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REPRODUCTIVE BEHAVIOR AND VOCALIZATIONS OF THE BONIN PETREL

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The Bonin Petrel (*Pterodroma hypoleuca*) is an abundant, colonially-breeding seabird in the central Pacific Ocean. It breeds in winter and spring, being ashore between August and June. The population of this species in the Northwestern Hawaiian Islands exceeds one million birds; about 10,000 breed at Midway Atoll (Harrison and Hida 1980). Until recent studies of egg development and chick growth (Pettit et al. 1982a, 1982b; Grant et al. 1982) the species had been little studied (mainly because it usually digs breeding burrows in loose sand and because it nests on islands of difficult access), although some details of breeding biology had been reported (Howell and Bartholomew 1961, Woodward 1972, Amerson et al. 1974, Clapp and Wirtz 1975). This paper deals with courtship behavior, vocalizations, pre-laying activities including the pre-laying exodus, egg-laying and hatching, and incubation shifts.

METHODS

Many nest burrows on Sand Island, Midway Atoll (28°13′N, 177°23′W) in the Leeward Hawaiian Islands are excavated under lawns. Burrows may be 3 m long and over 1 m deep. The single white 39-g egg is laid in an enlarged nest chamber which is lined with grasses and needles of the ironwood tree (*Casuarina equisetifolia*). The structural integrity of these sites allowed repeated examination of the same nests throughout the breeding season.

Vertical shafts 15–20 cm in diameter were dug to the nest chambers. The shafts were covered with plywood and the nests inspected during the prelaying, incubation, and nestling periods—almost daily from 30 December 1979–25 March 1980 and from 10 December 1980–23 May 1981. Small sticks were placed across burrow entrances to detect nocturnal visits. If the fences were disturbed the nest contents were checked. "Nest-days" refers to the number of nests examined multiplied by the number of days checked.

Behavioral observations were made at dusk and after dark with the aid of street lights, moonlight, and partly obscured flashlights. We detected no differences in behavior of petrels nesting under dim street lighting and those in unlit areas. Recordings of vocalizations made with a Uher 4000 IC machine using a Nagamichi CM 300 microphone and a tape speed of 19 cm/sec were analyzed with a Kay 6061B Sona-Graph. Most behavioral observations and vocalizations were recorded in December and early January, prior to egg-laying.

Times referred to here are local. The time of sunset was obtained from the U.S. Navy Meteorological Station on Midway Atoll. Color-marked birds were sexed by assuming that a bird on top during copulation was male. Where appropriate, means are given ± one standard error.

STUDY AREA

Much of Sand Island is covered with buildings, runways, and roads. The major petrel nesting colonies and the relative burrow densities are indicated in Fig. 1. Very few Bonin

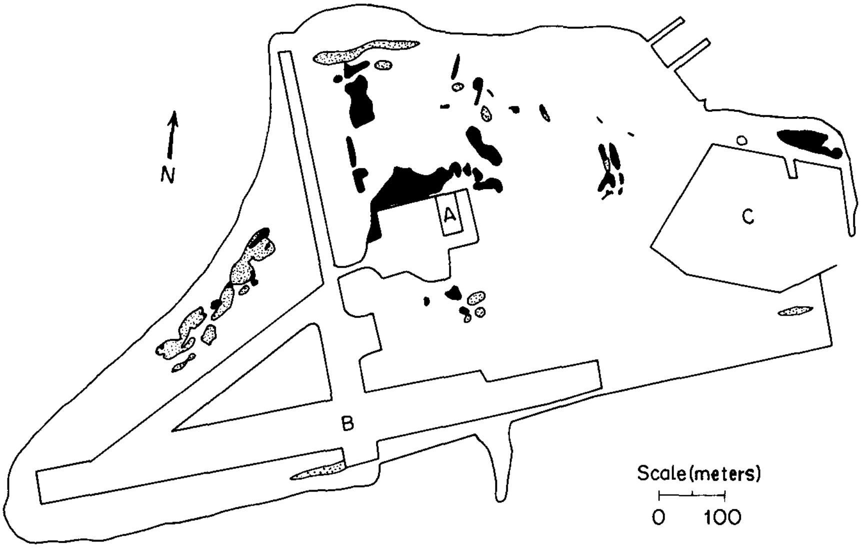

FIG. 1. Sand Island, Midway Atoll, showing locations of Bonin Petrel colonies. Filled square = Burrow density > 1 nest/10 m^2; dot filled square = Burrow density < 1 nest/10 m^2; A = airport hangar; B = runways; C = harbor.

Petrels breed on Eastern Island, Midway Atoll, due to the very dense rat populations (Grant et al. 1981). The largest petrel colonies on Sand Island are on the man-made hills near the harbor, under the *Casuarina* trees and on the fringes of the golf course, near the chapel and school, the area stretching northwest from the hangar to the dunes, and in Area 7 (a restricted zone). The Area 7 and golf course colonies support substantial Wedge-tailed Shearwater (*Puffinus pacificus*) nesting populations during the summer. The larger shearwater often evicts and may kill Bonin Petrel chicks when it takes over and enlarges the petrel burrow for its own use. Laysan Albatrosses (*Diomedea immutabilis*) nest on the surface of the ground above the petrel burrows in most areas but we saw little interaction between the albatrosses and petrels. The only impact of this association occurs when young albatross chicks occasionally become stuck in petrel burrow entrances. Typically the chick, if tightly wedged in the entrance, dies and blocks the passage of the petrels. We saw this happen only about 10 times during the course of our study.

NIGHTLY ARRIVAL

Bonin Petrels are strictly nocturnal in their activities over land. During 36 nights between 8 December 1980 and 28 January 1981, the first birds appeared overhead 13.2 ± 1.3 min after sunset, range 11 min before sunset–26 min after sunset. Only three birds, however, appeared before sunset, all under dark, rainy skies with 100% cloud cover. In general, the lighter the sky and the less the cloud cover, the later the time of arrival.

The first birds overhead at dusk flew quite high. As the light faded their numbers increased, and aerial pursuits with their associated chattering cries were heard. Soon many were circling just above the tops of the *Casuarina* trees and before long some were skimming the ground, particularly in open places near the burrowed areas; 15–25 min after the first high-flying birds had appeared, some had alighted, the earliest before the last daylight had gone.

On the Snares Islands, New Zealand, Mottled Petrels (*Pterodroma inexpectata*) (Warham et al. 1977) tended to arrive later with respect to sunset than did Bonin Petrels on Midway; but skuas (*Catharacta skua*) kill petrels at the Snares Islands whereas there is no natural predator on Midway Atoll.

BURROW EXCAVATION

Burrows in hard substrate were used year after year while those dug in loose coral sand frequently collapsed between breeding seasons. Bonin Petrels returned to Midway and nearby islands in August and September (Woodward 1972, Amerson et al. 1974, Clapp and Wirtz 1975) and began excavating new burrows or cleaning out old ones. When we arrived in early November digging had begun; some burrows were nearly completed but digging continued well into the laying period. Late season digging may have been done by prospecting pre-breeders or failed breeders. Both members of a pair dug. They picked with their bills to loosen the soil and then kicked it backwards with their webbed feet. The wrists and the unused foot supported the bird while the other foot kicked back the sand. Up to 3.3 kicks/sec were given and the ejected sand thrown 0.3–1.0 m beyond the burrow entrance. The bird typically kicked a few times with one leg, then a few times with the other, and so on.

In three instances, burrows were lengthened apparently because of our daily checks of burrow occupancy. The earlier lining was buried in these nests and the burrows were extended up to 0.4 m. The nest-chambers were relined 4–11 days later. Lengthening of the burrow in response to human disturbance has also been reported in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) (Gross 1935) and in Wedge-tailed Shearwaters (Shallenberger 1973).

Burrow entrances were often packed with vegetation both before and during incubation. The bird at the burrow entrance tugged and tore at grass stems and tossed them over its shoulder or packed them around the opening. The result was an eliptical hole about 10 × 7 cm through which the petrel had to squeeze to enter and leave. Nest blocking has been reported in several other petrels (e.g., Warham 1958, 1960, 1967; Warham et al. 1977; Bartle 1968). Bartle (1968) suggested that nest blocking disguised the burrow from predators and Warham (1960) thought it might be related to a preference for darkness while on land. *Pterodroma hypoleuca* may block the larger shearwater burrows so that they match their own smaller profiles.

OLFACTION

We were struck by the frequency of the "beak to the ground" posture when Bonin Petrels were near their burrows. Sand removed from burrows was "investigated" by the petrels who adopted this posture. Crude experiments indicated that olfaction may play a role here. On 14 December 1981 Warham placed both fists on the ground about 0.6 m apart, upwind of a pair of excavating birds. Both petrels ceased activities at their nest entrance and walked 1 m from the petrel burrow entrance, nibbled his fingers and investigated his notebook with the "beak to the ground" posture. He had handled another petrel extensively an hour earlier. The next night Grant repeated this experiment by handling a petrel (over 30 m from the experimental site) with his left hand only. He knelt down 2 m upwind from a burrow entrance where the male was digging and the female was below. The male immediately stopped and walked toward his right hand but then turned toward his left hand which the male nibbled (ignoring his right one). From this crude experiment, we suggest that olfaction is useful near the burrow entrance but not inside as the birds accepted domestic chicken (*Gallus gallus*) and other petrel eggs placed in the nest. This experiment extends the use of chemical communication by procellariiform birds (Wenzel 1980).

LOCOMOTION NEAR THE NESTING AREAS

Some petrels landed in open spaces and then walked to their nests where these were under trees, but the canopy was open enough to allow many to land through the trees at their burrows. Birds usually landed 3–7 m from burrows. They walked easily with a rather rolling gait, holding their bodies low and horizontal, head and neck outstretched and wings folded to the body. They pushed their way through patches of low grass but then often paused to lift their heads and view their surroundings. Some clambered onto low sloping fallen limbs and perched there. Occasionally a bird was seen climbing the vertical trunk of a *Casuarina* even though it could fly from unobstructed ground with ease, even in calms, in contrast with other *Pterodroma*, particularly larger members of the genus, and some shearwaters, which appear to need a sharp descent in which to gain air speed.

TERRITORIAL ACTIVITY

Much of the behavior of grounded birds apparently concerned the defense of a territory around a burrow entrance. Some birds patrolled an area within 2–3 m of their burrow entrances. Intruders were repelled by sudden dashes with outstretched wings. Most intruders shifted quickly, sometimes flicking up, part flying, part jumping, to alight a few meters away. Many repulsions occurred without vocalizations, but often loud *kik-ooo-er* calls caused some nearby petrels to scatter without any direct attack. Such calls tended to be contagious; presumably other territory-holders were responding. Some fights occurred; the birds spread their wings and pecked hard at each other's napes and heads. No injuries were known to have resulted. One bird entered a burrow *churring* loudly, continued this while briefly underground and then emerged, still calling, to chase away a nearby petrel which fled after responding with harsh cries.

SEXUAL ACTIVITY

Particularly in the pre-laying period of December and early January pairs were often seen with one bird walking close on the tail of another and reaching toward it. Such pairs tended to wander within a restricted area (in one instance within no more than a square meter) and their peregrinations were interspersed with quiet periods during which the pursuer preened the head and neck of the other. Some preening was so vigorous that the recipient drew back as if to disengage, but without actually doing so. Mutual allopreening also occurred, sometimes with the presumed female turning her beak to preen her partner's throat. These activities preceded copulation. In two instances, the leading birds gave a harsh *kuk-ku-er* at intervals and the followers gave a low rather continuous purring and churring sound (see below) during which the caller's throat pulsated. These same birds also used a higher pitched version of the other's call: *kik-ooo-er,* as described below. In both of these episodes the pursuer was on top of the pursued during mounting so it seems that the harsh *kuk-ku-er* was given by the female, the *churr* and the higher pitched call by the male. While it was usually the follower that *churred,* sometimes the leading bird did so when a silent pursuer trailed. As individual birds were not studied in earlier breeding seasons, it was not possible to determine if the petrels observed had been paired with each other the previous season or were prospecting for mates.

Nine pairs of Bonin Petrels were seen copulating on the ground between 10 and 21 December 1980. On 10 December a marked pair copulated at 20:28 and again at 20:45; the male attempted unsuccessfully to mount at 20:38. Copulation by this same pair was also seen at 19:19 on 11 December. With two marked pairs, copulation took place on the ground within 2 m of the mouths of their burrows.

During copulation the female swayed her head from side-to-side while the male nibbled with his bill at her crown and cheeks, shifting his attentions from one side of her face to the other. The birds were silent during copulation. The wings of the male were fluttered once to maintain balance during mounting and the female partly opened her wings to rest the wrists on the ground and moved her feet to keep her position. After cloacal contact was attained and the male had stopped thrusting, the female turned and gently nibbled his breast feathers. The male then dismounted. Copulation episodes lasted from 20 sec to 4–5 min.

In one instance post-copulatory behavior consisted of mutual preening of bills and faces. In another, the female walked to the burrow and began digging within a minute of the male's dismounting, leaving the male to preen himself.

AERIAL ACTIVITY

Bonin Petrels have a low wing loading ($33N/m^2$) (Warham 1977) and are very maneuverable birds. Their maneuverability was well shown by the frequent aerial chases 2–3 m above ground around small salients <8 m across at the edges of the belts of trees. The birds touched down gently and took off with equal facility without a headwind.

Before the pre-laying exodus, aerial activity involving the repeated circling of petrels above the colonies formed a major feature of their behavior. Immediately after dark, the noise of their callings was considerable, but tended to fade as the night advanced and more birds were on the ground. In the air the most discernible interactions were the high-speed pursuits of one bird by another. Typically, with many birds in the air, two would suddenly converge and for a few seconds one would chase hard on the tail of the other, both calling briefly. Longer chases also developed. Although no bird was individually recognizable, some of the aerial activity could be followed in the illumination provided by street lights. For example, single birds on the ground flew up and circled repeatedly a restricted area before alighting near their take-off point or close to another bird with whom they might display. We gained no evidence that birds calling in the air evoked vocal response from those on the ground or vice versa. Much of the behavior described may have been performed by pre- and failed breeders.

Petrels in flight may become disoriented by mercury and sodium vapor street lights or other sources of artificial lighting. Such disorientations may result in collisions with trees, buildings, or other objects; injuries sustained in this manner are not uncommon. The effect of artificial lighting upon fledging petrels is not known but high density of lights is the worst hazard to fledglings of Newell's Shearwater (*Puffinus puffinus newelli*) on the island of Kauai (Telfer 1979). Individual shearwaters and petrels may be brought down to the ground by following a bird in flight with a high-intensity light beam. Warham (pers. obs.) used similar techniques successfully in obtaining petrels in flight in the Southern Hemisphere.

VOCALIZATIONS

Most of the calls were of short duration; prolonged duetting as occurs with shearwaters (pers. obs.) was not noted. All appeared to be given on expiration of breath unlike those of some other petrel groups, e.g., *Diomedea* and *Puffinus*, whose vocalizations are given both on inspiration and expiration.

Calls of grounded birds.—There was much variation in the tempo, structure, and pitch among the calls given by different birds (Fig. 2 [1–9]), and some of this variation was so extreme that certain calls could not be categorized. Many were also incomplete; only one or two syllables of a trisyllable call were used—a *kuk* or a *ti-ti*—but we have concentrated here on fully developed vocalizations used by actively courting or threatening petrels. Many called in response to play-back of their calls but these responses were only brief. Most recordings were made with the microphone less than 2 m from birds that were often literally at our feet. The most recognizable calls were as follows:

(1.) A harsh, raucous cry, phonetically *kuk-u-er,* and often rising abruptly in pitch at the end. This call usually lasted 0.5–0.9 sec, occasionally as long as 1.1 sec, and was often preceded by a short burst of *kuks,* and such calls or *kuk-ers* were often interspersed among the more extended trisyllabic utterances. Most of these harsh cries consisted of almost unstructured noise with the main frequency between 1 and 4 kHz. Call (B) of the spectrograms of Fig. 2(1, 2) show typical examples.

Such calls were usually repeated only two or three times during one song burst, but occasionally were repeated seven or eight times. During repetition the structure of each phrase might change. Fig. 2(8A, 8B) shows two harsh *kuk-u-er* given by the same bird during a single burst of song. The longer call was the last of a short series and shows how the mainly unstructured and "noisy" vocalization can be modified into a more harmonic one. Despite the harmonics, the second call still sounded raucous and unmusical, the harmonics were only 300–350 Hz apart and were typical of the harmonic pattern of this type of call.

(2.) A high-pitched call made up of a series of 3–8 staccato syllables uttered in rapid succession (Fig. 2[4]). This loud chattering sound was roughly transcribed as *ti-ti-ti* . . . or *kik-kik-kik* . . . . There are four clearly defined harmonics reaching to 6 or 7 kHz, hence the high pitch and more piping character than the generally rasping and lower pitched *kuk-u-er.* Each *ti* is a simple noise-free cry (Davis 1964). As with the *kuk-u-er*

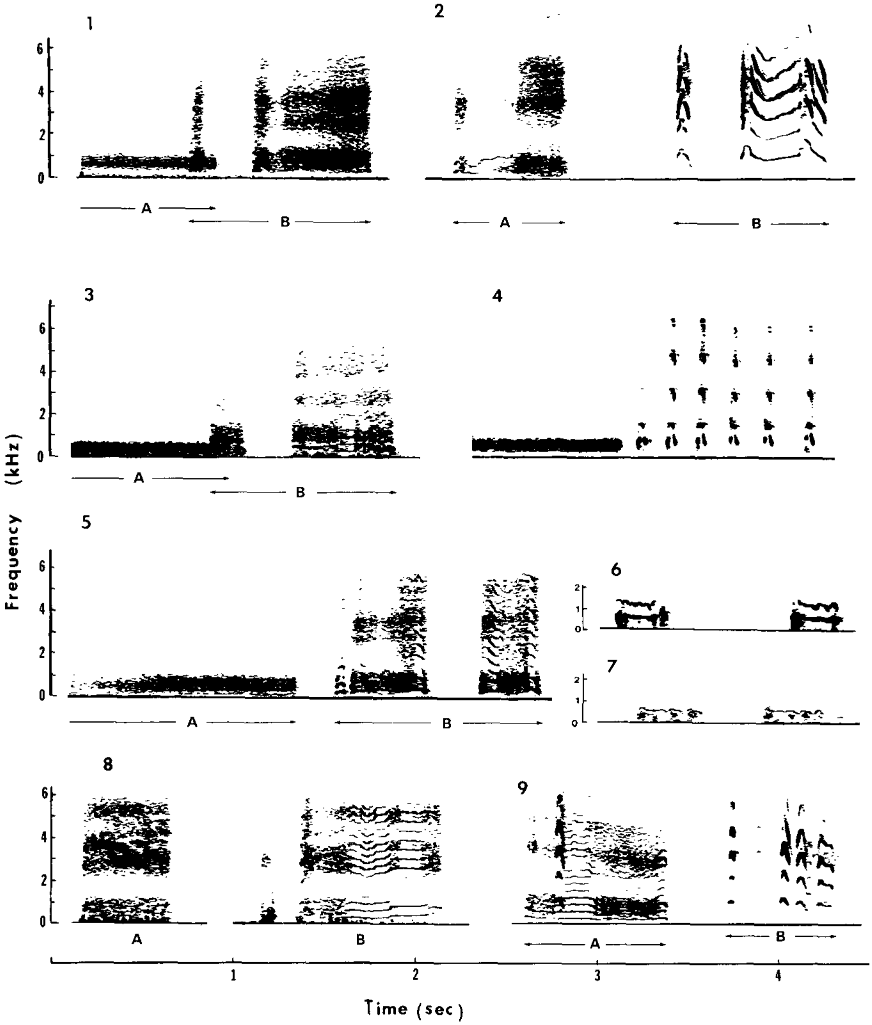

FIG. 2. Calls of grounded Bonin Petrels. (1) Part of duet: the *churr* of (A) stopped when its partner gave the hoarse *kuk-u-er* cry (B). (2) Two courting birds: (A) giving a harsh *kuk-u-er* with little pattern to the sound, and (B) a clearer, high-pitched *kik-ooo-er* with strong harmonics about 1 kHz apart. (3) Duetting: a *churring* bird call (A) overlaps with its partner's low pitched *kuk-u-er* call which was similar in form but of lower pitch than that of the bird in (1) above. (4) A *churr* and staccato *ti-ti-ti* . . . given by a lone bird. (5) A duet between a *churring* bird (A) and one (B) using the harsh *kuk-u-er*. (6) Part of a series of very low-pitched cooing cries from a bird underground. (7) Part of a series of gasping whimpers from a bird in a burrow, pitched at less than 1 kHz. (8) Development of the *kuk-u-er* call: phrase (B) followed (A). Note that the harmonics in (B) are only about 350 Hz apart. (9) Duetting: one bird (A) gives a harsh *kuk-u-er* and the other (B) gives a single and then a series of *ti* calls.

these notes could develop into longer more complex calls like those of the second series in Fig. 2(9B). Such calls sounded like clearer and higher-pitched versions of the *kuk-u-er* cry and were written down as *kik-ooo-er.* A more extreme example is shown in the analysis of Fig. 2(2B) where a simple abrupt *ti* or *kik* is expanded into a raucous high-pitched cackle.

The main frequency in this class of calls was between 4 and 7 kHz, with the harmonics well separated by 1.0–1.5 kHz, quite different from harmonics, if any, of the *kuk-u-ers.*

(3). The *churr* (Fig. 2[1A, 3A, 4, 5A]) is a quiet, very low-pitched call made up of a broad band of sound between 0.5 and 1.0 kHz. It was sometimes sustained at constant volume for 4–6 sec, but punctuated by silences of 0.3–0.5 sec long. Although the *churr* often sounded like a low, continuous growl, not all birds called alike; some had a more crackling quality. The sonograms mostly showed a broad, unstructured band of noise, e.g., in Fig. 2(5A), but sometimes a pulsed pattern was clearly audible (Fig. 3[1]). Indeed the field description of this call as a *churr* or *purr* implies a pulsed structure and other calls of this nature that appeared to be only noise proved to be a series of regular pulses. An example is given in Fig. 3(2)—note the rapid changes of amplitude with time. Fig. 3(3) provides a different example of a *churr,* one seemingly composed of a series of very close, slightly modulated harmonics. Wide band and amplitude analyses showed that this too had a structure of short and regular pulses of sound. The pulse rates in the examples analyzed varied from 78–190 pulses/sec and the *churrs* with the lower rates of pulse were those whose rhythmic character was clear to the unaided ear.

(4.) Miscellaneous calls. Birds in burrows and on the ground also used a variety of quiet chitterings, whistles and whimpers. These were imperceptible except at very close range, but were easily recorded, particularly when the birds were underground. Fig. 2(6) shows two calls from a series of very low pitched cooing cries and Fig. 2(7), part of a long series of even lower pitched calls, was described as "gasping whimpers." These calls were apparently only given when two birds were together.

(5.) Duets. By watching and recording duettists it was found that one used the harsh *kuk-u-er* and the other used the higher pitched chattering cry or its extended equivalent Fig. 2(2, 9). Two duettists never used the same type of song. Duets also occurred with one bird *churring* and the other giving the low *kuk-u-er* (Fig. 2[1, 5]). In the first the *churring* bird did not fall silent until after its partner responded—a sequence noted repeatedly; the *churring* bird abruptly stopped when its partner began.

Birds that *churred* could also switch to the *ti-ti-ti* call like the solo birds of Figs. 2(4) and 3(3). *Churring* birds did not use the hoarse *kuk-u-er.* These observations support the hypothesis confirmed by watching vocal-

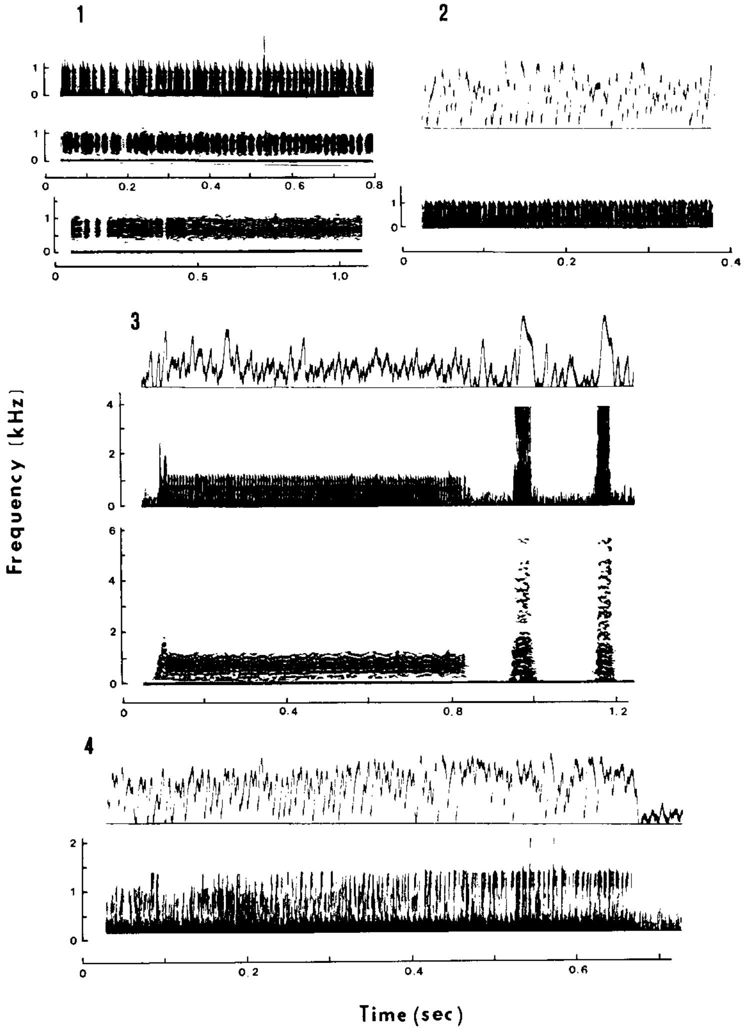

FIG. 3. Analyses of Bonin Petrel calls using an extended time scale. (1) Top: a *churr* analysed at half speed and (bottom) tape played at normal speed. Middle spectrograph used a narrow band filter, upper one a wide band filter; both show that call was composed of a series of rather regular pulses. (2) Part of an analysis of the *churr* of Fig. 2(4) slowed down four times. The amplitude trace (top) and the wide band analysis (bottom) emphasize the pulsed character of this call. (3) Bottom: a slowed down *churr* followed by two *ti-ti* calls from the same bird. The *churr* seems to be based on a series of very close harmonics (narrow band analysis) but the broad band and amplitude traces above show that the call is made from very fine pulses. (4) The low aerial moan of Fig. 4(3) is also composed of a rapid succession of pulsed sounds.

izing birds that eventually copulated, that the birds using the *churr* and the *ti-ti-ti* sequence are males, the others female.

Calls from flying birds.—It was difficult to get clear records of aerial song (Fig. 4[1–8]), but by placing the microphone about 2 m high and pointing vertically, lone and dual-flying petrels were recorded as they passed within 5 m. During aerial chases, both chased and chaser called but we could not see which bird gave which call. Most close flying lasted only 1–4 sec and the duets were likewise brief. Essentially, the calls given in flight were the same as those used on the ground, but were Doppler shifted when recorded, e.g., Fig. 4(2).

The harsh *kuk-u-er* calls (e.g., Fig. 4[1, 7]) have sonagrams similar to those of such calls from grounded birds (c.f. Fig. 4[1, 4, 7] with Fig. 2[1, 2, 9]). Both are made from broad bands of noise with underlying bands of close harmonics in some individuals (Fig. 4[4]). Some such calls were preceded by short pulses or *kuks* as shown in that figure.

The *ti-ti-ti* call as delivered in flight had clear, well-separated harmonics and a high pitch (Fig. 4[2]). These calls were far-carrying and were largely responsible for the overall chattering character of the aerial chorus. The development of the *ti-ti-ti* sequence appeared to be related to the intensity of the pursuit and some quite complex vocalizations resulted, e.g., Fig. 4(5, 8).

The third common call was a low, coarse, slurred moan lasting 2–3 sec, ending quite abruptly; most of the sound lay just below 1 kHz (Fig. 4[3]). The call has obvious similarities with the *churr* (Fig. 2[4]), but to our ears this aerial call did not have the pulsed structure revealed with finer analysis. This is shown by the sonagram and amplitude trace of the slurred aerial call of Fig. 4(3), re-analyzed in Fig. 3(4). Presumably the slurred effect is a consequence of the rapid movement of the calling bird and the inability of our ears to detect the underlying pulsations.

The details of the aerial duets showed their affinity with duets of grounded birds. Typically one of the pair used the moan and the high-pitched *ti-ti-ti* or its variants, the other the hoarse *kuk-u-ers* (Fig. 4[6]). In Fig. 4(7), about 100 msec after the moaning bird stopped, the other responded with a loud *kuk-u-er.* The high pitched chatter of the *ti-ti-ti* aerial cry was often described as *wik-wik-wik* . . . in field notes, and toward the end it was often drawn out into a loud crowing squeal, much as in the ground call analyzed in Fig. 2(2).

Most aerial chases involved birds that used the moan and the *ti-ti-ti* . . . call and its many variations; they were the chasers and the others with their deeper voices, the chased. We concluded, based on call groups, that the males were the chasers and the females, the chased.

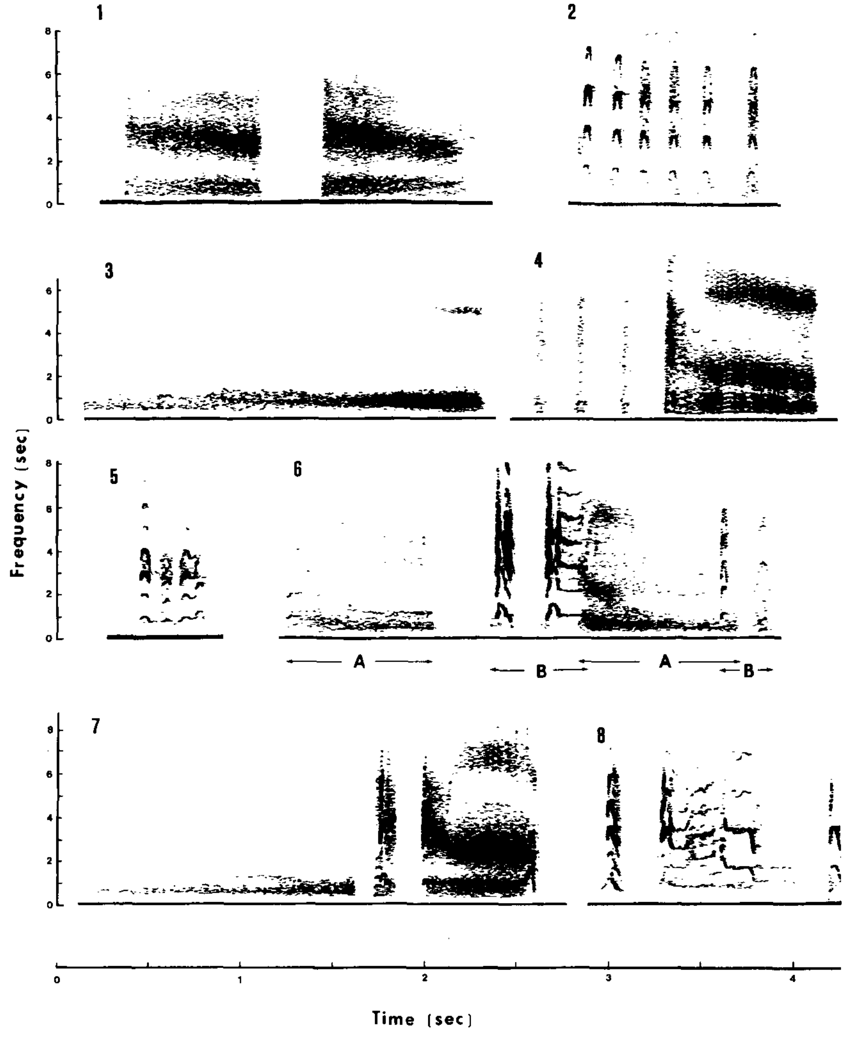

FIG. 4. Calls of Bonin Petrels in flight. (1) Two successive, deep harsh *kurr* calls from the same bird, variants of the trisyllabic *kuk-u-er* cry. (2) A succession of chattering *ti-ti-ti* calls from a bird flying past the microphone: the main energy was at about 5 kHz. (3) The low, coarse, slurred moan; note trace of a harmonic at about 5 kHz. For magnified analysis of this call see Fig. 3(4). (4) A harsh *kuk-u-er* preceded by three staccato *kuks*. (5) An elaboration of the chattering *ti-ti* call. (6) Duet with one bird using a harsh low-pitched call (A), the other an elaboration of the *ti-ti* sequence (B). (7) Duettists: the bird using the low moan fell silent and its partner gave a loud *kuk-u-er* about 100 ms later. (8) An elaboration of the chattering *ti-ti* call.

We noted a great deal of intraspecific variation in calls. This presumably helps in individual recognition in nocturnal species such as the Bonin Petrel where visual cues are limited or non-existent.

BREEDING

Pre-laying period.—Bonin Petrels lined their nests with bits of grass and *Casuarina* needles 36.0 ± 2.7 days (N = 6) before the egg was laid. One nest (not included in the above) was found already lined 48 days before the egg appeared. The lining was generally added in one night (N = 5), but in one case the lining was begun on one night and completed on the following one.

Twenty-three nests were checked daily for a total of 930 "nest-days" before laying, to establish occupancy by day. The burrows were empty on 847 nest-days (91%) and occupied by at least one petrel on 83 (9%) nest-days—the earliest time of daytime occupancy prior to laying was 48 days. Both members of a pair were present on only 19 of the 83 occupied nest-days, i.e., only 2% of the total nest-days. Four burrows (17%) held no petrel by day before egg-laying, the mean number of consecutive days on which no petrels were present being 39.0 days, range 29–48. Fourteen burrows (61%) never had two petrels present during the daytime, while in one burrow both members of pair were present on 7 days (during one consecutive 4-day and another consecutive 3-day period). Before egg-laying, daytime occupancy by other *Pterodroma* was infrequent (Warham 1967, Harris 1970, Warham et al. 1977).

Thirty petrel nests were checked in the morning, by fencing over the burrow openings to determine the frequency of nocturnal visits before laying. Nightly visits declined from ca. 80%–ca. 10% (Fig. 5) during the pre-laying exodus. The maximum pre-laying exodus interval recorded was 24 days (nest #70 of Fig. 6). Intact fences showed that nothing had entered the burrow during the night. Displaced sticks provided less certain information because sticks were shifted by rats, by Laysan Albatrosses stumbling into them, and by other petrels. One Bonin Petrel briefly entered four different burrows within 10 min during the pre-laying period. Many of the visits shown in Fig. 6, immediately before egg-laying, were probably made by rats or by birds other than the owners. However, in four instances marked birds were present in the burrows 2–3 days (N = 2), 1 day (N = 1), and on the eighth day (N = 1) before the egg was laid. In six nests (Fig. 6) lack of disturbance the day before egg-laying indicates that both sexes had left (nest chambers were inspected and found to be empty).

Thus, some Bonin Petrels exhibited a marked pre-laying exodus of up to 24 days while others occasionally returned to the nest in the 2 weeks before laying. Copulation was seen on the ground near burrows on the

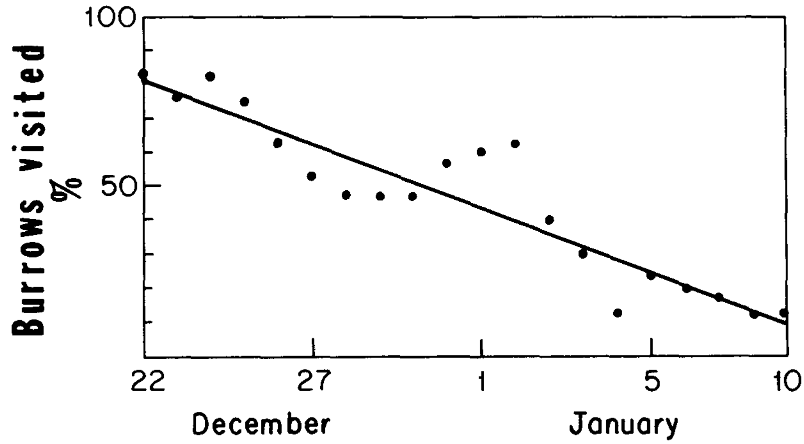

FIG. 5. Visitation rates of Bonin Petrels to 30 burrows before egg-laying. Regression line is fitted by least squares ($r = 0.888$, N = 20 days).

nights of 10–21 December, 21 or more days before the first egg was laid. We were unable to follow successfully a marked pair of petrels from copulation to egg-laying. Warham et al. (1977) found that the pre-laying exodus in *Pt. inexpectata* lasted from 9 to at least 16 days while Imber (1976) suggested the pre-laying absence by females may average 60 days in *Pt. macroptera gouldi.*

Egg-laying.—In 1980 the mean egg-laying was 27.2 January ± 0.5 days (range 13 January–7 February); 92% of the eggs were laid in a 13-day period (Fig. 7A). In 1981 the mean egg-laying date was 27.1 January ± 0.8 days (range 11 January–11 February), but only 81% of the eggs were laid in a 13-day period.

No evidence of relaying was found. Some eggs were collected on the day of laying for physiological measurements and many were lost to rats during incubation. Twenty-nine burrows where eggs were lost between 16 January and 15 March were checked on several occasions in February, March, April, and May for the presence of a new egg. In only one instance was a second egg found, and this was laid 2 days after the first was collected. Because yolk formation requires 15 or more days in the Bonin Petrel (Grau et al., unpubl.) this egg was laid by another female. In three nests a second egg appeared during incubation alongside the first but one of them was invariably buried in the burrow within a few days. Egg neglect occurred, though rarely (Grant et al. 1981), and thus the second egg was probably laid by another female during a temporary absence by the "owners." Bonin Petrels that had lost an egg visited their burrows up to 40–50

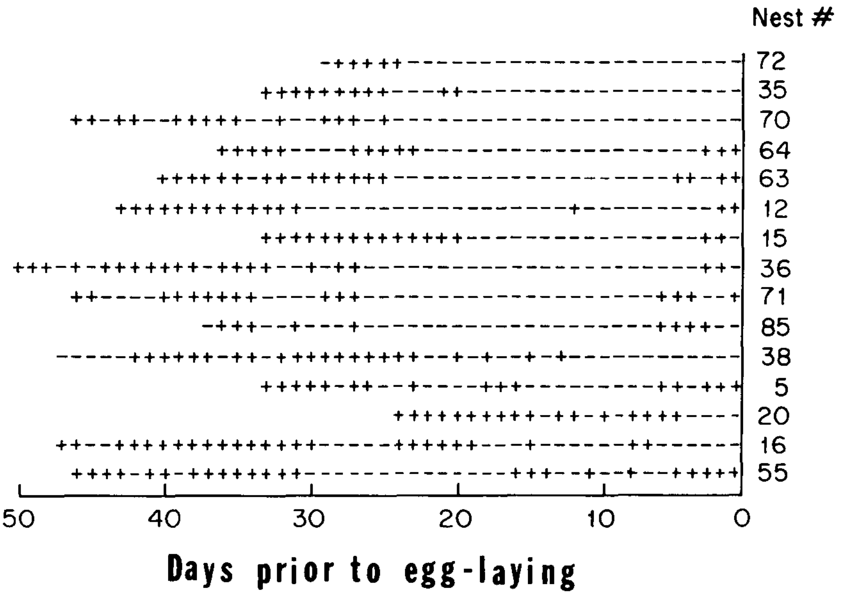

FIG. 6. Visits to individual Bonin Petrel nests before egg-laying: plus = visited, minus = not visited.

days after their loss. If an egg was then laid by another female during an absence of the original owners, we hypothesize the returning original pair might evict the newcomers and incubate the egg, thus appearing to have renested.

Incubation.—The incubation period averaged 48.7 days (Grant et al. 1982) and consisted of several alternating spans or bouts of incubation by both members of the pair. Incubation spans were short during egg-laying (1–3 days, $\bar{x} = 2.0 \pm 0.3$ days, N = 9) and later they were longer (2–15 days, $\bar{x} = 8.8 \pm 0.7$ days, N = 22). The average of 31 spans was 6.8 ± 0.8 days. Incubation duties were shared almost equally by both sexes, assuming that the first short bout associated with egg-laying was by the female. Data from the subsequent two spans at six nests were used to calculate the roles of the sexes in incubation. Long bouts averaged 8.3 ± 1.3 days for males and 7.0 ± 1.0 for females. On only 1 of 245 nest-days during the incubation period were both members of the pair in the burrow during the day.

Hatching.—The mean hatching date was 11.6 March ± 1.0 days in 1980 and 17.9 March ± 1.7 days in 1981 (Fig. 7B). The difference between the mean laying and mean hatching period gives an incubation period of 44.4

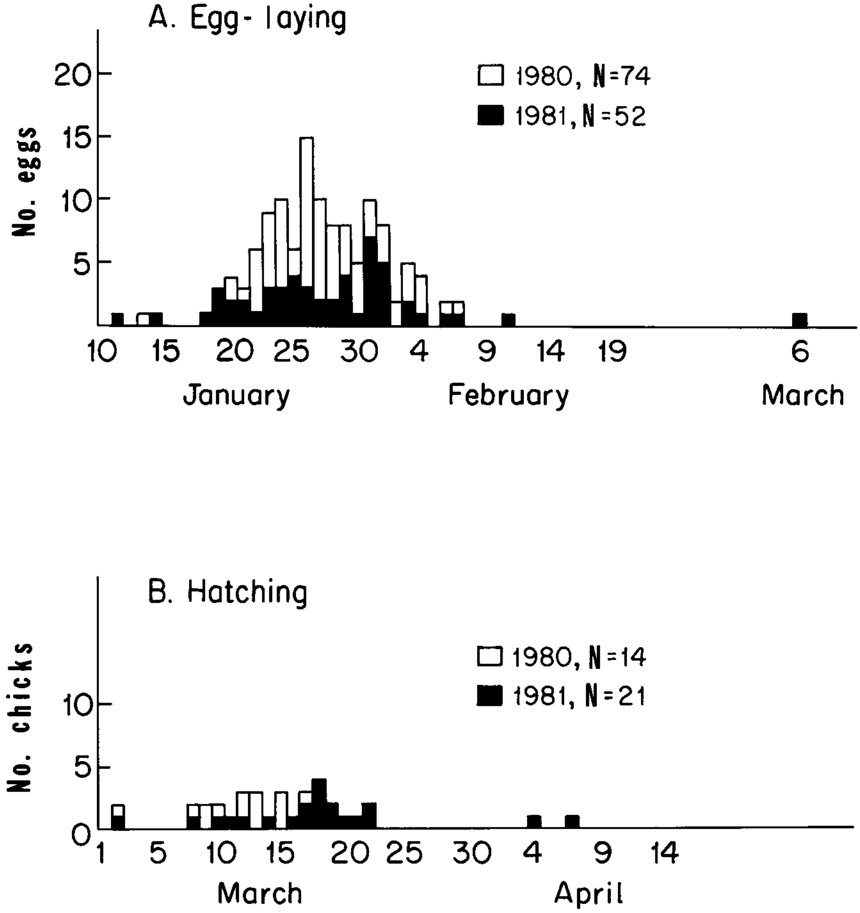

FIG. 7. Chronology among Bonin Petrels of (A) egg-laying and (B) hatching, in 1980 and 1981.

days in 1980 and 49.8 days in 1981, not substantially different from the 48.7 days (Grant et al. 1982) actually measured.

Hatching success was greatly affected by rats (*Rattus* sp.). In 1980 at the chapel colony only 1 of 26 eggs hatched; the remainder were taken by rats. In the nearby school colony, however, 19 of the 21 eggs laid subsequently hatched and the two which did not were broken by petrels (Grant et al. 1981). In 1981 no eggs hatched in the chapel colony and rats took some eggs in the school colony. Of 44 nests monitored, 21 (48%) eggs subsequently hatched. Losses were due to: rat predation—20% (N = 9);

crushing by petrels—7% (N = 3); desertion—5% (N = 2); eggs being addled—5% (N = 2); burial in nest by petrels—2% (N = 1); burrow cave-in caused by people—2% (N = 1); burrow cave-in—2% (N = 1). The cause of 9% (N = 4) of nest-losses was unknown. All 14 chicks examined daily in 1981 during the nestling period survived a minimum of 62 days. At least five of these fledged (R. Shea, pers. comm.).

SUMMARY

Observations on Bonin Petrels (*Pterodroma hypoleuca*) breeding on Sand Island, Midway Atoll, Northwestern Hawaiian Islands were made in 1979–80 and 1980–81. At Midway, many pairs were observed on the ground with the help of street lighting.

The birds' behavior and locomotion, their courtship, copulation, and territorial activity are described. Aerial activity included high-speed dual flights with loud calls. These and the calls of grounded birds are described.

Petrels lined their nest chambers about 36 days before the single egg was laid and there was a pre-laying exodus of up to 24 days. The mean laying date was 27.2 January and the eggs hatched, on average, 48.7 days after incubation began. Both sexes incubated in alternating spans of about 6.8 days. Mean hatching dates were 11.6 March 1980 and 17.9 March 1981. Due to differential rat predation, hatching success varied between colonies and from one year to the next.

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