teractions of the Shiny Cowbird and the Yellowshouldered Blackbird. Condor 79:176-184.

- ROBINSON, S. K. 1986. Benefits, costs, and determinants of dominance in a polygynous oriole. Anim. Behav. 34:241-255.
- ROBERTSON, R. J., AND R. F. NORMAN. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78: 166–173.
- ROTHSTEIN, S. I. 1977. The preening invitation or head-down display of parasitic cowbirds: I. Evidence for intraspecific occurrence. Condor 79:13– 23.
- ROTHSTEIN, S. I. 1980. The preening invitation or head-down display of parasitic cowbirds: II. Experimental analysis and evidence for behavioural mimicry. Behaviour 75:148–184.
- ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1986. Social dominance, mating and spacing sys-

tems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. Curr. Ornithol. 3:127–185.

- Scott, T. W., AND J. M. GRUMSTRUP-Scott. 1983. Why do Brown-headed Cowbirds perform the head-down display? Auk 100:139–148.
- SELANDER, R. K. 1964. Behavior of captive South American cowbirds. Auk 81:394–402.
- SELANDER, R. K., AND C. J. LA RUE, JR. 1961. Interspecific preening invitation display of parasitic cowbirds. Auk 78:473–504.
- WEATHERHEAD, P. J., AND D. J. HOYSAK. 1984. Dominance structuring of a Red-winged Blackbird roost. Auk 101:551–555.
- WILEY, J. W. 1985. Shiny cowbird parasitism in two avian communities in Puerto Rico. Condor 87: 165-176.

The Condor 94:1002–1006 © The Cooper Ornithological Society 1992

VOCALIZATIONS OF NESTLING LEACH'S STORM-PETRELS

CHRISTOPHER T. NAUGLER

Department of Biology, Queen's University, Kingston, Oniario K7L 3N6, Canada

Peter C. Smith

Department of Biology, Acadia University, Wolfville, Nova Scotia BOP 1X0, Canada

Key words: Leach's Storm-Petrel; Oceanodroma leucorhoa; nestling; vocalization; ontogeny.

Leach's Storm-Petrel (*Oceanodroma leucorhoa*) is a burrow-nesting seabird which breeds in colonies, often on off-shore islands. A single egg is incubated alternately by the adults for 41–42 days (Palmer 1962:232). After hatching, the chick is brooded continuously for up to five or six days (Gross 1935, Wilbur 1969). Adults forage at sea and return independently to feed the chick at intervals of about three days (Wilbur 1969, MacKinnon 1988) until the chick fledges at about 63–70 days of age (Palmer 1962:223). The vocal repertoire of adults is well-known, and consists of three main call types: the flight or chatter call, the burrow or purr call and the screech call (Hall-Craggs and Stellar 1976; Ainley 1980; Taoka et al. 1989a, 1989b).

In contrast, vocalizations of nestling Leach's Storm-Petrels have not been fully described, despite brief references by several authors (Palmer 1962:228, Hall-Craggs and Stellar 1976, Cramp and Simmons 1977: 172). In this paper we describe the nestling vocal repertoire of Leach's Storm-Petrel and present sonagraphs of call types. Such descriptions are important for two reasons. First, in the absence of visual cues, nestling vocalizations are probably of central importance in adult-chick interactions for nocturnal, burrow-dwelling species such as Leach's Storm-Petrel. Second, vocal behavior and vocal development of nestlings of nonoscine bird species in general is poorly known (Kroodsma 1982).

We studied Leach's Storm-Petrels breeding on the Evelyn and Morrill Richardson Field Station property, Bon Portage Island, Nova Scotia, Canada (43°26'N 65°45'W). This 150 ha island lies 3 km off the southwest tip of Nova Scotia. MacKinnon (1988) estimated the population size of this colony at 54,000 pairs.

We made audio recordings of nestling vocalizations on 21-27 August 1988 (5 chicks), 27 July-15 August 1990 (33 chicks) and 28 July-14 October 1991 (30 chicks). Individual burrows were marked and nestlings were recorded nightly in 1988 and 1990 and every few nights until fledging or nest failure in 1991. Nestlings were aged using allometric equations developed for this population by MacKinnon (1988). Recordings were made between dusk and dawn using a Realistic 14-812 recorder and a Realistic 33-992C microphone in 1988 and 1990, and a Sony Walkman Professional recorder WM-D60 and a Sony PC-62 microphone in 1991. Three different recording methods were employed. First, we recorded spontaneous vocalizations during adult-nestling interactions. We then examined burrows in an attempt to determine the behavioral context of the call. Second, we recorded responses of nestlings to burrow disturbances by us when adults were not present. These

¹ Received 9 January 1992. Accepted 27 May 1992.

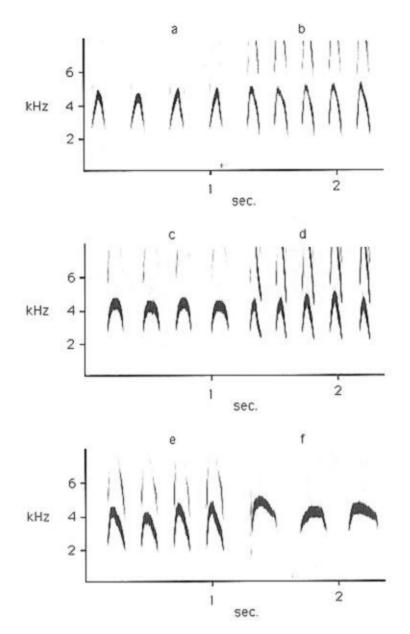


FIGURE 1. Rhythmic calls of nestling Leach's Storm-Petrels: (a) age 1 day, (b) age 2 days, (c) age 11 days, (d) age 14 days, (e) age 21 days and (f) age 45 days. Each call was made by a different individual.

consisted of either tapping the soil near the burrow entrance or reaching into the burrow and removing the nestling. Third, to determine vocal responses of nestlings to parents and strangers, we artificially introduced known parents (n = 25 birds) and strangers (n = 25birds) into nesting burrows containing only the chick. For these experiments an adult inside or entering a burrow was presumed to be a parent, while an adult removed from another burrow was presumed to be a stranger. Some burrows were used more than once and the actual numbers of nestlings tested is given where appropriate.

Recordings were analyzed using a DSP Sona-Graph model 5500 and printed on a Kay Elemetrics Corp. Gray Scale Printer model 5509, using a 234 Hz analyzing filter. Call types were classified by visual examination of sonagraphs.

We recognized three different types of vocalizations

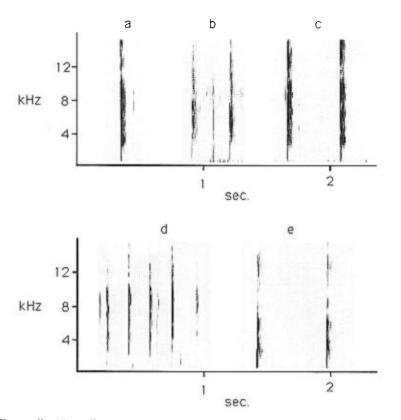
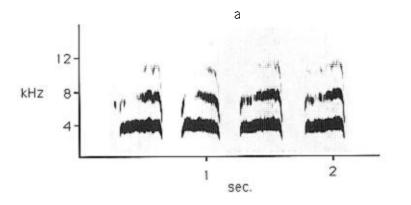


FIGURE 2. Short calls: (a) nestling age 4 days, (b) nestling age 8 days, (c) nestling age 18 days, (d) nestling age 26 days, (e) defense call of adult. Each call was made by a different individual.

from nestlings, which we called the short call, rhythmic call and high call. The rhythmic call (Fig. 1a-f) was a series of narrow band notes, each 100-200 msec in length, repeated at intervals of about 200 msec. Each note consisted of an upward sweep in frequency followed by a downward sweep, in the 2-4 kHz range. This call appeared to function as a food begging call as it was often given by nestlings when a parent entered the nesting burrow (62 of 70 observations on 55 nestlings). On several occasions the adult then fed the nestling and the nestling ceased vocalizing. In nestlings up to seven days of age, this call was also given in response to being handled by us (24 of 27 observations on 14 nestlings) or in response to a parent (14 of 14 observations on 10 nestlings) or stranger (12 of 12 observations on 10 nestlings) placed in their burrow. Nestlings possessed the rhythmic call from hatching to fledging with little variation in call structure apparent over this period (see Fig. 1). On several occasions, we observed introduced strangers apparently brooding a nestling which had been giving rhythmic calls.

The short call (Fig. 2a–d) was a short (50 msec), broad spectrum vocalization given either singly or repeated at intervals of varying length. The short call was used in apparent defense or threat situations and was often associated with a head thrust and bill snapping motion. These calls were given by all chicks in response to handling and removal from the burrow by us from hatching to fledging and, in chicks over about one week of age, in response to an introduced stranger (18 of 18 observations on 13 nestlings). Nestlings younger than one week gave the short call only in response to handling by us. This vocalization was highly similar among individuals throughout the nestling period (Fig. 2). The differences in repetition rate among examples in Figure 2 appeared to be related to the intensity of disturbance, with greater levels of disturbance (e.g., handling by us) eliciting more calls repeated at a faster rate. Our observations support Palmer's statement (1962:228) that adult Leach's Storm-Petrels possess a call given in apparent threat situations (Fig 2e) which strongly resembles the nestling short call.

The high call (Fig. 3a-c) consisted of a series of narrow spectrum notes of varying length and pitch. This call was given by chicks from about seven days of age until fledging in apparent alarm/distress situations, such as when we handled them (44 of 60 observations on 35 nestlings), or when a stranger was placed in the nesting burrow (14 of 18 observations on 13 nestlings). It was often preceded by the short call (13 of 14 observations on 13 nestlings). The high call showed little change over time, but was sometimes more drawn out in older chicks (compare Figs. 3b and c). This call appeared to develop from the rhythmic call. Nestlings



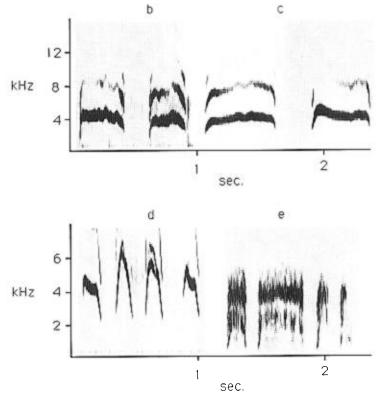


FIGURE 3. High calls: (a) nestling age 14 days, (b) nestling age 21 days, (c) nestling age 45 days, (d) altered begging call given by nestling age 3 days in alarm situation, (e) screech call of adult. Each call was made by a different individual.

age 3–6 days gave an altered version of the rhythmic call (Fig. 3d) in response to apparent alarm situations. The high call was fully developed by about seven days, while the rhythmic call remained essentially unchanged during this period (Fig. 1). The response of strangers to the short or high calls was to leave the burrow or move to a corner of the burrow away from the nestling. This differed markedly from the response to the rhythmic call (see above).

The main difference we observed between the be-

havioral contexts of the short and high calls was that the former call was generally given when the source of disturbance was non-tactile. The latter call was used when the source of disturbance actually contacted the nestling. Thus disturbance around the burrow entrance elicited short calls, but the chick switched to the high call when the observer's hand, microphone, or strange petrel touched it.

Previous references to nestling vocalizations in this species are confusing. Hall-Craggs and Stellar (1976)

state that the "food-begging calls of the female Leach's Petrel closely resemble those of the young." Adult Leach's Storm-Petrels give a "screech call" (Fig. 3e) which closely resembles the high call we describe in this paper (for other spectrographs of the screech call see Hall-Craggs and Stellar 1976, Cramp and Simmons 1977:172). It is possible that Hall-Craggs and Stellar were referring to the adult screech and nestling high calls. The "plaintive *peece peece peece ...* more prolonged in older chick" described by Palmer (1962:228) probably refers to both the rhythmic and high calls, as we found that younger nestlings give rhythmic calls give the longer and more emphatic high call (see above).

There is a paucity of information on the nestling vocal repertoires of other petrel species. Chicks of Wilson's Storm-Petrel (*Oceanites oceanicus*) uttered but a single type of call (Bretagnolle 1989). This call is similar to the rhythmic call of Leach's Storm-Petrel. Chicks of fulmarine petrels give coughing and lunging noises in defensive situations (Warham 1990:344), but no sonagraphs have been published.

Among other non-passerines, vocal repertoires and ontogeny have been examined in nestling Scaled Quail (Callipepla squamata, Anderson 1978), Aldabra White-Throated Rails (Dryolimnas cuvieri aldabranus, Wilkinson and Huxley 1978), American Coots (Fulica americana. Cosens 1981) and penguins (Jouventin 1982). Additionally, a more limited study was conducted on Northern Bobwhites (Colinus virginianus, Baker and Bailey 1987). The call repertoire of Leach's Storm-Petrel nestlings was smaller and more stereotyped than that reported for many of these other nonpasserine species. This may be due in part to the isolation of individual chicks in burrows and the resulting small number of different behavioral interactions experienced by the chick. For example, situations requiring a "contact call" such as Scaled Quail and American Coots possess (Anderson 1978, Cosens 1981), would never arise for Leach's Storm-Petrel chicks. Likewise, because nestlings do not leave the burrow until fledging, a call informing the parent of the location of the chick (e.g., the "chatter" call of Black-headed Gull chicks Larus ridibundus; Impekoven 1971) is not required either. Another possible factor may be the infrequent contacts between parents and young. This may have favored the existence of stereotyped, unambiguous vocalizations, which were easily interpreted by the parent, in the absence of visual cues. Finally, the relative absence of nestling predators on offshore islands may have obviated the need for diverse nestling alarm calls. This may be especially true for Leach's Storm Petrel because the nestlings are alone in the burrows for most of the time and so adults are not in a position to respond to nestling alarm calls.

We would like to thank L. Ratcliffe for the use of her sound analysis equipment, Richie and Bonnie Watkins for field assistance, and S. A. Shackleton, L. Ratcliffe, and C. M. Mackinnon for reading earlier drafts of the manuscript.

LITERATURE CITED

- AINLEY, D. G. 1980. Geographic variation in Leach's Storm-Petrel. Auk 97:837–853.
- ANDERSON, W. L. 1978. Vocalizations of Scaled Quail. Condor 80:49–63.
- BAKER, J. A., AND E. D. BAILEY. 1987. Ontogeny of the separation call in Northern Bobwhite (*Colinus* virginianus). Can. J. Zool. 65:1016-1020.
- BRETAGNOLLE, V. 1989. Calls of Wilson's Storm Petrel: functions, individual and sexual recognitions, and geographic variation. Behaviour 111:98–112.
- COSENS, S. E. 1981. Development of vocalizations in the American Coot. Can. J. Zool. 59:1921–1928.
- CRAMP, S., AND K. E. L. SIMMONS (eds.) 1977. Pp. 168–173. In Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the Western Palearctic, Vol. 1. Oxford Univ. Press, New York.
- GROSS, W. A. O. 1935. The life history of Leach's Petrel (Oceanodroma leucorhoa) on the Outer Sea Islands of the Bay of Fundy. Auk 52:382–399.
- HALL-CRAGGS, J., AND P. J. STELLAR. 1976. Distinguishing characteristics in the burrow-calling of Storm and Leach's Petrels. Brit. Birds 69:293–297.
- IMPEKOVEN, M. 1971. Calls of very young Blackheaded Gull chicks under different motivational states. Ibis 113:91–96.
- JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. Advances in Ethology No. 24. Verlag Paul Parey, Berlin.
- KROODSMA, D. E. 1982. Introduction, p. xxi-xxxi. In D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds, Vol. 2. Academic Press, New York.
- PALMER, R. S. (Ed.). 1962. P. 225–234. *In* Handbook of North American birds, Vol. 1. Yale Univ. Press, New Haven, CT.
- MACKINNON, C. M. 1988. Population size, habitat preferences and breeding biology of the Leach's Storm-Petrel Oceanodroma leucorhoa (Vieillot) on Bon Portage Island, Nova Scotia. M.Sc.thesis, Acadia University, Wolfville, Nova Scotia.
- TAOKA, M., T. SATO, T. KAMADA, AND H. OKUMURA. 1989a. Heterosexual response to playback calls of Leach's Storm-Petrel Oceanodroma leucorhoa. J. Yamashina Inst. Ornithol. 21:84–89.
- TAOKA, M., T. SATO, T. KAMADA, AND H. OKUMURA. 1989b. Sexual dimorphism of chatter-calls and vocal sex recognition in Leach's Storm-Petrels (Oceanodroma leucorhoa). Auk 106:498–501.
- WARHARM, J. 1990. The petrels. Academic Press, San Diego, CA.
- WILBUR, H. M. 1969. The breeding biology of Leach's Petrel, Oceanodroma leucorhoa. Auk 86:433-442.
- WILKINSON, R. AND C. R. HUXLEY. 1978. Vocalizations of chicks and juveniles and the development of adult calls in the Aldabra White-throated Rail Dryolimnas cuvieri aldabranus (Aves: Rallidae). J. Zool. (London) 186:487–505.