were: 85 lost without trace, 77 addled, 33 washed away by sea, 8 rolled out of nest, 8 died during hatching, 5 squashed by incubating bird, 5 never incubated, 5 destroyed by sea lions, 4 dented, 2 broken by falling stones, 2 taken by *L. fuliginosus*, and 1 adult died. Young usually just disappeared, but 6 were washed away by the sea, 3 fell over cliffs, 2 dislocated wings, 2 were eaten by Short-eared Owl *Asio (flammeus) galapagoensis*, and 2 died apparently of starvation. Predation appeared to be slight though the owl took a few, as probably did the egret (*Casmerodias egretta*) and Gray Heron (*Ardea herodias*), both of which the gulls mobbed. Frigate birds doubtless took some small young but were uninterested in eggs, as four I placed on exposed rocks remained untouched for several weeks. Cannibalism was unrecorded, nor were any young seen to be killed when wandering, or chased accidentally, into a strange territory. A proportion of the failed eggs were deserted and/or addled, and these were left in case they affected the occupation of the site by other pairs. Of eggs later opened, 26 had signs of development and 15 did not. Egg losses were equally spread throughout the incubation period, whereas the majority of chick losses occurred within the first few days after hatching.

In extremely few species does breeding occur throughout the year at a less than annual interval and birds in individual groups breed synchronously. Hailman (1964b) concluded that breeding in *Creagrus* was entirely induced by social factors, as the ecological conditions appeared to him to rule out possible synchronizing effects of the physical environment. Snow and Snow (1967) showed that on Plaza adverse weather affected breeding success and might be important if birds were to delay laying in the more exposed sites during the rougher months of the year, but I think this unlikely. A third possibility is that a period of severe food shortage might similarly synchronize breeding as in Audubon's Shearwater (*Puffinus lherminieri*) on Plaza (Harris, 1969).

Conditions on Galápagos are far from uniform with a windy, cool, and misty "garua" season from July to October and a hot, sunny, and calm season from January to May when most of the rain occurs. Although the sea temperatures show considerable seasonal changes, I was unable to detect any seasonal fluctuation in plankton. During the windy season some parts of Plaza are subject to considerable spray, but in this respect the colony is atypical, and Snow and Snow (1967) considered that new pairs coming to breed at this season occupied mainly the more sheltered places and that, possibly every few years when the peak of breeding coincided with the windy season, breeding might be delayed. Rough weather during my stay did not prevent birds laying, and some successfully sat through hours of driving spray. Some birds whose nest sites were washed away just before laying moved up the cliffs and laid without making a nest—perhaps the pairs that Snow and Snow (1967) considered young but, although some then constructed nests around the egg, none was successful as the eggs were soon cracked on the bare lava or rolled away. The roughest seas I experienced on Plaza were in May, a normally calm month, and it is probably impossible for birds to predict rough weather. Indeed in all probability a peak of laying occurred in the rough season of 1967 (Figure 4).

Nesting success varied but was lowest for eggs laid August–September

TABLE 10
NESTING SUCCESS OF *CREAGRUS FURCATUS* ON PLAZA IN RELATION TO NEST SITE, COLONY DENSITY, AND LAYING DATE

	Eggs		Young		Overall nesting success (%)
	Laid	Hatched (%)	Hatched	Fledged (%)	
Nest site					
On top and exposed	33	64	16	37.5	24
On top and sheltered	44	61	23	39	24
Among boulders	215	65	116	57	37
Exposed on boulders	25	56	13	61	34
Under boulders	81	60.5	44	61	37
On cliff ledge	149	67	95	62	42
Colony density					
Dense	34	44	14	64	28
Dense	44	54.5	21	43	23
Dense	26	69	15	73	51
Less dense	48	56	27	33	19
Very low	138	64	85	51	32
Date of laying within the cycle of a subcolony					
First half of spread	99	60	55	58	35
Second half of spread	88	57	53	49	28
Peak of laying	106	64	60	65	42
Out of peak	87	63	46	54	34

1966 and January–February 1967. In the former period most of the losses were during the egg stage (some to the sea) while in the latter some chicks failed to survive, though this was not correlated with any marked decrease in feeding of the young that were weighed. March and April 1967 were the only months when I noted starvation as a cause of death in young, but even at this time several pairs managed to raise two young (provided experimentally).

Although a high proportion of the losses were due to addled eggs, this was no more important than in *L. argentatus* and *L. fuscus* (Paludan, 1951, Harris, 1964). At the time I thought that eggs laid in a subcolony after the peak of laying were the most frequently deserted but analysis of the results has failed to confirm this.

Nesting success was considered in relation to nest site, colony density, and date of laying within a subcolony (Table 10). The last factor had no effect and is not discussed further. Nest sites were classified as to exposure to aerial predators, whether on the flat top of the island, on cliff ledges, or among or on boulders, areas subject to wave action being excluded. Nest site had no effect on hatching success, but chicks on the top of the island had a significantly lower fledging rate than those from other areas. Snow and Snow (1967) found that nests on the exposed top of the island were invariably unsuccessful unless near places where chicks could shelter. Predation is probably the important factor here where it must be harder for adults to protect their young than on ledges or among boulders.

Density of nests of birds nesting on cliffs or among boulders is extremely difficult to measure, but it was possible to classify subjectively five colonies among boulders as dense (in coves with nests usually closer than 6 feet although sometimes separated by boulders), less dense (in a cove but with an obviously lower density of nests), and very low (spread over about 200 yards of reasonably straight coast with nests up to 30 feet apart but all synchronized as a subcolony). There was no relation between colony density or position of nest within the colony and nesting success, and even isolated nests, as long as not on the exposed top of the island, were frequently successful. Nor did pairs from dense colonies show any tendency to return and breed earlier than isolated pairs. In *L. ridibundus,* Patterson (1965) showed that birds breeding in the center of a gullery had a higher nesting success than those at the fringe, while the few breeding outside the colony produced very few young; also that pairs laying during the peak of nesting had the highest nesting success. Neither of these points could be shown in *Creagrus* possibly because in *L. ridibundus*, as in *L. argentatus* and *L. fuscus* (Harris, 1964), predation and cannibalism caused most losses.

Most discussions on the advantages of synchronous breeding (e.g. Darling, 1938) have been concerned with the effects of predation and, although this certainly occurs in *Creagrus*, it is difficult to believe that it is of more importance than the disadvantage inherent in competing for food in a synchronously breeding colony of inshore feeding birds. In this species it could be important as a protection against cleptoparasitism, and to a lesser extent predation, by frigate-birds during times of food shortage.

Population Dynamics

Of the 42 color-marked adults at the start of the season, at least 40 were alive two seasons later—a mortality of only 2.4 per cent per season. Moreover it is by no means certain that the two missing birds were dead, as they might possibly have lost their color rings.

Breeding adults had previously been ringed on Plaza by the Snows (53 birds) and Lévêque (18 birds). I have excluded three birds marked with aluminum rings that they are likely to have lost from wear on the rocks. Of the Snows' 53 birds we recaught 45, with an average interval between ringing and last retrap of 43 months—an average seasonal mortality of 3.2 per cent (assuming an average breeding interval of 9 months). The corresponding data for the birds Lévêque ringed were 7 retraps, an average gap of 71 months, and a seasonal mortality of 7.7 per cent. Whereas the Snows' rings were of different design than mine, Lévêque's were identical to mine, so I probably overlooked some of Lévêque's birds. This small mortality might be accounted for by accidents (i.e. density independent) as I found two adults dead after getting feet jammed between rocks, and two more crushed by bull sea lions.

I found three breeding birds that had been ringed as young: one on Tower was aged 50 months (just over 4 years); one on Plaza 68 months (5½ years) old had certainly not bred the previous season; the third, color-ringed as a juvenile 40–44 months previously, had certainly not bred before, and was probably young for a breeder.

During their study Snow and Snow (pers. comm.) color-ringed large numbers of chicks on Plaza with green plastic, (126 young February–July 1963) and split celluloid rings of red (35 young July–October 1963), black (34 young November 1963–March 1964, and blue (55 young January–March 1964). From April 1966 onward numbers of these birds returned to the colonies. From the dates and places seen and behavior I calculated that I saw at least 18 green-ringed birds (14 per cent of those ringed), three red (9 per cent), and four black (12 per cent). The minimal times that young from these groups must have spent away from Plaza were 38, 39, and 41 months respectively. Postfledging survival appears to be high, as the 14 per cent of the green birds seen was probably far less than the numbers actually present in the colonies when I was there, and takes no account of any returning after I left. From observations on adults ringed with celluloid rings it was obvious that many soon fell off, especially those colored blue. Of 23 the Snows placed on adults, all had gone within 3-years. Therefore differences in the number of observations of different colored rings do not indicate differences in postfledging survival. No color-ringed birds were seen at other colonies, not even at North Plaza only 200 yards away.

Immature birds returned to the colonies in fully adult plumage and soon took up residence in a subcolony and defended a territory, but few built nests in their first season. One bred during its second season at the colony but the majority did not. On average birds probably breed after spending four breeding seasons away from the colonies and two more at the colonies as prospecting birds, i.e. when almost 5 years old.

To judge from studies made on tropical seabirds on Ascension Island by the B.O.U. Centenary Expedition (in Ibis, 103b: 1962–63) and in Galápagos (pers. data on food shortages in several species) it is unlikely that conditions in Galápagos are as uniformly favorable as they appear to have been during the present study. Periodic food shortages might well

TABLE 11

AGES WHEN LAST SEEN OF YOUNG *CREAGRUS FURCATUS* THAT FAILED TO FLEDGE

	Days after hatching					
	1–10	11–20	21–30	31–40	41–50	51–60
Singles	60	13	15	7	6	4
Artificial twins	12	3	4	4	4	2

reduce the production of young and perhaps the survival of adults. In 1965 a periodic change of oceanic currents ("El Niño") that caused a large scale die-off of guano birds in Peru also affected the Galápagos, but it appears to have had little influence on the *Creagrus* adult survival, for it is difficult to envisage a much higher adult survival than the 97 per cent indicated by the birds the Snows ringed prior to this and I retrapped later.

SIGNIFICANCE OF THE SINGLE-EGG CLUTCH

Although *Creagrus* is unique among gulls, a single-egg clutch is common among many groups of seabirds, as Sternidae (several species), the Sulidae (two species), Procellariiformes (all), Fregatidae (all), Phaethontidae (all). Lack (1954, 1967), supported by many workers such as Ashmole (1963), argues that either the adults cannot collect enough food to produce more than one egg, or that this is the most productive clutch size, some factor, presumably food, acting so that young in larger broods either die in the nest or have a lower postfledging survival. The tendency to lay more than one egg would then be soon eliminated from the population. On the other hand, Wynne-Edwards (1962) interprets the data on clutch size and deferred maturity in many seabirds as factors restricting the number of young recruited to the breeding population. In theory it is quite feasible to test these hypotheses by giving adults larger than normal clutches, but in practice it has proved exceedingly difficult to eliminate all the variables.

Some *Creagrus* pairs were given additional eggs to test if they could hatch more than the normal clutch. Some of the added eggs were known to be addled before being added to newly laid eggs, others were freshly laid and taken from nests used for repeat laying experiments. Of 31 living eggs 16 hatched (52 per cent), which was not significantly lower ($P > 0.05$) than the hatching of normal eggs (65 per cent). Therefore the species appears not to need the two brood patches to incubate its single egg, but this is to be further tested by eliminating one brood patch and looking at survival of single-egg clutches.

Thirty pairs, with laying dates spread throughout the study, were given an additional young on the hatching of their own egg. Of these 60 young,

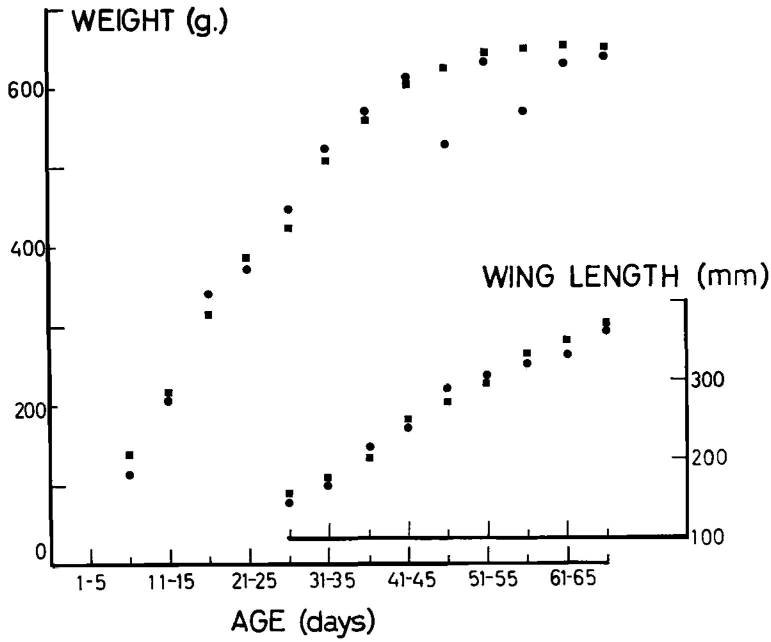

Figure 8. Average growth curves for 84 single chicks of *Creagrus furcatus* (indicated by squares) and 16 young in artificially produced sets of twins (indicated by circles).

31 fledged (51 per cent or one per pair) as compared with 56 per cent fledging success of single young hatched during the same period. The pattern of chick losses at different ages was identical to that of single young (Table 11). As the growth curves and wing length curves (Figure 8) and the feeding frequencies and feed sizes (Table 8) show these twins grew as well as single young, the parents were presumably able to bring twice the normal food to the nest. The parents of some of these twins were caught; they showed no loss of weight and their feathers were in good condition. No adult was known not to have survived to breed again, so presumably this additional burden did not affect their survival. Unfortunately several aspects of these experiments cannot be resolved. It is conceivable that the female cannot obtain sufficient food to produce more than a single egg at one time, which might explain the low incidence of replacement layings and the long intervals between the loss of an egg and the replacement. However as many adults are feeding young when others are forming eggs, and the female receives much food from the male during courtship (for discussion see Royama, 1966), it is unlikely

that food shortage prevents the laying of a second egg; I have no information on the requirements of other materials, but it would seem an unlikely explanation. The survival of these young after fledging is not known, and could conceivably be lower than that of single chicks if (again I think it unlikely) adults feed the young for long after they leave the colonies.

Similar experiments with larger than normal broods have been carried out on other seabirds. The Glaucous-winged Herring Gull (*L. a. glaucescens*) and *L. fuscus* have both been shown to be able to raise up to 5 or 6 young (Vermeer, 1963; Harris and Plumb, 1965), *R. tridactyla* 4 young instead of the normal 2 or 3 (Coulson *in* Lack, 1967), and the Gannet (*Sula bassana*) 2 instead of the normal 1 (Nelson, 1964). All these experiments were undertaken only for a single season in species that are all increasing in numbers, suggesting a superabundance of food. Stonehouse (1962) noted a single pair of *Phaethon aethereus* successfully raising 2 young instead of the normal 1.

Within the Procellariiformes twinning experiments have been carried out on the Laysan Albatross (*Diomedea immutabilis*) (Rice and Kenyon, 1962), Leach's Petrel (*Oceanodroma leurrhoa*) (Huntington *in* Lack, 1966), the Madeiran Storm-petrel (*O. castro*) (Harris, 1969), and the Manx Shearwater (*Puffinus puffinus*) (Harris, 1966). In all but the last species the production of young was much lower than normal and in another species, *P. lherminieri*, the adults had difficulty in feeding even the single young (Harris, 1969). The evidence for *P. puffinus* is confusing. In one season the production of young from pairs with two young was much lower than the normal controls, but in the next season, and a much larger sample, the fledging success of individual young from broods of one or broods of two was almost identical. In this species it has been possible to follow the postfledging success as shown by the numbers of young later returning to the colonies. In both years it appears that postfledging survival was similar in both normal and experimental birds. Therefore it seems that this species can, at least in one year, successfully raise more than the normal one young.

The evidence available on the significance of clutch-size in these long-lived seabirds is inconclusive and points to the need for a long-term experiment including data on postfledging survival.

Adaptations to Cliff Nesting

Most authors (for instance Cullen, 1957) have assumed, probably correctly, that the typical and ancestral gull was ground nesting. The detailed study of Cullen (1957) indicated the many adaptations shown by *R. tridactyla* associated with its nesting on steep cliffs. Hailman (1965) considered that in some aspects of its ecology *Creagrus* was intermediate between *R. tridactyla* and the ground nesting gulls. In many ways this conclusion is justified, especially if one considers the series *R. tridactyla-Creagrus-L. argentatus* (the eastern North American or some European populations) or, better, *L. fuscus*. If gene pools of the species as a whole are considered, then *Creagrus* is intermediate between the ground nesting species and the cliff nesting *R. tridactyla* but little, if any, difference in nesting habitat and nest sites exists between *Creagrus* and the populations of *L. argentatus* I have studied in Wales where the latter interact with the much more typical ground nesting *L. fuscus*. In some aspects of its behavior *Creagrus* shows some "Kittiwake-like" modifications (Snow and Snow, 1968).

Inaccessibility of the nests has virtually eliminated nest predation by mammals in *R. tridactyla*, but some few are still lost to other gulls. In Galápagos the only native ground predators were the rice-rats (*Oryzomys* spp. and *Nesoryzomys* spp.), which appear to be largely vegetarian and also absent from most seabird colonies. The avian predators would certainly not be deterred by the cliff nesting of *Creagrus* whose young would appear to be much safer among the boulders.

The platform of lava stones effectively prevents the egg rolling away, but the reduction of the clutch is hardly likely to have been evolved as an adaptation to cliff nesting.

Among the most striking adaptations shown by *R. tridactyla* is the behavior of the young, which spend most of their time in the nest, crouch when attacked or frightened, show few flight intention movements, usually face away from the cliff edge, are fed from the parent's throat, and have an associated lack of a parental feeding call (see Cullen, 1957). In most aspects of its behavior the *Creagrus* young is like the typical gulls, except that they face away from the cliff edge most of the time, possibly away from the direct light, as do the adults. Young avoid the deep side in visual cliff experiments, as did young *L. argentatus* and Laughing Gulls *L. atricilla* (Emlen, 1963; Hailman, 1965, 1968), but young *L. ridibundus* placed in nests of *R. tridactyla* wandered off the cliffs (Cullen, 1957). It may well be that chicks of all species are hatched with the ability to perceive and avoid a cliff edge, and only later do those reared on cliffs "learn" to crouch and not run away (Hailman, 1968). Although *Creagrus* young often rushed away from any disturbance, once they reached the edge they always stood their ground and faced the cause of the disturbance. Never once in many hundreds of hours of handling *Creagrus* did I see a chick fall over the cliff as a result of my activities. This is in marked contrast with most cliff nesting *L. argentatus* whose young often rush headlong over cliffs at any disturbance but some, and also the few young

L. fuscus raised in such atypical sites as small ledges, seem to crouch facing away from the edge and to be far less mobile than normal young.

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SUMMARY

The Swallow-tailed Gull (*Creagrus furcatus*) was studied at a colony of about 400 pairs on Santa Cruz, Galápagos from November 1965 to July 1967. The species is an atypical gull in feeding at night, laying only a single egg as a clutch, and breeding at less than annual intervals, 9 months for successful birds and even less for birds losing eggs. Food is entirely fish and squids, some heavier than the birds, with the proportions varying with time and place. The distribution and sizes of the colonies and the few data on times of feeding of the young suggest that the birds feed young from a food source reasonably close to the colonies.

Within any large colony are several subcolonies with birds breeding synchonously, but subcolonies are often out of phase with each other. Similarly there are unreleated peaks of breeding on different islands at different times. External factors could not be shown to be primarily responsible for synchronizing breeding.

Although one egg is the normal clutch, one female probably laid two eggs. Examination of the ovaries of a few birds showed that only a single follicle enlarged greatly before laying. Repeat eggs, which were not common, were not laid until about 3 weeks after the loss of the first egg.

Replacement of the primaries started when birds were feeding young and continued until the start of the next breeding cycle. Apart from the low fledging success of birds hatched on the flat cliff tops, nesting success was not affected by nest site, time of laying within the spread of laying in a subcolony, or colony density. The advantage of synchronous breeding was not clear but might offer protection against frigate birds.

Survival of breeding adults from one season to the next was about 97 per cent and young birds did not normally breed until at least 5 years old. Experiments showed that adults could successfully incubate two eggs and

rear two young with no apparent difficulty. Although *Creagrus* shows some adaptations to cliff nesting, it is more like the ground nesting gulls than the cliff nesting Kittiwakes.

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