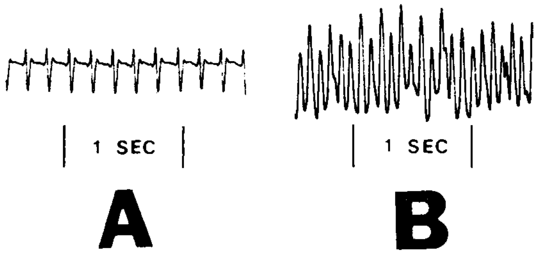

FIGURE 4. Two samples of ECG's from a kestrel, recorded from electrodes placed in its keel. A, ECG of a resting bird; B, ECG of a flying bird.

from the skin and connects to the dorsally mounted transmitter. Second, electrocardiograms recorded from the keel-anchored electrodes during flight have much less EMG interference than those recorded by surface electrodes (fig. 4). The reduced interference may be due to multiple factors. One possible reason may be that the sternum bone shields the keel electrodes from the EMG potentials more effectively than subcutaneous tissue shields surface electrodes. Another is that since the EMG potentials along the keel are determined by the electrical activity in both pectoral muscles, the EMG's from the pectorals may tend to cancel out along the keel which separates these two muscles. Third, the electrodes are anchored into the bird's skeleton, thus rigidly fixing the distance between them even though the bird is in flight. Fourth, the electrodes will remain in the same position for months in a free-living bird.

With this method we have telemetered ECG's from birds in the field for 2–3 week periods. One kestrel was implanted and released into the field in June 1971. Nine months later it was retrapped and the electrodes were still functional.

Two problems were encountered in using this method. One, the bird must be anesthetized to implant the electrodes. A few kestrels died when sodium pentabarbital was used as the anesthetic. Its effect varies among individual birds and with the age of the pentabarbital. We do not recommend its use on birds. Ketamine hydrochloride has been recommended by Kittle (Mod. Vet. Prac. 52:40, 1971) and Mattingly (Raptor Res. 6:51, 1972) as an anesthetic for birds of prey. The second problem, a small percentage (about 10%) of the kestrels and two of three Snowy Owls (*Nyctea scandiaca*) studied at the Naval Arctic Research Laboratory in January 1973 were able to reach the short electrode leads between the skin and transmitter. These birds pulled on the leads with their beaks, causing them to break away from the No Knot Eyelets at the soldered connections. Birds then usually continued to pull at a lead wire until it was pulled free of the body. The Snowy Owls could turn their heads more easily and get at the transmitter leads better than the kestrels.

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THE INCUBATION PATCHES OF CASSIN'S AUKLET

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During the beginning of the breeding season, certain areas of the ventral thoracic and abdominal skin of most birds undergo morphological and physiological changes that result in the formation of bare regions called incubation or brood patches. These changes include defeathering, hypervascularization, edema, and hyperplasia (Bailey 1952). An extensive review of the incubation patches of birds is given by Jones (1971).

This paper discusses the morphology and ecological significance of the brood patches of Cassin's Auklet (*Ptychoramphus aleuticus*). It is based on research conducted during 1969–71 on Southeast Farallon Island, California, 27 miles offshore from San Francisco. Cassin's Auklet is a small alcid that breeds on islands from southern Alaska to south-central Baja California. It is a nekton-feeder and is nocturnal with respect to its activities on the island. The nests are located in burrows or rock crevices, usually in colonies, and the normal clutch is a single egg. Both parents share the activities of incubation and nestling care.

Bailey (1952) separated birds into two major groups based on the distribution of the brood patches. Most birds belong to the group having a single large median patch corresponding roughly to the large median apterium. The other group develops a large patch from two large lateral apteria and a small median apterium. Most of the Charadriiformes follow this pattern but several species, including Cassin's Auklet, Crested Auklet (*Aethia cristatella*), Least Auklet (*A. pusilla*), Parakeet Auklet (*Cychlorrhynchus psittacula*), and the Rhinoceros Auklet (*Cerorhinca monocerata*), have no ventral median apterium but instead have two separate and distinct brood patches, one beneath each wing on the lateral ventral apterium (this study; Sealey 1968). All of these species lay just a single egg and it is placed beneath the wing on one side or the other of the abdomen.

Although Cassin's Auklets have been reported to lack brood patches (Payne 1966), intensive study of the birds through all seasons reveals that auklets incubating clutches early in the nesting season do have patches, but those nesting later often do not. I examined patches of birds that were either incubating or brooding and of those captured by a large net (see Ralph and Sibley 1970) during morning departure flights. I preserved brood-patch tissue samples in 10% formalin and stained sample slices (10) with eosin and hematoxylin for study. I classified brood patches of Cassin's Auklet in the following manner.

MORPHOLOGICAL CHARACTERISTICS

Type 3. Well-developed Brood Patch

The outstanding characteristics include the large amount of epidermal folding and increased vascularization (figs. 1 and 2). No feathers or down are present on the deep-pink surface contact area, but feather papillae can be found in subepidermal tissue. Edema appears to be moderate.

Type 2. Regressing Brood Patch

This is similar to Type 3 but folding is decreased and there is little or no edema. The patch surface

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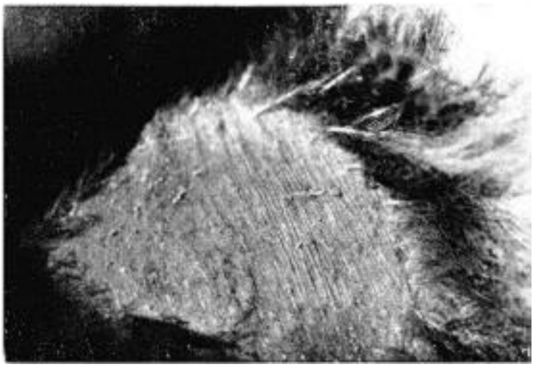

FIGURE 1. Photograph of a fully developed Type 3 incubation patch of Cassin's Auklet showing the bare, slightly wrinkled contact surface.

is partially covered with light-gray down and pin feathers are visible through the skin.

Type 1. Regressed Brood Patch

There is little folding and the surface is undergoing keratinization. The patch surface is completely covered with down and growing feathers.

Defeathering occurs rapidly in most birds, and I could not detect sufficient histological differences in the potential patch area of birds just prior to egg-laying to describe a patch type representing the condition during that stage. Consequently, the preceding brood patch types 1 and 2 refer to patches that are regressing, not to developing ones. In addition, Type 1 patches have lost most of the edema and have a sufficient covering of down and feathers to be considered mostly nonfunctional.

Average brood patches (Type 3) of 17 auklets examined during early incubation measured 43 × 23 mm. This is similar to the measurements for the Crested, Parakeet, and Least Auklets on St. Lawrence Island, Alaska (Sealy 1968) (table 1).

CYCLIC NATURE OF THE BROOD PATCHES

The egg-laying pattern of auklets on Southeast Farallon Island is complex, and in most years there may be three types of clutches laid. A first clutch is the first breeding attempt of the year and is laid at the beginning of the season (March–May). A replacement clutch is laid by auklets that have either lost or deserted their first clutch egg. These eggs may be laid from late March to mid-June. Second clutches (Manuwal 1972) are laid by auklets that have already raised a first brood chick during the same breeding season. This clutch is usually laid in June or early July.

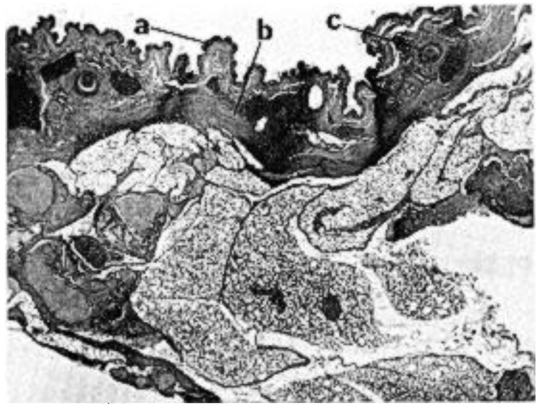

FIGURE 2. Cross section of a Type 3 incubation patch. Note the epidermal folding. 60×. a = stratified squamous epithelium; b = connective tissue of dermis; c = feather follicle

The cyclic nature of the brood patch must be examined with respect to three breeding situations. The first is the patch of a bird that lays a single clutch and successfully raises a nestling. Defeathering of the patch usually occurs 24–48 hr prior to egg-laying, although less than 1% of the birds examined initiated incubation before the patch defeathered. There is a very rapid increase in vascularization and edema (fig. 2) during the first week of incubation, although the edema does not seem to reach the same relative level as in passerine brood patches.

Refeathering begins during mid-incubation and is usually complete by the last few days of the nestling period. This cycle represents what occurs during a normal breeding cycle uninterrupted by the laying of a replacement clutch or extended by a second brood attempt.

A second situation involves a bird that either deserts or loses the first clutch and lays a replacement clutch. In this case, the progression of refeathering of the patch is partially inhibited. This slight departure from the normal regression of the patch from Type 3 to 0 is shown by the dashed line in figure 3. This inhibition is apparently induced by further courtship and other visual and tactile stimuli involved in laying of the replacement clutch. Even so, the patch is refeathered (Type 1 or 0) at hatching time.

A third situation exists with auklets that attempt to raise a second brood. Here, the patch of most auklets continues to refeather despite the second breeding attempt (fig. 3). A few auklets that attempt to double brood were found with remnants of a brood patch (table 2).

The adaptive value of the brood patch of Cassin's

TABLE 1. Measurements of brood patches, eggs, adult weight, and temperatures of Cassin's Auklet and St. Lawrence Island Auklets.

Species	Brood patch (mm)	Egg (mm)	Mean adult weight (g)	Temperature (°C)			Source
				Body	Patch	Body – patch	
Cychlorrhynchus psittacula	44 × 27	53.3 × 37.3	280.6	40.4	36.9	3.5	Sealy 1968
Aethia cristatella	43 × 27	56.8 × 37.2	286.6	40.1	38.1	2.0	Sealy 1968
A. pusilla	25 × 15	39.8 × 28.3	92.0	40.7	38.0	2.7	Sealy 1968
Ptychoramphus aleuticus	43 × 23	46.2 × 33.5	167.0	38.8	37.5	1.3	Manuwal 1972

TABLE 2. Condition of brood patch of auklets incubating first egg clutch, replacement clutch, or second clutch.

	Brood-patch types				
	0	1	2	3	Total
First clutch					
No.	4	0	9	12	25
%	16	0	36	48	
	0	1	2	3	Total
Replacement clutch					
No.	9	2	4	2	17
%	53	11.5	24	11.5	
	0	1	2	3	Total
Second clutch					
No.	27	11	10	8	56
%	48.2	19.5	17.9	14.3	

Auklet may be questioned because of the high percentage of birds found incubating without brood patches. Table 3 shows the distribution of brood-patch types among 228 auklets found either on eggs or brooding chicks. The small fraction of those birds with functional brood patches (Types 2 and 3) that were sitting on eggs and the 94% of birds brooding chicks that did not have a functional brood patch are a result of the rapid refeathering of the patch midway through incubation. The condition of the brood patch can be examined further with respect to birds that are incubating an egg from the first clutch, second clutch, or replacement clutch (table 2).

As previously stated, brood patch Types 0 and 1 cannot be considered functional brood patches. Consequently, of birds incubating their first egg of the season only 84% have functional brood patches (table 2). Sixty-four percent of the birds that lose their first egg and lay a replacement egg do not have functional brood patches. Finally, 69% of birds that attempt double-brooding do not have brood patches. It appears, then, that functional brood patches develop in auklets when the first clutch is laid and regress to a nonfunctional state in most individuals. In some auklets, however, the rate of regression may be slowed or stopped if a replacement or a second brood attempt is made. Less than 15% of these birds retain a fully developed patch.

It would appear that Payne's (1966) discussion of selection against heat loss in Cassin's Auklet may be inappropriate. The Least Auklet of northern Alaska weighs considerably less than Cassin's Auklet, but it does have two well-developed lateral brood patches (table 1). Surely if heat loss through brood patches were important, the Least Auklet which lives in a colder marine environment would show

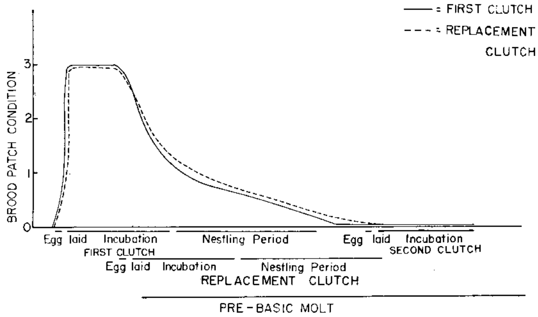

FIGURE 3. The incubation patch cycle of Cassin's Auklet with reference to the first clutch, replacement second clutch, and prebasic molt.

some modification or lack of brood patches. Cassin's Auklets are able to successfully incubate eggs with poorly developed brood patches. Despite the relatively warm temperatures characteristic of sea-bird burrows, this by itself does not explain the brood patch condition in Cassin's Auklet since all other burrowing sea birds have well-developed brood patches. While the brood patch of this species appears to be unusual, the reproductive cycle of auklets composing the Southeast Farallon population is even more unusual (Manuwal 1972).

If one examines the patch development and regression of auklets laying only one clutch per season, there is nothing unusual about the cycle. However, when replacement clutches and second brood clutches are laid, irregularities appear. Sealy (1968) found that replacement clutches were rare in auklets on St. Lawrence Island, Alaska. This seems to be the rule among arctic and subarctic birds. Double-brooding has not been documented previously for seabirds (Manuwal 1972), so this is an unusual occurrence. Until more information is collected on other aspects of the brood patch of auklets occupying Southeast Farallon Island and elsewhere, I can offer only the following explanation.

The nesting environment in the vicinity of the Farallones is obviously very favorable for extended breeding. This is most likely not the case in the colder, far northern, Pacific waters where this species originated (Udvardy 1963). Therefore, the brood-patch cycle of Farallon auklets remains approximately the same as that for auklets laying only one clutch per year. However, in this population, environmental conditions allow frequent laying of replacement clutches and double-brood attempts, but instead of the patch remaining in an advanced stage, it regresses without apparent hormonal influence. The small percentage (11.5–14.3%, table 2) of auklets that have fully developed patches after they lay additional clutches may represent a genotype that has evolved in response to the unique Farallon Island environment. It might also indicate those individuals in the population that are more stimulated than others.

TABLE 3. Distribution of types of brood patch among 228 auklets found either on eggs or brooding chicks.

	With eggs Brood-patch condition					With chicks Brood-patch condition				
	0	1	2	3	Total	0	1	2	3	Total
No.	54	39	40	78	211	9	7	1	0	17
%	25.6	18.5	19.0	36.9		53	41	6		

Whatever the reason may be, the brood patches of Farallon Cassin's Auklets are peculiar in their development because they regress early in the nesting cycle and do not persist when birds make additional nesting attempts. The functional importance of these patches in the successful incubation of the single egg is questionable under the nesting conditions present on the Farallon Islands.

This paper represents partial results of a study on the population ecology of Cassin's Auklet on Southeast Farallon Island. Financial support was received from a National Science Foundation departmental grant to the Department of Zoology, UCLA, and generous grants in 1970 and 1971 from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, New York. I thank L. Barajas and R. Cloney for advice concerning histological aspects of the study, and Thomas R. Howell and Donald S. Farner for their review and comments on the manuscript. I extend appreciation to personnel at the Point Reyes Bird Observatory for their assistance. This is Contribution No. 50 from the Point Reyes Bird Observatory.

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