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Vocal recognition by little penguins (Eudyptula minor) on Phillip Island, Victoria, Australia

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Fadely, Janey Burger, M.S.

San Jose State University, 1991

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VOCAL RECOGNITION BY LITTLE PENGUINS

(Eudyptula minor)

ON PHILLIP ISLAND, VICTORIA, AUSTRALIA

A Thesis
Presented to
The Faculty of Moss Landing Marine Laboratories
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
Janey Burger Fadely
May 1991

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ABSTRACT

VOCAL RECOGNITION BY LITTLE PENGUINS (Eudyptula minor) ON PHILLIP ISLAND, VICTORIA, AUSTRALIA

by Janey Burger Fadely

Playback experiments were conducted at the Phillip Island Penguin Reserve, Victoria, Australia, to test whether Little Penguins recognize one another on the basis of vocalizations. Cardiac changes were monitored in response to mate and non-mate calls to test for recognition between mates. Changes in mean and peak heart rate (HR) were significantly greater following non-mate calls, indicating vocal recognition occurred. Differences in HR were statistically significant for males and females. Recognition of adults by chicks was tested by monitoring chick movements inside a test box in response to playback of parent and non-parent mutual vocalizations. Although chicks responded indiscriminately when young, chicks older than 5 weeks demonstrated recognition of parent calls. Variability was great between and among structural parameters of individual adult display calls. Duration of syllables was the most stable parameter within individuals, and may be important for individual recognition.

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INTRODUCTION

Individual recognition, the discrimination of one individual from another (Falls 1982), is essential for successful reproduction among species that maintain pair-bonds or provide extended parental care. Coordination of the breeding effort between mated individuals and restriction of parental care to the correct offspring requires accurate recognition systems (Thorpe 1968). Selection pressures should therefore be high among species in which family groups frequently reunite to successfully raise young, and among those with colonial breeding systems. Many seabird species exhibit these characteristics and are ideal for the study of individual recognition.

Individual recognition by seabirds has been studied recently (see Falls 1982, Beecher 1982) relating recognition systems to the environments in which they occur. Complexity of a recognition system is correlated positively to the degree of coloniality (Beecher 1982, Jouventin 1982), and negatively with presence of a permanent nest site. The most complex recognition systems occur in species that breed in dense aggregations without nests such as the Common Murre (Uria aalge; Tschanz 1968) and the Emperor Penguin (Aptenodytes forsteri; Jouventin and Roux 1979).

Penguins breed in a wide variety of environments from the Antarctic to the Galapagos Islands; coloniality varies between dense huddles of Emperor Penguins to widely spaced nests of Yellow-eyed Penguins (Megadyptes antipodes). Vocal recognition is common among penguins, but exceptions may occur relating to breeding biology and environment of particular species. Playback experiments and observations indicate that vocal recognition occurs in Emperor Penguins (Prevost 1955, Jouventin 1972, Jouventin and Roux 1979, Jouventin et al. 1979), King Penguins (Aptenodytes patagonicus; Derenne et al. 1979), Adélie penguins (Pygoscelis adeliae; Sladen 1955, Penney 1968, Thompson and Emlen 1968, Thompson 1974, Ainley 1975, Spurr 1975, Jouventin and Roux 1979, Aoyanagi and Tamiya 1981), Macaroni Penguins (Eudyptes chrysolophus; Jouventin 1982), Rockhopper Penguins (Eudyptes chrysocome; Pettingill 1960, Warham 1963), Chinstrap Penguins (Pygoscelis antarctica; Sladen 1955), Jackass Penguins (Spheniscus demersus; Eggleton and Siegfried 1979), and Snares Crested Penguins (Eudyptes robustus; Proffitt and McLean 1990).

Vocal recognition may occur in Yellow-eyed Penguins, (Richdale 1946, 1951), although recent playback experiments indicated that in contrast to all other penguins studied thus far, Yellow-eyed Penguin chicks could not recognize their parent's calls (Nordin 1988). This result is not unexpected because the Yellow-eyed Penguin is the least colonial of all penguin species, with large inter-nest distances that may reduce the likelihood of encountering other individuals.

The study of species that exhibit unique behavioral patterns is important in the continuing development and refinement of existing theories. Little Penguins (Eudyptula minor) are nocturnal on their breeding grounds, a behavior unique among penguins. Although theory would predict reduced need by Little Penguins for a complex recognition system on the basis of their loose coloniality and use of a permanent nest site, observations indicate otherwise. Mates frequently remain with the same partner annually (83%, Reilly and Cullen 1981) and perform mutual displays if they meet away from the burrow (pers. obs.). Parents rarely feed the wrong chick on Phillip Island (Peter Dann, pers. comm.), and frequently were observed feeding their older chicks away from the burrow. Although a permanent burrow site may aide reunions, it is apparently not necessary for individual recognition. This implies that some other mechanism allows recognition of individuals.

Mechanisms for individual recognition in birds can involve olfactory, visual, and vocal cues (Wilson 1975). It is unlikely that olfactory cues contribute to communication in the Little Penguin because the external nares are occluded by bone (Zusi 1975). Jouventin (1982) reported that obstruction of olfactory ducts in four species of penguins did not interfere with partner recognition and concluded that communication among penguins was primarily visual and vocal.

Although penguin vision may be adapted for dim underwater conditions (Stahel and Gales 1987), vision in Little Penguins has not been tested and there is no indication that any penguin species possesses specialized night vision. In general, penguin night vision is about equal to that of humans (Martin and Young 1984). Visual communication in Little Penguins is therefore limited by their nocturnal behavior as well as by densely vegetated habitat in which many burrows are excavated. It seems likely that individual recognition may be based on vocalizations in the Little Penguin. Anecdotal observations of Little Penguins suggested that individual calls are highly distinctive (Stahel and Gales 1987), and that vocal recognition occurs (Richdale 1951, Jouventin 1982, Burger 1987b), but experiments for verification have not heretofore been performed.

Vocal recognition experiments should include manipulative experiments in the field and analysis of call structure in the laboratory (Catchpole 1982). Analysis of call structure can demonstrate whether individual cues exist. An acoustic variable which is constant within calls of one individual relative to calls among individuals can potentially be used for individual recognition (Falls 1982, Jouventin et al. 1979, Brooke 1986).

Playback experiments test an individual's ability to discriminate between call types. Playback studies examining vocal recognition in seabirds typically have involved monitoring overt behaviors (such as orientation or approach toward a speaker) following playback of different pre-recorded calls to an individual on the nest or in a natural setting (e.g., Jones et al. 1987, Proffitt and McLean 1990). This technique was appropriate for Little Penguin chicks in this study since chicks are usually less sensitive to a small amount of handling and manipulation than adults.

However, behavioral observations may be impractical or invasive for some species or groups because of environmental and behavioral characteristics. Monitoring of a physiological response to playback calls is an alternative which has been used successfully on Belted Kingfishers (Ceryle alcyon) by Davis (1986). In addition, physiological responses may provide a more objective measure of a reaction to a stimulus than observed behavioral responses, because of reduced subjectivity in recording or analyzing data. Cardiac responses to mate and non-mate playback calls were used as an indication of discrimination between the two call types by adult Little Penguins in this study.

This study tests the general hypothesis that vocal recognition occurs in the Little Penguin. Specifically, experiments were conducted to test the following hypotheses: 1) Increases in heart rate of adult Little Penguins will be significantly greater following non-mate playback calls than mate playback calls, and 2) Chicks will approach playback of parent calls significantly more than playback of non-parent calls after the age at which chicks wander from the burrow (5 weeks-old). Call individuality was examined to determine whether cues for individual recognition exist.

MATERIALS AND METHODS

Research was conducted from September to December during the 1988-89 penguin breeding season at the Penguin Reserve on Phillip Island, Victoria, Australia (38°31'S, 145°08'E; Fig. 1). All work was conducted between dusk and dawn when Little Penguins were socially active on the breeding colony. No supplementary lighting was used beyond that normally used at the Reserve.

Adult mated pairs were banded by the research staff at the Penguin Reserve as part of a long-term study on breeding biology. Sex was determined at banding by bill depth or cohabitation with birds of known sex (Reilly and Cullen 1981). Pairs were chosen from among those nesting in artificial burrows constructed by the Reserve staff. These burrows had removable tops which allowed access for identification of individuals, placement and removal of the heart rate monitor, and removal and replacement of chicks with minimum disturbance to the birds.

Recordings of calls, used for playback tapes, were made using a Marantz PMD430 recorder and Maxell XLII 90-min cassette tapes. These were recorded using a Unitech shotgun microphone (flat ±3 db from 50-18000 Hz), with a parabolic reflector when needed, or with a Realistic lapel microphone placed inside the burrow. Tapes were played back using a Sony WM-D6C cassette recorder and Aiwa portable speakers.

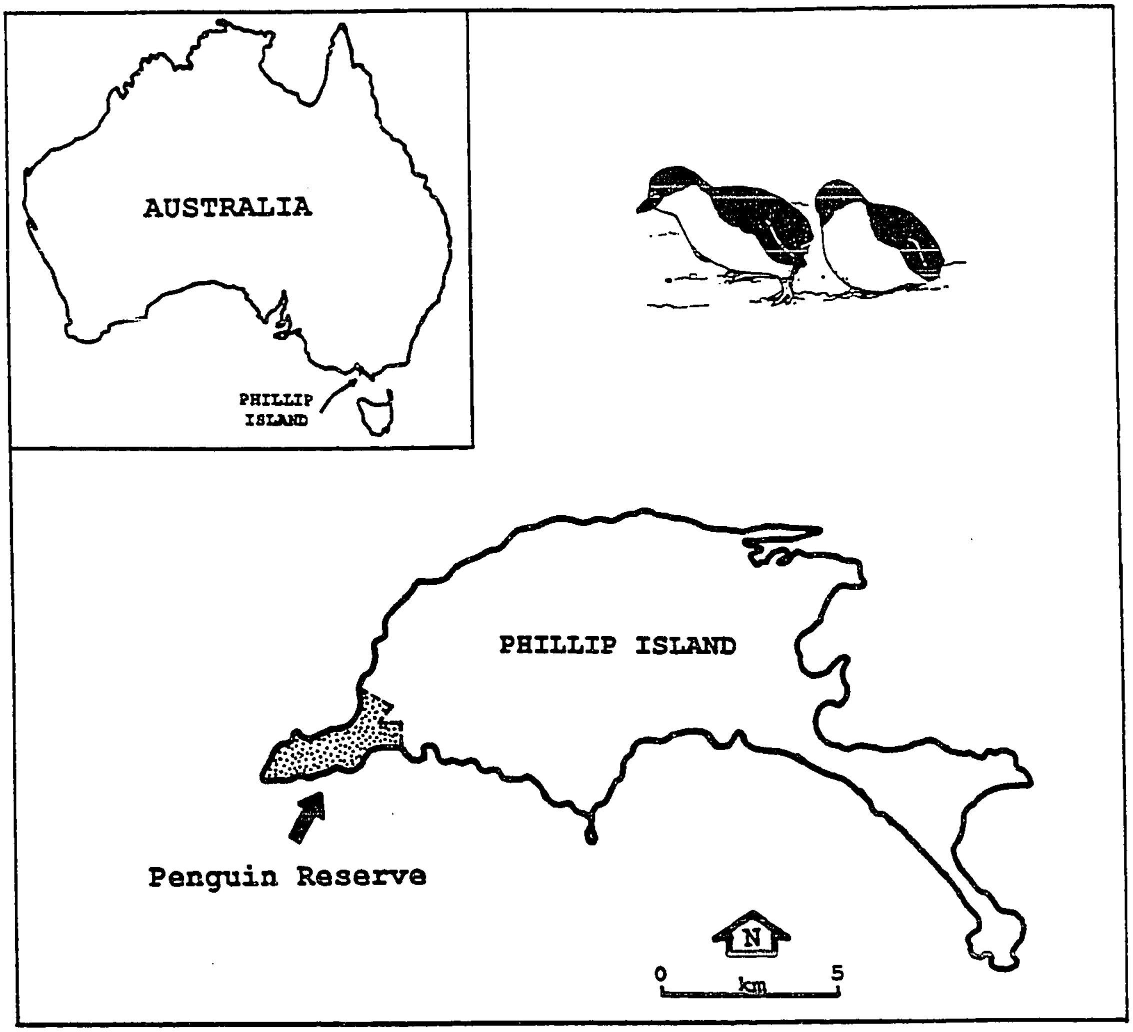

Figure 1. Location of Phillip Island Penguin Reserve study site.

Mate Recognition Experiments

Playback experiments were conducted with adult Little Penguins to test the hypothesis that vocal recognition occurs between mates. Experiments were designed to minimize disturbance and handling of birds. Adults were extremely aggressive when handled and could not be removed from their burrows without significantly altering their behavior. Observation of birds inside their burrows at night was not practical. Therefore, a simple inexpensive instrument was developed, based on a design by Davis (1986), to monitor a physiological response to playback calls. Davis monitored cardiac responses of hole-nesting Belted Kingfishers to familiar and unfamiliar vocalizations. In this study, cardiac and vocal responses of Little Penguins to mate and non-mate playback calls were recorded. Significant differences in responses were used to indicate discrimination between the two call types.

"Display Calls," which are used by males to attract females early in the breeding season, and by both sexes in territorial and mutual displays (Burger 1987a, 1987b), were used for playback calls. Calls were recorded during peak social activity after birds returned ashore in the evening (Burger 1987a, 1987b). It was difficult to obtain clear recordings of display calls from known individuals because many birds typically vocalized at the same time, and individuals were extremely difficult to locate and capture for identification after a successful recording. Waas (1988) reported that playback of display calls to Little Penguins facilitated calling from both single birds and pairs. Therefore, in this study clear recordings of known adults (individuals and pairs) were obtained by recording their vocal responses to unfamiliar calls. Calls were played outside the burrow entrance, and birds responded with aggressive Display Calls in defense of the territory. This technique, suggested by Gulledge (1977), was also used to obtain clear recordings of nocturnal burrow-nesting petrels (Brooke 1986).

Playback tapes were produced from recordings having the highest signal-to-noise ratio, as determined by ear. Mate calls and non-mate calls were always from the same sex, and were matched in length and intensity whenever possible. The two call types were alternated on the playback tape with 2-min pauses between each call. Each call was played twice, the initial call alternated for each experiment and cardiac response of the incubating bird was measured using a heart rate monitor (HRM).

Nineteen mate-recognition experiments were conducted. The bird's own eggs were removed from the nest and incubated nearby. The HRM was introduced into the nest, speakers were placed 20 cm from the burrow opening, and the bird was left alone for 30 min to recover from the disturbance. HR was recorded for 3 min before the start of the playback tape, and the playback tape was paused during the playback period whenever HR was not audible due to shifting in the nest. At the end of the experiment, the HRM was removed and the eggs replaced.

The HRM was modified from a design by Davis (1986). However, rather than measure heart rate through the breast, the HRM was built in the shape of an egg (Fig. 2), which came into direct contact with the brood patch of an incubating

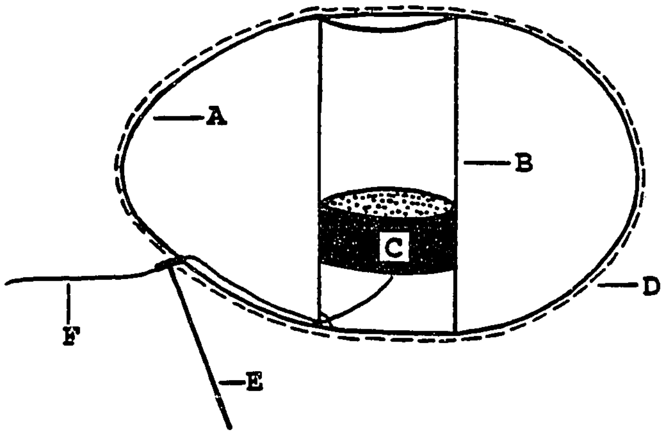

Figure 2. Heart rate monitor for Little Penguins. A. plastic egg, B. PVC cylinder, C. condenser microphone, D. rubber membrane, E. nail, F. wire leading to cassette recorder.

bird. Most breeding birds readily incubated the HRM. Heartbeats were clearly audible (Fig. 3) when the HRM was correctly positioned relative to the penguin's body.

To build the HRM into the shape of an egg, a small Radio Shack condenser microphone (without plastic casing) was mounted in a 3.0 cm long, 2.5 cm diameter cylinder of PVC. The PVC cylinder was mounted inside an artificial white plastic chicken egg, approximately the size of a Little Penguin egg. The egg was cut in half for mounting, and then sealed together. The open end of the cylinder fit against a 2.5 cm diameter opening in the side of the egg. The PVC cylinder was sanded at either end to conform to the shape of the egg, and glued into the egg with an airtight seal between the cylinder and egg. A wire to the microphone exited a small hole drilled in one end of the egg, and extended 3-5 m to the Marantz recorder, a distance that avoided interference with the experiment. A thin, flexible vinyl membrane (prophylactic) was stretched over the egg and secured with tape. A 7-cm nail was attached at the point where the wire entered the egg. This nail was driven into the floor of the burrow when positioning the monitor, and prevented the bird from rolling or kicking the egg out of position.

HR recordings were analyzed on a DSP Sona-Graph Model 5500 (Kay Elemetrics Corp.). Analysis was limited to experiments in which HR was clearly discernable before, during and after playback call (n=11 experiments with 8 individuals, 5 females and 3 males). Elapsed time for three heartbeats was measured consecutively in the 10 sec before and in the 10 sec following the start of

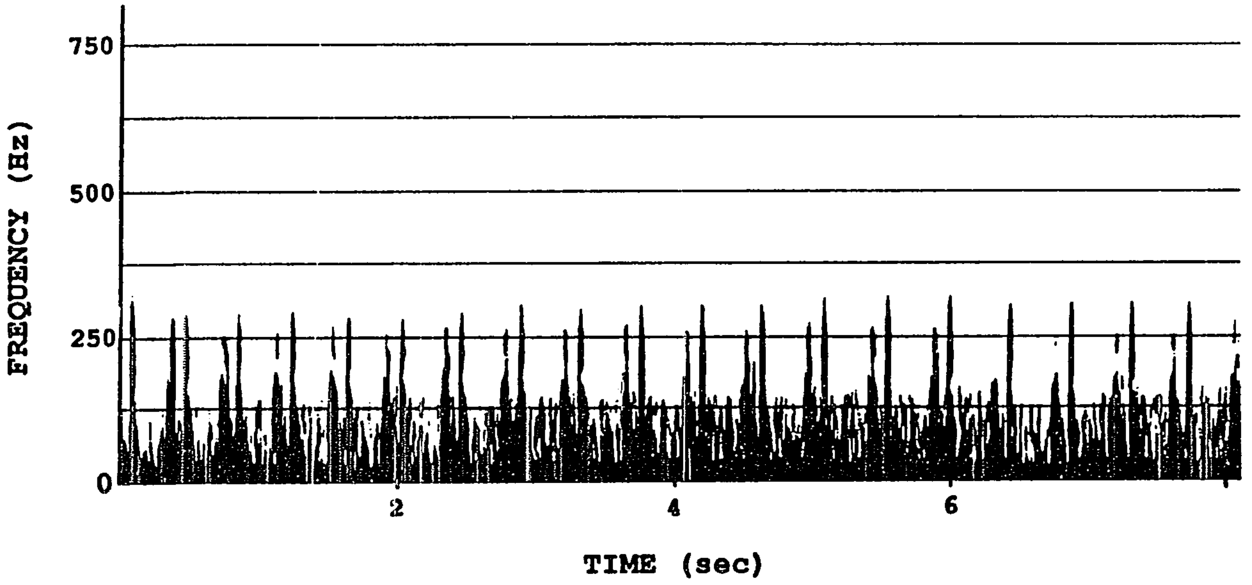

Figure 3. Spectrograph of heart rate of a Little Penguin recorded through the HRM.

the playback call, and these values were used to calculate HR before (baseline) and after playback. Mean changes in HR and changes in peak HR in response to mate and non-mate playback calls were compared using paired t-tests, as were differences between males and females. One mate and one non-mate trial per individual were used for analysis (n=8 experiments). Homogeneity of variances were tested using an F-test, and distributions were examined graphically for normality.

The duration of change from peak heart rate (which always occurred shortly after the start of the playback call), to baseline HR was defined as the recovery time. A paired t-test was used to compare recovery times following mate and non-mate playback calls. Recovery times were also compared between males and females. Durations of vocal responses were measured; differences between mate and non-mate playback, and differences between males and females were tested using paired t-tests. Equality of variances and normality were examined as above. Number of vocal responses to each type of playback call was compared with a Chi-Square contingency table.

Culik et al. (1989) demonstrated an increase in HR of Adélie Penguins during aggressive interactions. Little Penguin heart rates could therefore be expected to increase following playback of all calls since calls were recorded in an aggressive context. However, Spurr (1974) noted that individual recognition and mutual displays (ritualized behavior between members of a mated pair), reduced aggressive behavior between individuals. In some circumstances, aggressive responses may be mitigated by individual recognition. Playback experiments in this study test the specific hypothesis that heart rate increases will be significantly larger following non-mate playback calls than following mate playback calls.

Sonagram Analysis

The following acoustic characteristics of calls were measured among and within individuals for both inhalent and exhalent phrases: 1) main frequency (the frequency with the highest concentration of energy); 2) phrase duration (the time elapsed for one inhalent or exhalent phrase); 3) sideband interval (interval between the main frequency and the first harmonic or sideband); and 4) syllable duration (the time elapsed for 5 syllables). Time measurements (phrase and syllable durations) were made directly from sonagrams (Figs. 4 and 5), and frequency (main frequency and sideband interval) determined from power spectra (Fig. 6). Three calls from each of 11 individuals were analyzed.

Coefficients of variation for mean values of each acoustic characteristic were calculated for each individual, and these values averaged for an overall intra-individual ("individual") coefficient of variation for each characteristic (Falls 1982, Jouventin 1982). An inter-individual coefficient of variation was calculated using characteristics of one call from each of the 11 individuals. Population/individual ratios were calculated and used for comparisons among characteristics and with other studies.

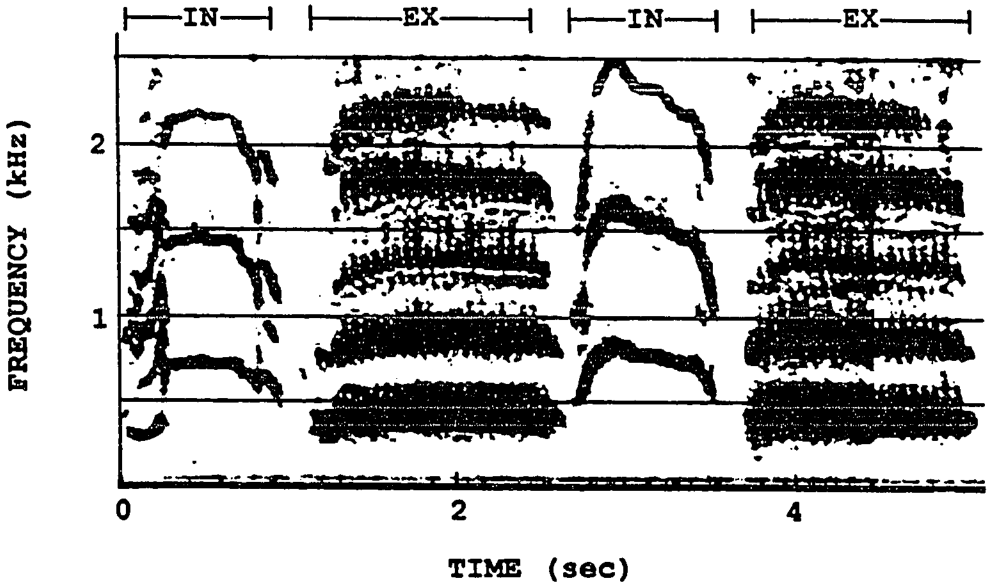

Figure 4. Sonagram of a portion of a Little Penguin Display Call showing 2 inhalent phrases (IN) and 2 exhalent phrases (EX). Duration of phrases was measured directly from sonagrams. Phrases are made up of a series of syllables, clearly visible in Fig. 5.

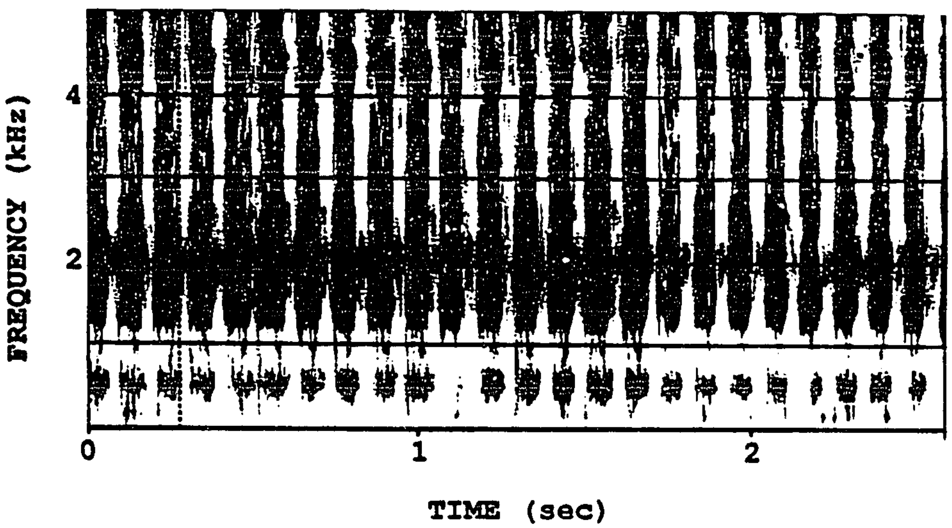

Figure 5. Sonagram of a portion of one exhalent phrase of a Little Penguin Display Call showing individual syllables (vertical bars). Time scale is smaller than Fig. 4. Duration of syllables was measured directly from sonagrams.

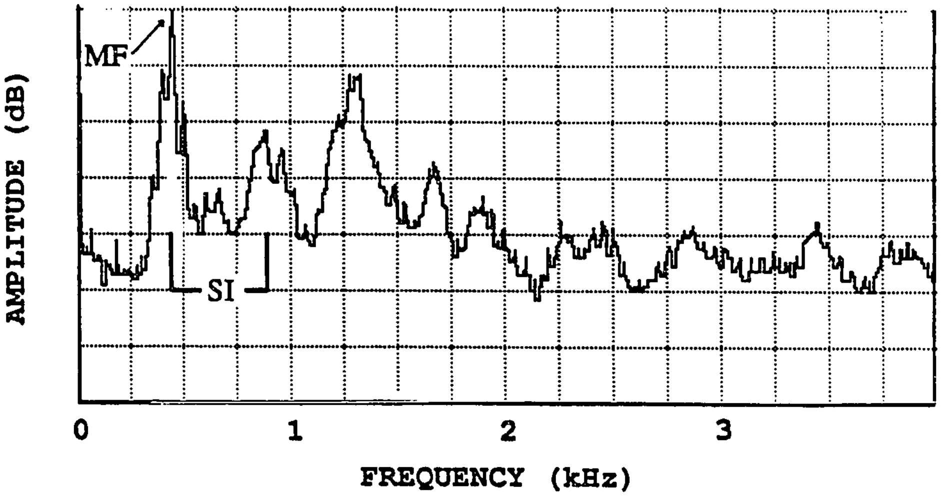

Figure 6. Power spectrum of one exhalent phrase of a Little Penguin Display Call. Peaks correspond to horizontal dark bands in sonagram display (Fig. 4). Main Frequency (MF) and Sideband Interval (SI) were measured from power spectra.

Chick Recognition Of Parent Calls

Recognition of parent calls by chicks was tested by monitoring chick movements in response to parent and non-parent calls in a modified artificial burrow. This technique was used because chicks were less sensitive to handling than adults and because the HRM could not be used with chicks since they do not incubate eggs. Experiments were designed to make some observation possible with minimum disturbance to the chicks and their parents.

Recognition of a parent call by a chick in many species does not appear until the onset of brood mobility. At this point, it becomes advantageous for the chick to discriminate parents from other adults to facilitate parent-chick reunion and feeding, and to avoid aggressive rebuffs from other adults (Falls 1982, Beecher et al. 1985).

Chicks were tested for recognition of parental calls in three different age categories: less than 2 weeks old (n=8), 2-4 weeks old (n = 27) and 5-8 weeks old (n = 32). These represent ages before (1-4 weeks) and after (5-8 weeks) chicks begin to wander from the nest (Reilly and Cullen 1981). Age of chicks was estimated by size and general appearance with help of the Penguin Reserve research staff.

Experiments were conducted just after dusk when adults were returning to their burrows. A chick was removed from the burrow and placed at the centerline of a long narrow plywood box (2.5 m x 0.5 m x 0.5 m; Fig. 7). The box was open to the ground and closed with a lid during experiments to simulate the burrow

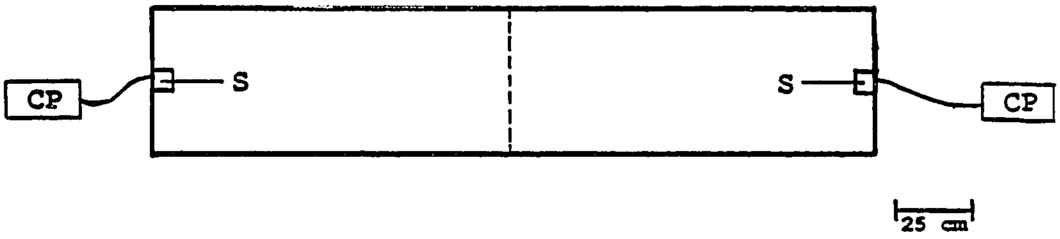

Figure 7. Schematic of box design for chick recognition experiments. CP = cassette players. S = speakers. Removable box top not shown. Dotted line indicates centerline of box.

environment. The ground inside the box was covered with sand so footprints of chicks were visible and could be noted after each trial. Mutual-display calls of parents and of non-parent mated pairs (recorded from a different area of the Reserve) were alternated from a speaker at each end of the box. Non-parent calls that approximately matched the length and intensity of parent calls were chosen. Volumes of the two calls were matched by ear with those normally heard from displaying birds. Four calls were played from each speaker, and the initial call was alternated between experiments.

At the end of each trial, the chick's position was classified into one of 3 categories: 1) still in the center starting position; 2) in the parent area (the half of the box toward the speaker playing parent calls); or 3) in the non-parent area. Chick positions were scored as 25%, 50%, 75% or 100% of the distance from centerline to speaker. Numbers of chicks in the parent versus non-parent areas were compared with a Chi-Square test. Mean distance moved toward parent or non-parent speakers was compared using a Student's t-test, and the effect of order of playback calls was tested with a Chi-Square contingency table. The number of begging calls heard from chicks during parent and non-parent playback calls was noted and compared using a Chi-Square test.

RESULTS

Mate Recognition Experiments

Heart rate increased immediately following the beginning of playback calls in all trials but increases were larger following non-mate calls. Mean change in HR (paired t_s=5.44, $P<0.01$; Fig. 8) and mean change in peak HR (paired t_s=5.12, $P<0.01$; Fig. 9) were significantly greater following non-mate trials than following mate trials. Mean HR differences were significant for males (paired t_s=5.33, $P<0.05$; Fig. 10) and females (paired t_s=4.09, $P<0.02$). Similarly, peak HR differences were significant for males (paired ts=4.82, $P<0.05$; Fig.11) and females (paired t_s=3.35, $P<0.05$).

Mean recovery time was not significantly different between mate and non-mate trials (paired t_s=1.09, ns; Table 1). Differences between the two trials were not significant for males (paired t_s=1.73, ns) or females (paired t_s=2.31, ns). Mean recovery time was not significantly different when birds responded vocally to playback calls (t_s=0.07, ns; Fig. 12).

Adult birds responded vocally to playback calls in 50% of mate trials and 38% of non-mate trials. The mean duration of vocal response was not significantly different for mate (11.12 ± 4.72 sec.) and non-mate (11.78 ± 5.62 sec) playback trials (paired t_s=0.31, ns).

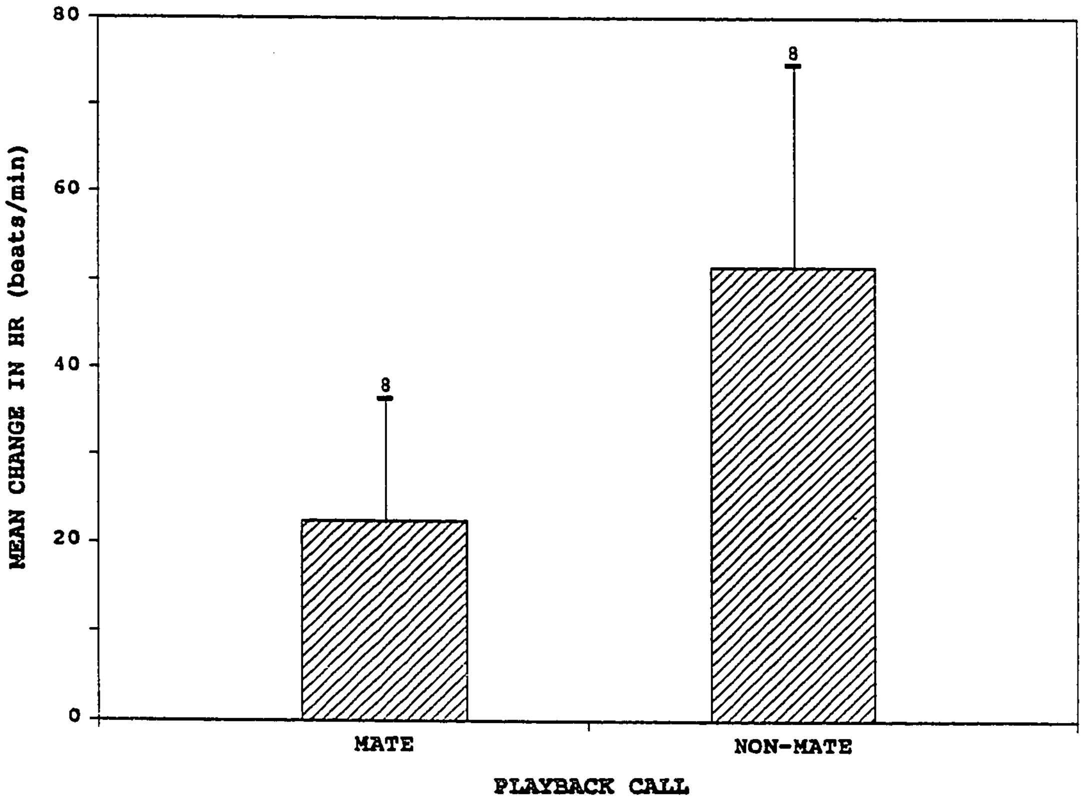

Figure 8. Mean changes in HR (± SD) following playback of mate and non-mate calls. Sample size indicated for each group.

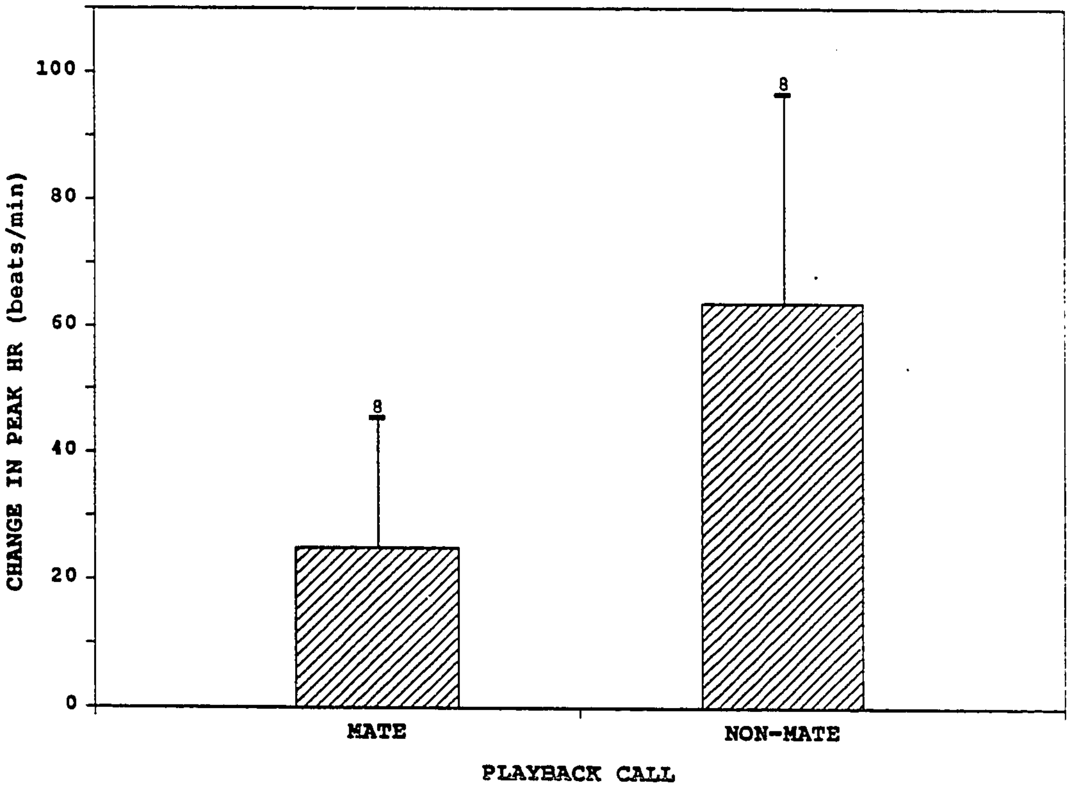

Figure 9. Mean change in peak HR (± SD) following playback of mate and non-mate calls. Sample size indicated for each group.

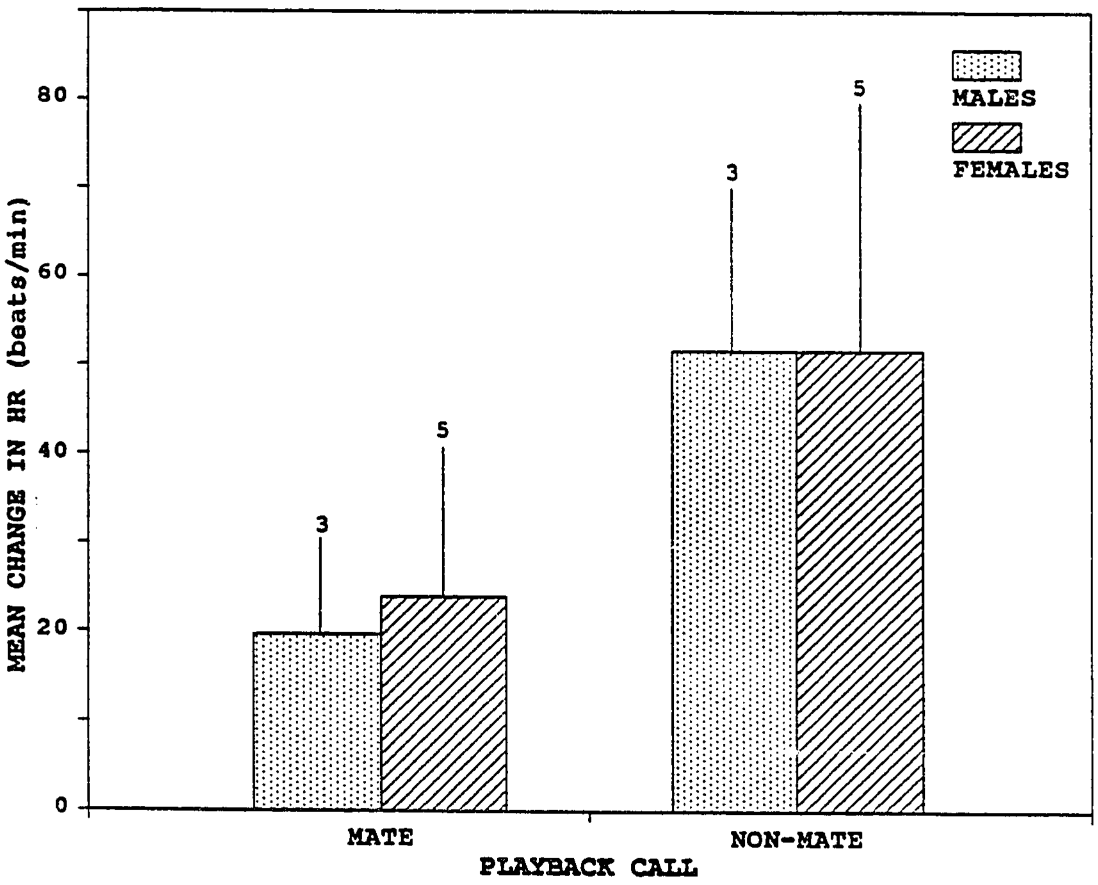

Figure 10. Mean change in HR following mate and non-mate playback calls for males and females separately. Sample size indicated for each group.

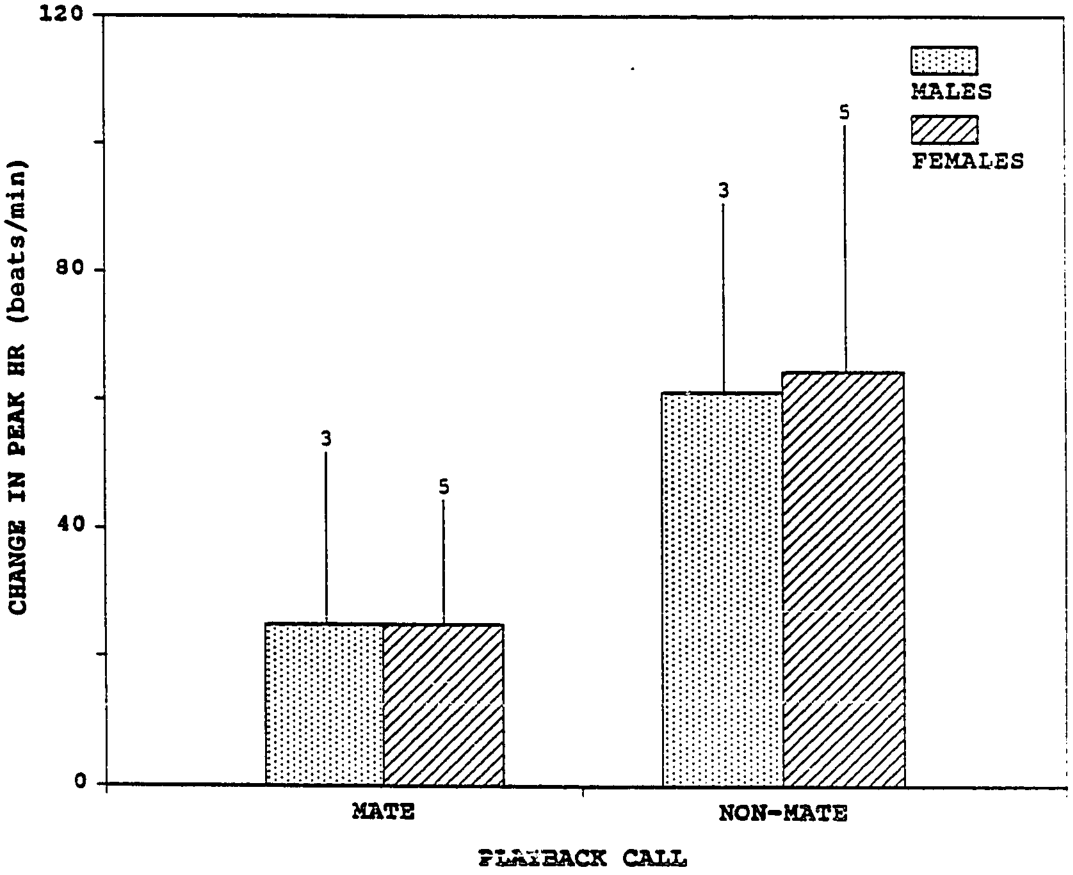

Figure 11. Mean change in peak HR (± SD) following playback of mate and non-mate calls for males and females separately. Sample sizes indicated for each group.

Table 1.
Mean recovery time (sec) following playback of mate and non-mate calls.

	Mate Call			Non-Mate Call		
	x	SD	n	x	SD	n
Both Sexes	15.3	5.6	8	17.9	7.5	8
Males	11.0	5.0	3	16.8	9.6	3
Females	17.8	4.5	5	18.6	7.1	5

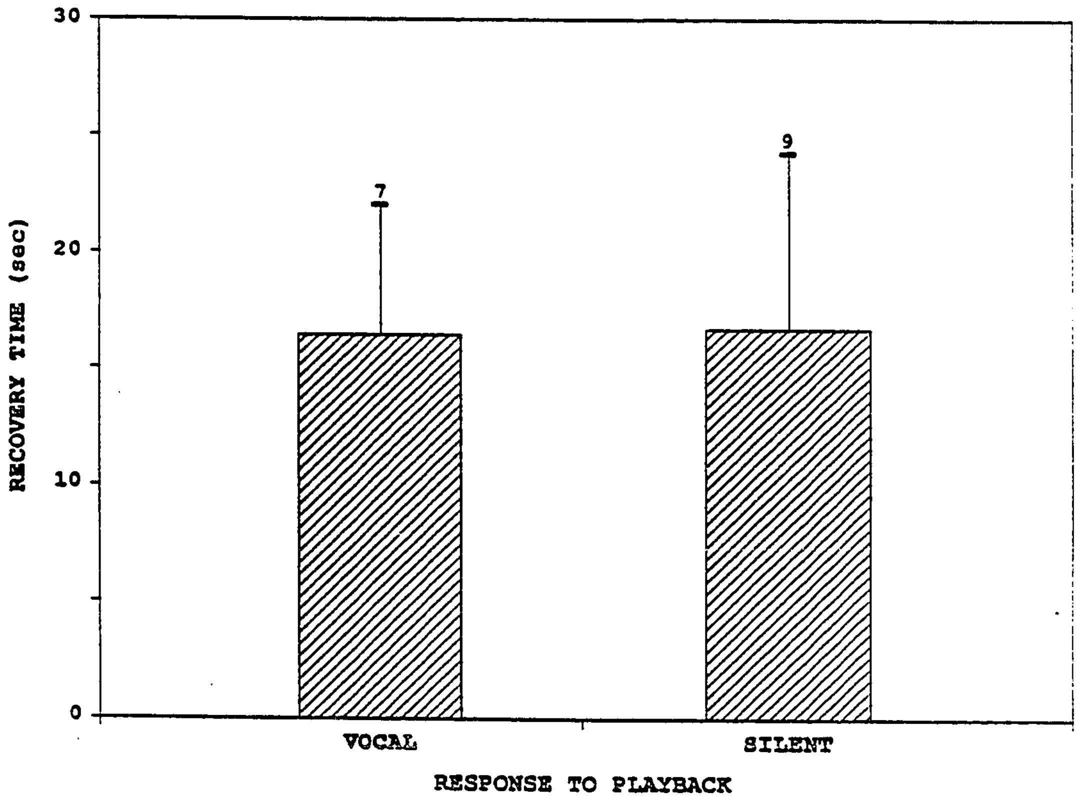

Figure 12. Mean recovery time (± SD) of birds that vocalized following playback calls versus birds that were silent following playback calls. Sample size indicated for each group.

Sonagram Analysis

Inter-individual (population) and intra-individual coefficients of variation (Table 2) indicated that structural features of Little Penguin Display Calls were highly variable. Main frequency of calls was the most variable, indicated by the largest coefficient of variation. The duration of 5 syllables for both inhalent and exhalent phrases had the smallest coefficients of variation both within and among individuals, and the largest population/individual ratios.

Visual inspection of 20 sonagrams of mutual displays indicated that the structure was very similar to individual display calls (Fig. 13). Therefore, information on structural consistency of display calls of individuals also may be relevant to mutual displays.

Calls of individuals and mutual displays could not be recognized individually in the field because of the large amount of variation in quality and timing of calls in different contexts.

Chick Recognition Of Parental Calls

All chicks less than 2 weeks old remained in their starting position at the center of the box for the duration of the trial (n=8). No begging calls were heard from these chicks during playback trials.

Chicks between 2 and 4 weeks old were more mobile than those less than 2 weeks old; 11 of 23 chicks (48%) moved from the center starting position during the trial. The number of chicks that approached the parent speaker was not

Variable	Pop. CV	Ind. CV	Ratio
INHALENT PHRASE			
Phrase Duration	52.31	27.78	1.88
Main Frequency	79.31	27.00	2.94
Harmonic Interval	65.22	21.20	3.08
Duration of 5 Syllables	50.61	7.27	6.96
EXHALENT PHRASE			
Phrase Duration	36.12	31.99	1.13
Main Frequency	79.34	42.00	1.89
Harmonic Interval	65.25	35.82	1.82
Duration of 5 Syllables	20.07	9.14	2.30

Table 2.
Coefficients of variation for four variables of Little Penguin Display Calls. Population CV (Pop CV) values represent inter-individual variability (n=11 individuals, 1 call per individual). Individual CV (Ind CV) values represent intra-individual variability (n=11 individuals, 3 calls per individual). See text for explanation of variables.

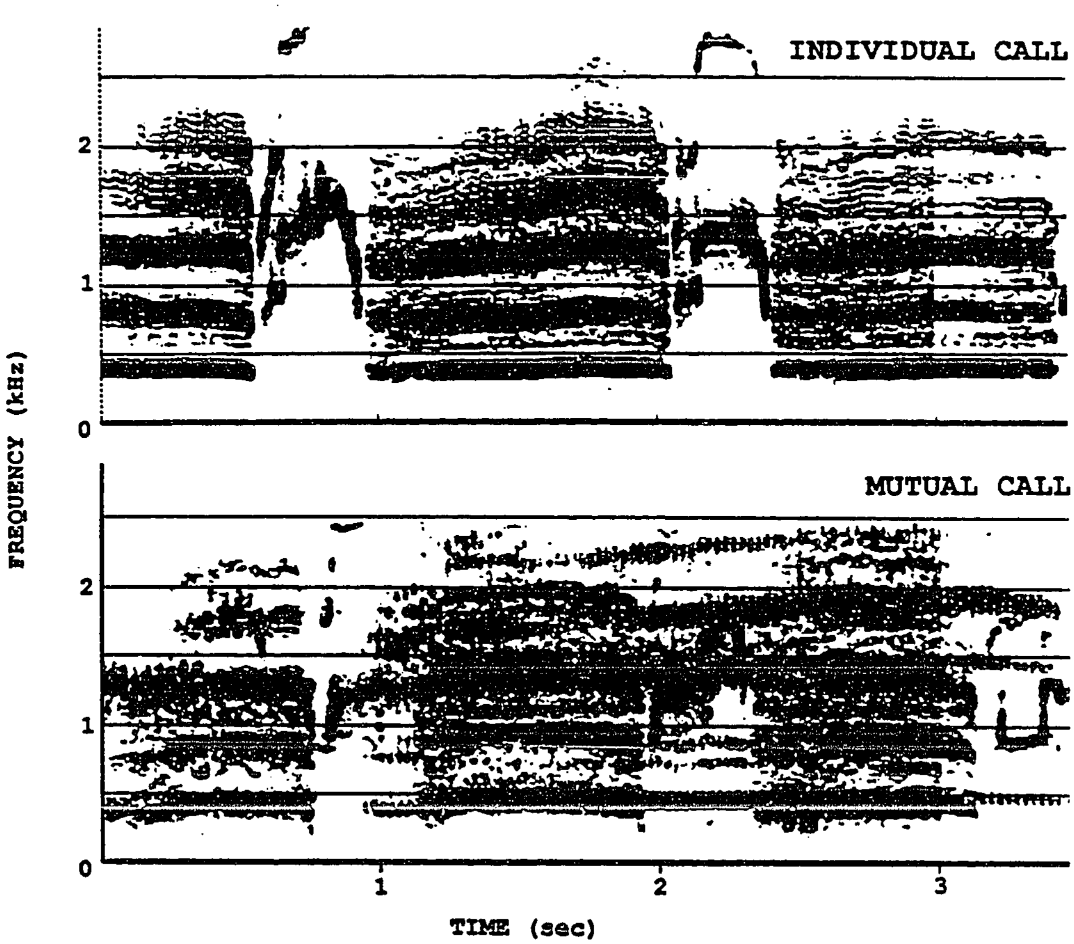

Figure 13. Sonagram of an individual call and a mutual call showing similarity in structure.

significantly different from the number of chicks that approached the non-parent speaker (X^2=0.09, ns; Fig. 14). The average distance moved toward a speaker was not significantly different between chicks in the parent area and chicks in the non-parent area (X^2=1.02, ns; Fig. 15). No begging calls were heard from these chicks during playback trials.

All chicks in the 5-8 week old category (n=24) moved during the trial. At the end of the trial, significantly more chicks were in the parent area than the non-parent area (X^2=9.78, $P<0.01$; Fig. 14). Mean distance moved toward a speaker was not significantly different for chicks in the two areas (X^2=0.01, ns; Fig. 15). Begging calls were heard in 42% of the playback trials with 5-8 week old chicks, and were heard more frequently at the parent speaker than the non-parent speaker (X^2=4.90, $P<0.05$; Fig. 16). Begging calls always began shortly after the start of the parent playback call.

The order of calls (parent or non-parent call first) had no effect on chick movements in the 2-4 week (X^2=1.02, $P>0.1$) or 5-8 week (X^2=0.01, $P>0.5$) age category.

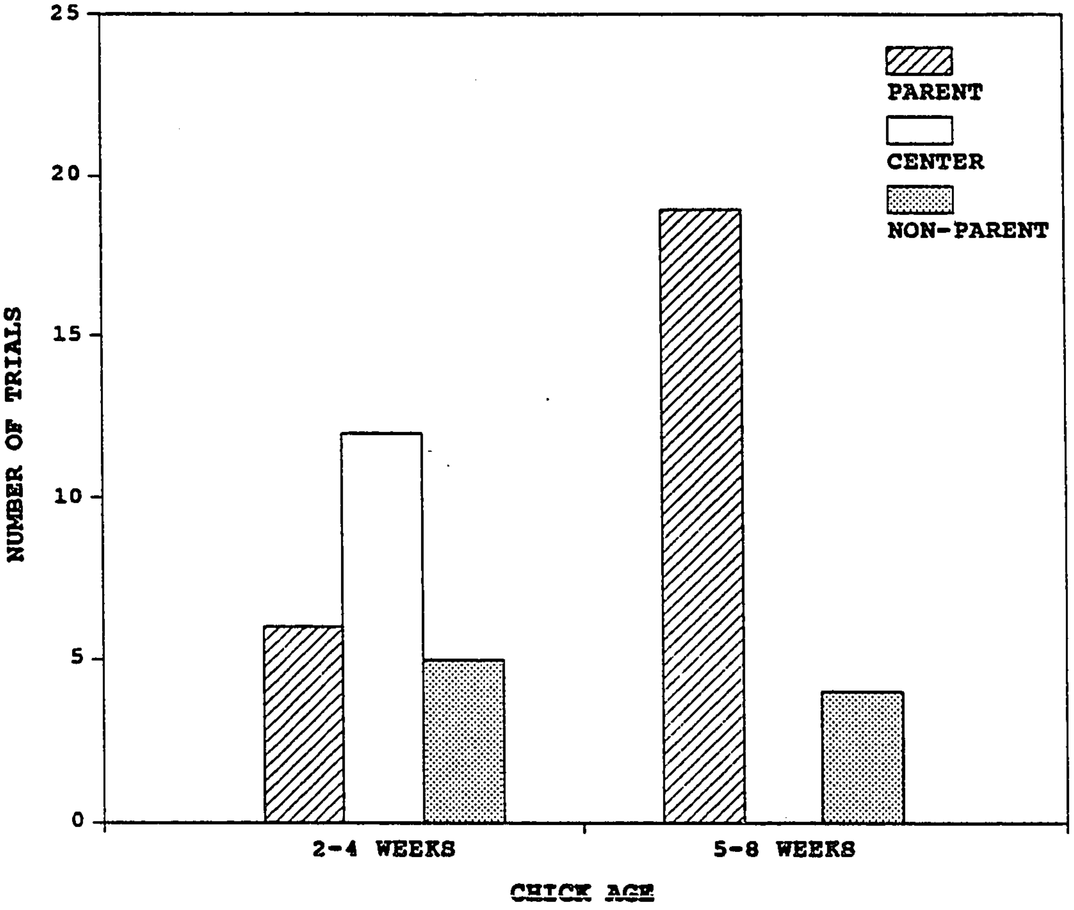

Figure 14. Number of trials during which 2-4 week-old and 5-8 week-old chicks moved into parent area (PARENT), stayed at centerline of box (CENTER) or moved into non-parent area (NON-PARENT).

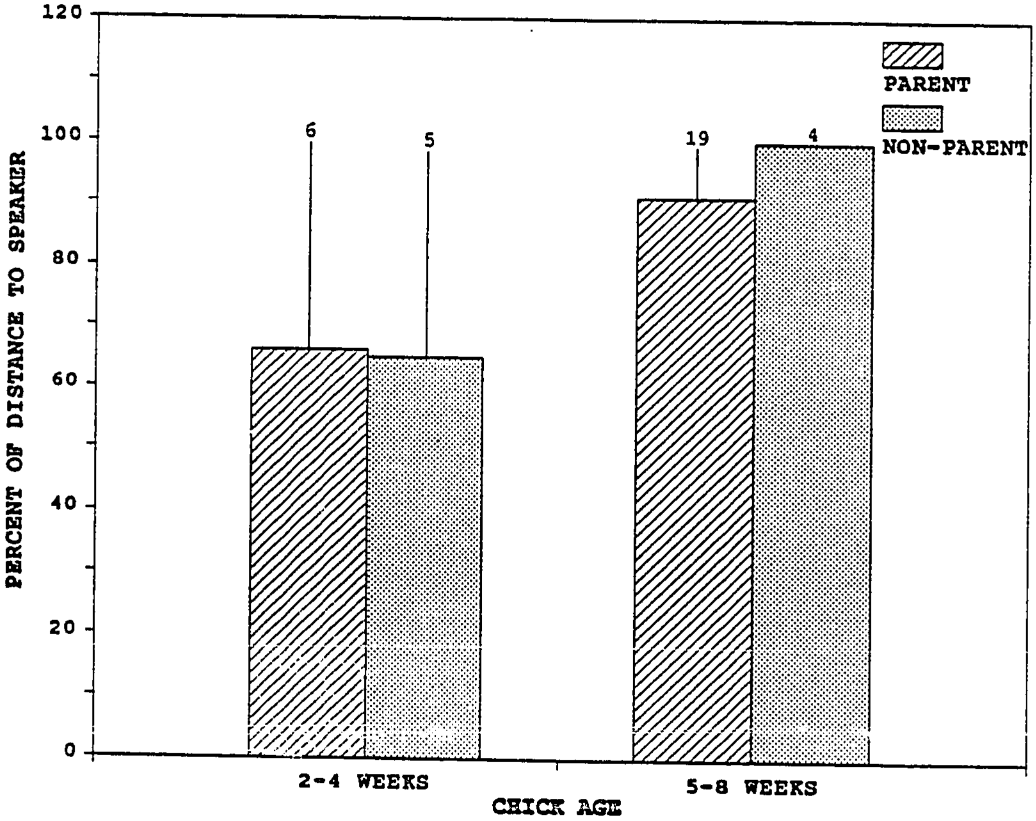

Figure 15. Mean distances moved (± SD) by 2-4 week-old and 5-8 week-old chicks into parent or non-parent area. Sample size indicated for each group.

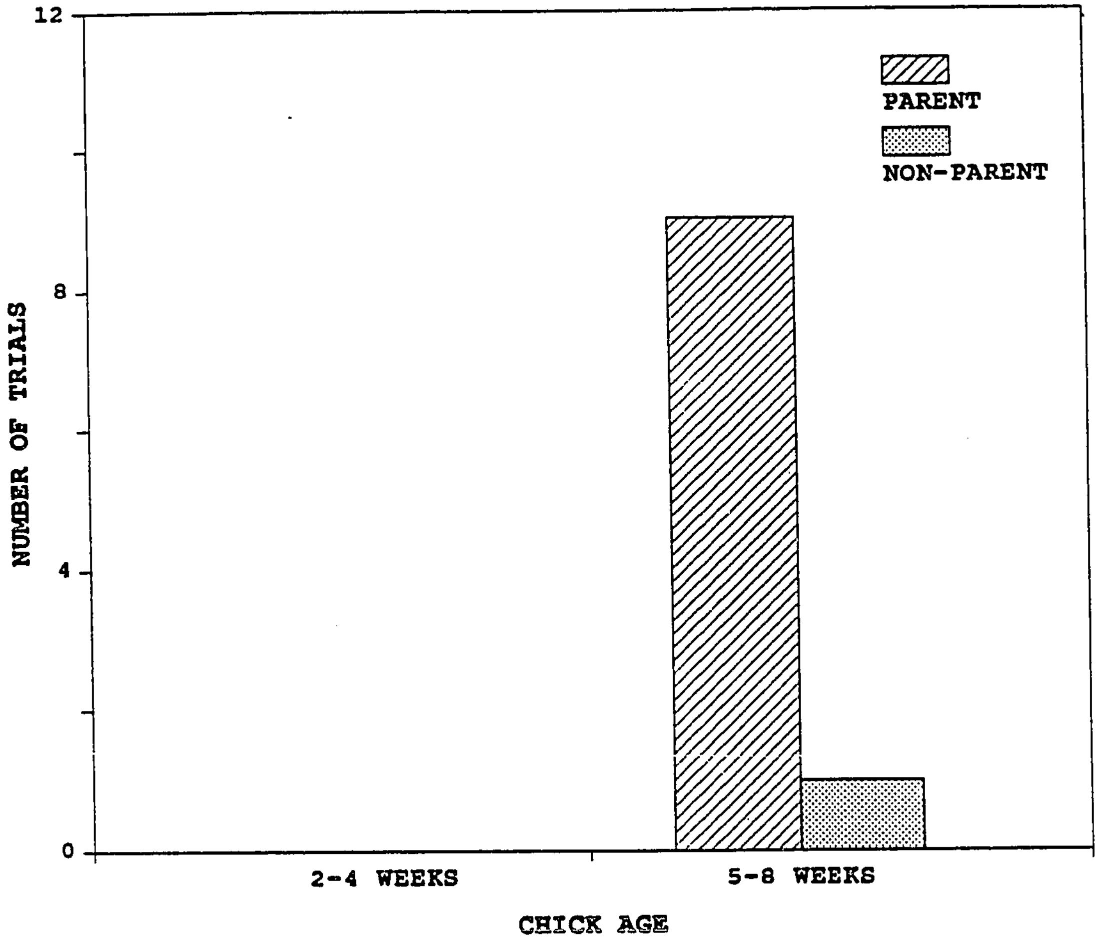

Figure 16. Number of trials during which begging was heard at parent or non-parent speaker by 2-4 week-old and 5-8 week-old chicks.

DISCUSSION

Mate Recognition

Increases in heart rates of Little Penguins were consistently different following mate and non-mate playback calls indicating that heart rate may be a useful index of recognition and the vocal recognition occurred between mates.

Heart rate has not been widely used as an indication of behavioral response to playback calls because environmental and physiological factors can cause variation in heart rate that cannot be controlled in field research situations. However, many environmental and behavioral factors were constant in this study because incubating birds remained inside their burrows; visual stimuli were minimal inside the burrow, and sounds of the colony audible to incubating birds were random with respect to call type. Thus it is unlikely that heart rates were affected by stimuli other than the playback calls.

Waas (1988) demonstrated that calling was socially facilitated in Little Penguins. Thus, neighboring birds may have increased their calls in reaction to the playback call, and subsequently intensified the reaction of the test bird. This effect also would be random with respect to call type, unless mate calls were recognized by neighbors. The unlikely bias introduced by neighbor recognition, however, would only be a problem if recognition were limited to neighbors and did not occur between mates.

Culik et al. (1989) found that heart rate in Adélie Penguins was not correlated with temperature, cloud cover, humidity, estimated solar radiation, or time of day but it increased with wind speed. For a Little Penguin inside a burrow, wind speed should not have been an important factor. Heart rate of Adélie Penguins also increased when birds preened and rearranged eggs, or when they were disturbed by congeners or researchers. This was expected because heart rate is correlated with energy expenditure in birds (Owens 1969, Ferns et al. 1980, Gessamen 1980). Little Penguin heart rates increased when birds shifted on the nest, but quickly returned to resting levels when activity stopped. Movements were clearly audible through the HRM, so any trials that were potentially affected by a shifting bird were omitted from analysis. Thus, in a playback experiment, changes in heart rate can result from factors other than the playback call. However, in circumstances where these factors can be minimized and monitored, heart rate is a useful measure of response.

Davis (1986) concluded that mate recognition occurs in Belted Kingfishers on the basis of a significantly different cardiac response following mate versus non-mate playback calls. Discrimination of conspecific songs by Swamp Sparrow (Melospiza georgiana) chicks was demonstrated on the same basis (Dooling and Searcy 1980). In contrast to the cardiac changes observed in Little Penguins, heart rates in these studies decreased immediately following playback calls. This was probably because non-aggressive calls were used in both studies. Heart rate may drop in response to a novel stimulus (McFarland 1987), but it will increase during aggressive encounters (Kanwisher et al. 1978). In the context of one experiment, discrimination will manifest in the magnitude of the response rather than in the direction of change in HR.

In some cases, heart rate may be a better measure of response to a stimulus than overt behaviors. Kanwisher et al. (1978) reported that cardiac acceleration preceded overt visual communication in Herring Gulls (Larus argentatus) threatened by conspecifics or approached by humans. In some cases, it may be advantageous for individuals to conceal or delay overt reactions to stimuli (Krebs and Dawkins 1984). Changes in alertness, aggressive intent, or fear that are not manifest in overt behaviors are potentially discernable using changes in heart rate. Further studies are needed to correlate changes in heart rate with overt behaviors in the same species.

Given the cooperative nature of the relationship between members of a mated pair, should heart rates have remained stable instead of elevating following mate calls? There are several possible reasons why heart rate would increase even when calls were recognized. An aggressive call from a mate outside the burrow entrance could be interpreted as a direct threat to the incubating mate, or as aggression directed towards a third party. The situation also may be threatening simply because mates do not normally call aggressively before entering the burrow. In addition, aggressive interactions between Little Penguins are characterized by an escalation process (Waas 1990). The aggressive calls used in playback trials may have been typical of an aggressive encounter that has already started to escalate, which would seem out of context in the playback situation.

Observations have indicated that vocal recognition occurs in Rockhopper Penguins (Warham 1963), Jackass Penguins (Eggleton and Siegfried 1979), and Yellow-eyed Penguins (Richdale 1946). Vocal recognition was confirmed with playback experiments in Emperor Penguins (Derenne et al. 1979), King Penguins (Jouventin et al. 1979), and Adélie Penguins (Speirs 1988). Although visual cues may contribute to recognition in several diurnal penguin species, recognition is primarily vocal (Jouventin 1982). Playback experiments also have indicated that mate recognition occurs in three other nocturnal, burrow-nesting seabirds: the White-chinned Petrel (Procellaria aequinoctalis; Brooke 1986), the Grey Petrel (Puffinus cinerea; Brooke 1986), and the Manx Shearwater (Puffinus puffinus; Brooke 1978). The ability of Little Penguins to recognize their mate's call is not surprising given vocal recognition between mates is common among penguins, and occurs in other seabirds with similar behavior patterns.

Chick Recognition Of Parent Calls

Recognition between parents and young generally develops when and where location of the nest is not adequate to insure family integrity. In these situations, parental care may be directed to the wrong offspring (Falls 1982, Jones et al. 1987). This may occur in species that breed in high density colonies, those that do not build nests, or those in which chicks gather in crêches. Recognition generally appears at the onset of brood mobility, when chicks first encounter other individuals that could be confused with their parents.

In breeding aggregations of Common Murres, a non-nest building species, young learn parental calls in the egg (Tschanz 1968). Adults gather in dense groups to breed where the chance of chicks encountering other adults at a very young age is high. Black-billed Gull (Larus bulleri) chicks which begin wandering from the nest in the first few days after hatching, learn their parents' calls by 4-days-old (Evans 1970). Ancient Murrelets (Synthliboramphus antiquum) depart the burrow as a family group several days after hatching, and remain at sea until chicks are fledged. Recognition in this species is clearly essential for chick survival. In playback studies, chicks several days old preferentially approached a speaker playing their parents' calls (Jones et al. 1987). Conversely, in a non-colonial species such as the Yellow-eyed Penguin, where chicks are unlikely to encounter many other adults when they leave the nest site, chicks do not recognize parental calls (Nordin 1988).

Results of playback experiments in this study demonstrated that Little Penguin chicks recognized their parents' mutual displays after the age that chicks began to wander from the burrow. Although Little Penguins nest in loose colonies, chicks may frequently encounter other adults when wandering outside the burrow. Chicks also gather in small crêches along pathways or in a burrow.

Coloniality does not always imply intermingling of young and subsequent confusion of parents with other adults. Northern Gannet (Sula bassana) chicks lack recognition capabilities despite coloniality because young do not leave the nest (White 1971). Manx Shearwater and White-chinned Petrel chicks are fed in burrows until abandoned, and both lack recognition of parent's calls at any age (Brooke 1978, 1986). Similarly, in Black-legged Kittiwakes (Rissa tridactyla), which nest on steep cliff ledges, recognition between parents and chicks does not develop (Wooller 1978). Location of the nest by adults is sufficient to insure that the correct chicks are fed because chicks cannot wander outside the nest.

It is clearly advantageous for parents to feed only their own chicks, but why is it an advantage for chicks to recognize their parents? Beecher et al. (1985) suggested that once parents can discriminate their young, they also discriminate among other young. Chicks that beg from adults other than their parents are likely to elicit an aggressive response. Older penguins in this study begged significantly more during parent calls than during non-parent calls. This was also true for Adélie Penguin chicks (Thompson 1974). Additionally, in some breeding situations, mutual recognition may be necessary for parents and offspring to consistently find one another. This appears to be the case in Adélie Penguins (Penney 1968, Thompson 1974), Emperor Penguins (Jouventin 1982), and Snares Crested Penguins (Proffitt and McLean 1990). Finally, my own observations on Phillip Island indicated that as Little Penguin chicks become older and more persistent and aggressive in begging, parents attempt to avoid them. It may be advantageous for chicks to recognize parents in an attempt to maximize parental investment (Trivers 1974).

Sonagram Analysis

Coefficients of variation for Little Penguin calls indicated individual calls were not highly stereotyped. Inter-individual variation of Little Penguin calls was approximately 2-3 times greater than intra-individual variation, whereas inter-individual variation of Emperor Penguin calls is 12 times intra-individual variation (Jouventin et al. 1979). There are several possible explanations for such a low degree of stereotypy in Little Penguin calls.

Breeding biology and environment ultimately dictate the degree of complexity needed for individual recognition (Jouventin and Roux 1979). During the breeding season, Emperor Penguins huddle together in groups of several hundred birds. There are no nest sites, and individuals are constantly shifting position within the huddle. Birds returning from foraging bouts at sea must find their mates among hundreds of individuals. Without highly stereotyped calls, this would be difficult. Little Penguins, however, nest in loose colonies and return to the same burrow. This reduces the number of birds from which an individual must discriminate its mate. A smaller degree of stereotypy may be adequate for the Little Penguin.

Secondly, the Little Penguin display call is a graded signal, used in a variety of situations from sexual advertisement to territory defense. Frequency and time characteristics of the call vary with context (Warham 1958, Waas 1990, pers. obs.). In contrast, temporal characteristics of the Emperor Penguin call are almost invariant (Jouventin 1982). Presumably, the need for a sophisticated recognition system imposed limits on the variation in signal characteristics. The opposite could be true for Little Penguins; nocturnal habits may have resulted in a more complex vocal communication system. This imposes limits on parameters that can be held constant and, thus, on call stereotypy as well. Grading in the Little Penguin call appears to occur both in temporal and frequency parameters (Waas 1990), and may limit the opportunity for call stereotypy.

A third possibility is that some parameter not measured in this study may be important in call stereotypy. Individual distinctiveness in call structure has been found in a variety of parameters from temporal patterning in Least Terns (Sterna albifrons; Moseley 1979) and Black-legged Kittiwakes (Wooller 1978) to consistent temporal changes in amplitude in the Northern Gannet (White and White 1970, White et al. 1970). The range of possible cues for recognition was greater than those measured in this study.

Comparison of coefficients of variation for parameters of Little Penguin calls revealed which parts of a call may carry most of the individually recognizable cues. The C.V. for the duration of 5 syllables was the most stable parameter within individuals, suggesting that stereotypy of individual calls was encoded in the temporal patterning of the calls, rather than in any frequency measure. Jouventin's (1982) assertion that individual penguin calls were characterized by syllable length was supported by results of this study.

Among penguins, stereotypy of call structure has been demonstrated in Emperor Penguins (Jouventin 1972, Jouventin et al. 1979), Adélie Penguins (Jouventin and Roux 1979) and King Penguins (Derenne et al. 1979), and was encoded in temporal patterns in all three species. Inter-individual call variation of Adélie Penguins, however, is only approximately 2 times intra-individual variation (Jouventin and Roux 1979), suggesting that Adélie Penguin calls are even less stereotyped than Little Penguin calls. This was attributed to the importance of the permanent nest site in facilitating recognition. This also may be a factor for Little Penguins.

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