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Measuring the Daily Energy Expenditure of Free-living Arctic Terns (*Sterna paradisaea*)

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Measurement of the energy expenditure of free-living birds plays an important role in many kinds of ecological and behavioral studies. For example, the concept of reproductive effort has become central to the study of the limits to reproductive output and, in particular, to whether and how effort can affect survival, future breeding attempts, and thereby lifetime reproductive success (e.g. Charnov and Krebs 1974, Drent and Daan 1980, Nur 1984, Winkler and Wilkinson 1988). Although it is doubtful that energetic considerations alone will ever adequately describe parental effort and its consequent costs (Ricklefs and Williams 1984, Bryant 1988), estimates of the energy expenditure of breeding birds have provided valuable insights into parental effort (e.g. Bryant and Westerterp 1983, Reyer and Westerterp 1985, Bryant 1988, Bryant and Tatner 1989). In addition, ecological energetics models, such as those that attempt to assess the amounts of prey that seabirds consume, rely among other things on estimates of energy expenditure that are representative of free-ranging individuals (e.g. Furness 1982, Wiens 1984). Field measurement of energy expenditure using the doubly-labelled-water (DLW) method (Lifson and McClintock 1966, Nagy 1980) has been extensively applied to free-living birds (e.g. Hails and Bryant 1979, Ricklefs and Williams 1984, Bryant and Tatner 1988, Birt-Friesen et al. 1989). It is a physiologically robust measure of energy expenditure (Nagy 1980, Tatner and Bryant 1988), but for the results to be meaningful in an ecological or behavioral context, it is imperative that the behavior of the subject birds is not significantly disrupted by the technique, which involves disturbing operations such as capture, injection, and blood sampling. If the behavior of birds subject to the technique is not representative of undisturbed birds, the resulting measures of energy expenditure will be far less useful than otherwise, and could be seriously misleading.

We report on the results of a pilot study of the feasibility of studying the free-ranging energetics of

Arctic Terns (*Sterna paradisaea*) using the DLW method. In particular, we examine the impact of the technique on the behavior of birds at different locations and at different stages of the breeding cycle.

Methods.—The field metabolic rate (FMR; kJ day^{-1}) of Arctic Terns was measured in 1988 at three sites and during two stages of the breeding season. Measurements were attempted on four adults feeding chicks in the first week of life in Shetland ($60^{\circ}0'N$, $1^{\circ}10'W$; 27–29 June 1988), where Arctic Terns were known to be experiencing food shortage (Monaghan et al. 1989, Uttley et al. 1989), and on nine adults on Coquet Island, Northumberland ($55^{\circ}20'N$, $1^{\circ}32'W$; 20–21 June 1988), where food supply was adequate for young to be reared successfully (Monaghan et al. 1989, unpubl. data). Later in the season, measurements were made on four adults feeding chicks close to fledging in Orkney ($59^{\circ}22'N$, $2^{\circ}25'W$; 9–12 July 1988), another site where food appeared sufficient for successful breeding by terns (Uttley 1991).

Arctic Terns were trapped while feeding chicks using drop-in traps fitted with a lid that could be closed by an observer located in a nearby blind. The traps were constructed out of 13-mm wire mesh and placed around the nests during incubation, without the lids on, to accustom the adult birds to them. The traps caused very little disturbance, being essentially similar to enclosures put up around nests to prevent chicks from wandering (Nisbet and Drury 1972, Monaghan et al. 1989).

Captured birds were fitted with a numbered metal band and their wing lengths, head plus bill lengths, and mass were recorded. After processing for DLW, each bird was given a temporary, individual mark on the head using white typewriter correction fluid marked with a permanent, colored marker pen before release. Where no initial blood sample was taken, birds were processed and released in less than 5 min.

Once the birds had been processed a previously calculated dose of $D_2^{18}O$ from a 1-ml sterile syringe was injected intraperitoneally (under licence from the British Home Office) into each one. The dose was derived from predicted fractional turnover rates of oxygen (K_o) equal to 0.04995 and hydrogen/deuterium (K_D) equal to 0.03815 for a 120-g bird; these were

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calculated from the relationships between fractional turnover rates and body mass in breeding birds (Tatner and Bryant 1988: equations 8 and 9). The dose used was 0.9 ml of DLW (14.5 atom% ^{18}O and 5.04 atom% deuterium [D]) using equations 12 and 13 from Tatner and Bryant (1988). The time of injection was noted together with details of capture time, biometrics and individual color mark.

The first five birds caught on Coquet Island were held for 1 h in a cloth bag to allow the injectate to equilibrate with body water before the initial blood sample was taken from the femoral vein. Blood was collected in graduated 10- μl pipettes (Vitrex), which were then sealed by drawing off the ends under a flame from a butane gas torch (Tatner and Bryant 1988). Up to 10 tubes were collected from each bird. After initially sampling the first four birds, we became concerned that holding the birds captive for 1 h was affecting their subsequent behavior. The remaining birds, therefore, were released immediately after injection, without an initial blood sample being taken. A mean initial concentration was calculated from those birds that were held, and applied to the rest of the subjects. This latter method was also used in Shetland and Orkney, and had previously been used by Ricklefs et al. (1986). Two of nine adults captured on Coquet Island were members of the same pair, and they deserted their young. Subsequently, only one bird from each nest was captured, and no further desertions occurred.

Approximately 24 or 48 h after the initial injection, the experimental birds were recaptured and a second blood sample taken in a similar manner to the first. In the case of one individual on Shetland (AT10), a second sample was obtained after 24 h and a third after 48 h.

In addition to the experimental birds that were injected and then released, with or without an initial blood sample, five birds (one on Coquet, two on Shetland, and two on Orkney) were captured and their blood sampled at the same time as the experimental birds, but without injection, in order that natural abundance levels of ^{18}O and D could be determined. These birds were released immediately after sampling.

The nests of labelled adults were kept under continuous observation for all of the daylight hours from hides, and full time-budget information was collected for each experimental bird and its mate, except for one nest on Coquet Island (AT5), which was away from the main colony and could not be seen clearly. The data recorded were the number of feeds brought to the chicks by each bird and the total time spent by each bird in its territory. At the same time comparable data were collected from nonexperimental birds from within the colony as part of a wider study of Arctic Tern breeding biology (Uttley et al. 1989, Uttley 1991, 1992).

Analyses of the blood samples to determine ^{18}O /

^{16}O and D/H ratios were carried out at the Scottish Universities Research Reactor Centre, East Kilbride, using the techniques described by Tatner and Bryant (1988). The concentrations of the heavy isotopes (i.e. ^{18}O and D) were then determined by isotope ratio mass spectrometry (IRMS) on a VG-ISOGAS SIRA-10 (^{18}O) or a VG-ISOGAS SIRA-9 (D).

For FMR, CO_2 production was calculated using equation 4 of Ricklefs and Williams (1984), which allowed those initial samples that were collected to be used in the calculation of CO_2 production for birds from which an initial sample had not been taken. A comparison of the average daily metabolic rates (ADMR) obtained by this method with ADMRs obtained using the equation of Lifson and McClintock (1966) showed a mean difference of less than 2% in the estimated ADMR for the two birds with complete measurements of initial and final ^{18}O and D concentrations. The time period over which CO_2 production was measured was taken to be from the time of the last initial blood sample (where this was taken) to the time of the last recapture blood sample. For birds that were released without an initial blood sample, it was estimated as the interval between the time of injection and the time of the last recapture blood sample minus 1 h. The average fraction of body mass consisting of water (WF) was calculated from the ^{18}O dilution space (Nagy and Costa 1980). FMR was calculated from CO_2 production assuming an energy equivalent of 0.0247 kJ/ml CO_2 (Flint and Nagy 1984), and body mass was taken as the mean of mass measurements taken at the beginning and end of the measurement period.

Results.—Of the 18 birds labelled, three refused to enter the traps a second time and were not recaptured. In addition, a pair deserted on Coquet, and two birds on Orkney were not recaptured because the chick fledged in one case, while another died and its parents ceased to attend the nest. Eleven birds were successfully recaptured, but only eight of these yielded estimates of energy expenditures as three results (AT10, AT14 and AT15) were lost during the course of analysis.

The natural abundances of ^{18}O and D were calculated using data from two birds for ^{16}O and three birds for D. The mean levels were 1,996.2 ppm ^{18}O (individual measurements 1,989.3 and 2,003.2) and 151.2 ppm D (individual measurements 150.5, 150.4 and 152.7), both of which fall well within the range of natural levels found in a variety of temperate bird species (Tatner 1990).

The mean water fraction of four terns from which an initial blood sample had been taken and successfully analyzed for ^{18}O enrichment was $0.63 \pm \text{SD}$ of 0.08. This accords with a mean of 0.63 reported by Tatner and Bryant (1988) for seven species investigated by carcass analysis and is similar to 0.599 ($N = 2$) determined by Ricklefs and White (1981) for the closely related Common Tern (*S. hirundo*), again using carcass analysis.

TABLE 1. Mass, measurement period and energy expenditure of Arctic Terns subjected to doubly-labelled-water technique.

| Bird no. | Date in 1988 | Mean mass (g) | Time period (h) | ADMR (cm ³ CO ₂ g ⁻¹ h ⁻¹) | FMR (kJ day ⁻¹) | Notes |
|-----------------|--------------|--------------------|-----------------|-------------------------------------------------------------------------|-----------------------------|-----------------|
| Coquet | | | | | | |
| AT1 | 19 June | 96.5 | 47.7 | 3.62 | 207.08 | |
| AT2 | 19 June | 111.0 | 47.4 | 4.18 | 275.05 | |
| AT3 | 19 June | 92.0 ^a | — | — | — | Deserted |
| AT4 | 19 June | 120.0 ^a | — | — | — | Deserted |
| AT5 | 20 June | 94.5 | 25.7 | 4.91 | 275.06 | |
| AT6 | 20 June | 97.0 | 22.1 | 4.04 | 232.31 | |
| AT7 | 20 June | 106.0 ^a | — | — | — | Not retrapped |
| AT8 | 20 June | 105.0 | 23.2 | 6.18 | 384.67 | |
| AT9 | 20 June | 107.5 | 24.4 | 4.75 | 302.70 | |
| Shetland | | | | | | |
| AT10 | 27 June | 98.5 | 24.4 | — | — | Failed analysis |
| AT11 | 27 June | 98.0 | 24.3 | 7.43 | 431.64 | |
| AT12 | 27 June | 94.0 ^a | — | — | — | Chick died |
| AT13 | 27 June | 93.0 ^a | — | — | — | Not retrapped |
| Orkney | | | | | | |
| AT14 | 9 July | 104.0 | 47.8 | — | — | Failed analysis |
| AT15 | 9 July | 101.5 | 46.8 | — | — | Failed analysis |
| AT16 | 10 July | 99.5 | 48.3 | 9.64 | 568.45 | |
| AT17 | 10 July | 105.0 ^a | — | — | — | Chick died |
| AT18 | 10 July | 100.0 ^a | — | — | — | Chick fledged |

^a Initial mass measurements of birds not recaptured.

The initial ratio of excess ¹⁸O to excess D required to calculate carbon-dioxide production was determined using data from three birds for which initial enrichments of both isotopes were determined. The mean of the log_e-transformed values (input to equation 4 of Ricklefs and Williams 1984) was 1.12808 ± SE of 0.01516. Despite the small sample of birds available, the method appeared satisfactory since the coefficient of variation was small (1.2%). This initial isotope ratio figure was used in the calculations of FMR for the remaining birds where it could not be established directly due to the lack of initial blood samples.

The fractional turnover rate of oxygen (K_o) could be calculated for three birds and averaged 0.08062 ± SE of 0.01167. The fractional turnover rate of hydrogen (K_D) was estimated from three birds, averaging 0.06375 ± 0.00231. These values were 61% and 60%, respectively, higher than those predicted when calculating the injected dose of D₂¹⁸O. The similarity of the underestimates of hydrogen and oxygen turnover indicates that water turnover rates were higher than predicted, while CO₂ production was as expected. As a result of the higher than expected water turnover rates, the final levels of ¹⁸O and D came close to background abundance. In three terns (AT10, AT14, AT15) the final concentrations were too small for their energy expenditure to be reliably estimated. Analytical errors have a greater effect upon calculated CO₂ production as final isotope levels approach natural abundance (Nagy 1980).

The calculated FMRs for each bird are shown in Table 1. Treating the Coquet Island birds as a discrete subsample, they had a mean FMR of 279.5 ± SD of 61.8 kJ day⁻¹ (CV = 22.1%, $n = 6$). The Shetland bird, at the same stage of breeding, had a higher FMR of 431.6 kJ day⁻¹, while that of the Orkney bird feeding a 17-day-old chick was still higher at 568.45 kJ day⁻¹. Using a figure for BMR (active phase) of Arctic Terns of 77 kJ day⁻¹ (M. Klaassen, Univ. Groningen, pers. comm.), the Coquet birds were working at 3.63 ± SD of 0.80 BMR ($n = 6$), with the Shetland and Orkney birds working at 5.61 and 7.38 BMR, respectively.

Figures 1A and 2A show the territorial attendance and chick-feeding frequencies of the experimental birds in comparison with those of control (uncaptured) birds from other nests at a similar stage of the breeding season in each colony. Figures 1B and 2B provide the same data for experimental birds and their mates combined. The small sample sizes meant that statistical analysis could only be conducted on the attendance (Fig. 1B) and the chick-feeding frequency (Fig. 2B) of Coquet birds. Chicks at nests on Coquet, where DLW measurements of energy expenditure were conducted, were attended significantly less than the controls (Fig. 1B; Mann-Whitney test, $z = 2.40$, $P < 0.05$). However, there was no statistically significant difference in the rate chicks were fed (Fig. 2B). Examination of Figure 2A suggests that DLW birds on Coquet may have fed their young less than the controls. Thus, their mates may have increased

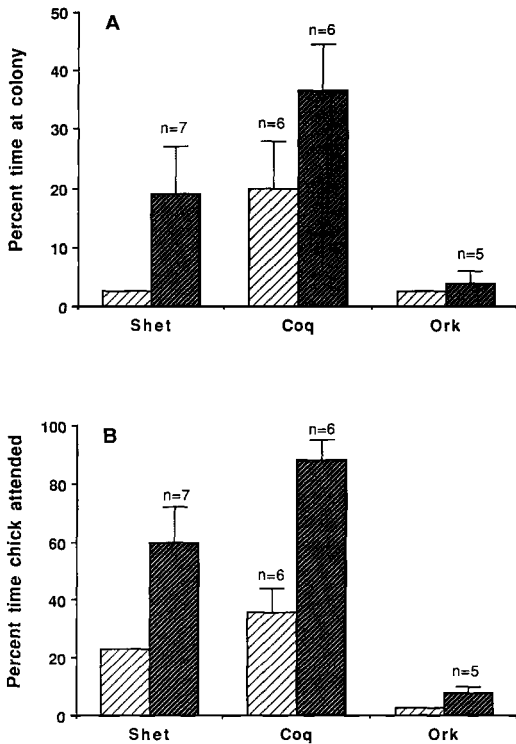


Fig. 1. (A) Proportion of time spent at colony by labelled birds in period between release and recapture (light hatching) and control birds from undisturbed nests (dark hatching). (B) Total time chicks attended by either parent for labelled birds (light hatching) during period between release of injected bird and its recapture and control birds (dark hatching). Error bars show 1 SE for control groups and labelled birds from Coquet Island.

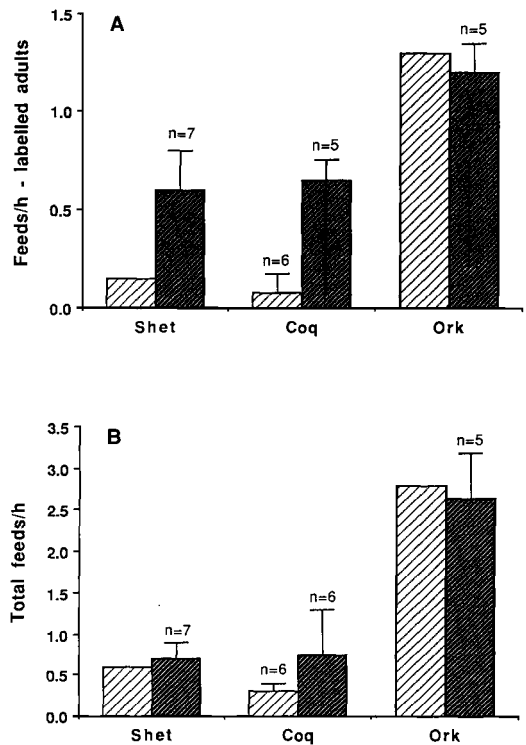


Fig. 2. (A) Number of feeds per hour given to chicks by labelled birds in period between release and recapture (light hatching), and control birds from undisturbed nests (dark hatching). (B) Number of feeds per hour given to chicks of labelled birds (light hatching) by either parent during period between release of labelled bird and its recapture and control birds (dark hatching). Error bars show 1 SE for control groups and injected birds from Coquet Island.

their feeding rates at the expense of spending less time with the young, leading to the reduced levels of attendance. There is some suggestion of a similar effect for DLW birds in Shetland (Figs. 1A and 2A), but the sample of birds is too small to establish statistical significance. Birds subjected to the DLW technique on Orkney, which had older chicks and were breeding in conditions of good food supply, did not appear to suffer such an effect.

The relationships between the birds' behavior and their energy expenditure were examined within the sample of birds from Coquet and for all birds combined. There were no significant statistical associations between parental energy expenditure and either the percentage of time spent away from the colony, or the number of feeds given to the chick per day (Fig. 3). Therefore, it was not possible to estimate either metabolism at the nest or away from it on the basis of incremental energy expenditure with time or

the metabolic cost of feeding young through incremental energy expenditure with feeding events.

Discussion.—The predictions of ^{18}O and D turnover rates made from equations 8 and 9 in Tatner and Bryant (1988) were incorrect because the water turnover rates were higher than expected. In our study, water turnover could be measured for three birds, and averaged 1.53 turnovers day^{-1} , 58% higher than the predicted value of 0.970 calculated from equation 9 (Tatner and Bryant 1988). Ricklefs et al. (1986) measured the water turnover rate of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) to be 1.01 day^{-1} , 18% lower than that predicted by Tatner and Bryant (1988). This raises the question as to whether water turnover rates may differ for different groups of birds. If so, there will be consequences for the calculation of dose rates in DLW studies.

Arctic Terns feeding young appear to have very

little flexibility in their time budgets when feeding young. This is especially so when they are brooding chicks (Pearson 1968, Uttley 1992). They might be expected to be working extremely hard and expending large amounts of energy at this time. This is supported by evidence from studies of adult mass change showing that mass loss is rapid at this time (Monaghan et al. 1992). The data on energy expenditure in our study are based on small samples of birds and, therefore, must be treated with caution. The level of energy expenditure of birds on Coquet Island feeding young chicks (3.63 BMR) is indeed close to that proposed by Drent and Daan (1980) as the "maximum sustainable work level" (MSR) in birds, but it is by no means exceptionally high. Among higher measurements of daily energy expenditures for seabirds are those for Brown Noddies (*Anous stolidus*; 5.2 BMR, stage of lifecycle not stated), Wedge-tailed Shearwaters (*Puffinus pacificus*; 4.8 BMR, stage of life cycle not stated; Ellis 1984), and Northern Gannets (*Sula bassanus*; 6.6 BMR, breeding, but stage of breeding season not stated; Birt-Friesen et al. 1989). Furthermore, two birds from our study whose FMRs were measured under different conditions had considerably higher rates of energy expenditure. One individual (AT11) feeding young chicks in Shetland, where food was in short supply, had an FMR 54.4% higher than the mean FMR on Coquet of birds at the same stage of breeding and 42.6% higher than the highest recorded FMR on Coquet Island, where food was adequate (Monaghan et al. 1989). For AT16, feeding a nearly fledged chick on Orkney where no food shortages were apparent (Uttley 1991), the equivalent figures were 103% and 87.8%. These figures highlight the apparent limitations of Drent and Daan's (1980) theoretical MSR of 4 BMR.

FMR also was estimated using the equation derived for nongliding seabirds in high latitudes in Birt-Friesen et al. (1989). For Coquet Island birds, it gave a mean predicted FMR of $328.5 \pm 16.3 \text{ kJ day}^{-1}$ of which the DLW measured value (279.5) was only 85.1%. However, the DLW determined FMRs of the Shetland and Orkney birds were 32 and 75% higher, respectively, than the predicted levels.

The results, although based on small samples, support intuitive ideas that energy expenditure during chick rearing will differ according to the energy demands of the young and the availability of food to the foraging adults.

In addition to the ecological conclusions that may be drawn from this data, there are implications for the methodology itself. A central assumption of the DLW technique is that the results obtained are representative of normal energy consumption. Validation studies that have been undertaken for a wide range of animals show that the technique gives results comparable to those produced by volumetric methods, but most of these studies were performed on captive animals in the resting phase, when ADMR is

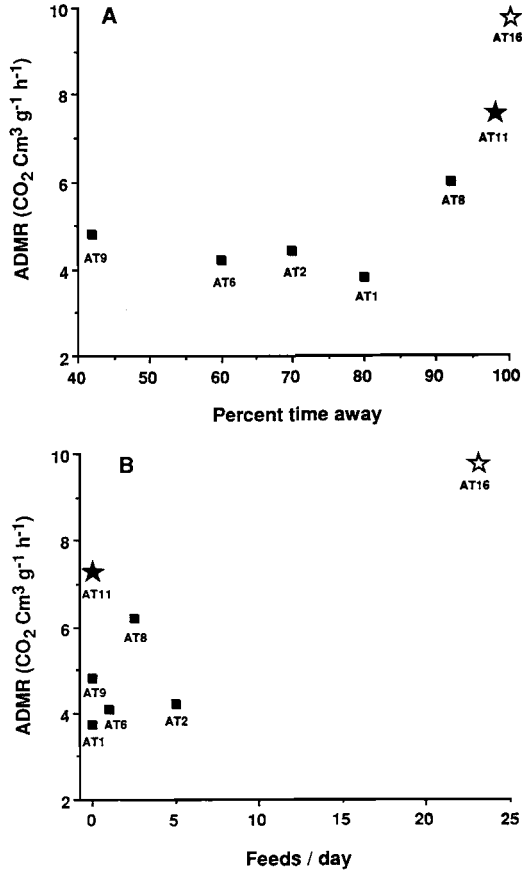


Fig. 3. Relationship between average daily metabolic rate of labelled birds to (A) amount of time spent away from colony, and (B) number of times they fed chicks. Squares = Coquet; solid stars = Shetland; open stars = Orkney.

several times lower than during the active phase (Tatner and Bryant 1988). Thus, these studies do not assess the possibility of changes induced in behavior by the technique and only show that captive animals do not incur any energetic stress due to the technique above those resulting from captivity.

Our study suggests that the behavior of Arctic Terns is altered by the technique. DLW birds feeding young chicks on Coquet and Shetland (although not significant at the latter) attended and fed them less than control birds. The disruptive effect appeared to be less marked with birds feeding older chicks on Orkney. The lack of a relationship between time away from the colony and ADMR suggests that much of the time away from the colony (by birds that were absent for a high proportion of the time) was spent in low-cost activities (i.e. not in flight or foraging), and that birds did not incur energetic costs above those that they would have incurred at the nest. We do not know whether it was the capture or blood

sampling or injection that disturbed the birds most. However, since all of these procedures are necessary for the use of the DLW method, it is not necessary to discriminate at this level. The effect of the method on behavior may vary with many factors, such as age and experience of the breeding birds, environmental conditions, and stage of the breeding season. Therefore, it is essential that, if DLW measured estimates of FMR are to be used as measures of daily energy expenditure (rather than as measures of cost of certain activities), the behavior of experimental birds be compared to control individuals not subjected to the procedure. However, although the majority of DLW studies report no adverse effects on the behavior of the subjects, this is often not done. Of the 13 DLW studies used by Birt-Friesen et al. (1989) to generate predictive equations for seabird metabolism, only one (their own) compared the behavior of DLW and control birds, while 10 made no mention of any such comparisons. One study of storm-petrels suggested that there were some adverse effects on the birds (Ricklefs et al. 1986), and Birt-Friesen et al. (1989) found that Northern Gannets subjected to the DLW method attended their nests less than control birds (not tested statistically). They concluded that this had little effect on measured FMR, since the birds appeared to spend more time sitting on the water and resting, in place of time spent at the nest; these two activities were of similar energetic cost. Several studies of energy expenditure of birds of other groups have incorporated comparisons with control birds. For example Ricklefs and Williams (1984) showed that there appeared to be no effect on nestling growth in European Starlings (*Sturnus vulgaris*) between experimental and undisturbed nests. Admittedly, it is very difficult to monitor the behavior of most seabirds, which spend long periods at sea, and many of these studies measured FMR while at sea. However, the increasing availability of ever-smaller telemetry devices for monitoring behavior of seabirds (e.g. see Cairns et al. 1987) should enable such measurements to be incorporated into future DLW studies, as has already been undertaken with Common Terns (P. Becker pers. comm.) and Northern Gannets (Birt-Friesen et al. 1989).

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Parental Recognition of Juvenile Begging Calls in the Florida Scrub Jay

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Previous research on parent-offspring recognition in birds suggests that acoustic recognition systems should be common in colonial species where unrelated young intermingle freely at early ages. Because the inability to recognize young in dense breeding colonies could result in parents neglecting their own offspring and caring for unrelated juveniles, natural selection would be expected to favor vocal recognition of offspring in colonial species (Davies and Carrick 1961, Beer 1970, Evans 1970, Buckley and Buckley 1972, Beecher 1981, Falls 1982, Colgan 1983).

The relationship between coloniality and vocal recognition of offspring has been explored most thoroughly in swallows. In two colonial species, the Bank

Swallow (*Riparia riparia*) and Cliff Swallow (*Hirundo pyrrhonota*), offspring leave the nest at around 18 days of age and form creches that contain many nutritionally dependent fledglings (Beecher 1981, Stoddard and Beecher 1983). Young develop individually distinctive "signature" calls prior to fledging, and parents learn to discriminate between the calls of their own young and those of other young (Burt 1977, Beecher et al. 1981, Stoddard and Beecher 1983, Loesche et al. 1991). However, in two species of non-colonial swallows, the Barn Swallow (*H. rustica*) and Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), dependent young seldom intermingle with those from other broods, nestlings do not develop distinctive signature vocalizations, and vocal recognition of offspring is apparently absent (Medvin and Beecher 1986, Beecher 1990, Medvin et al. 1992, 1993).

The four species of swallows studied by Beecher and colleagues provided an excellent opportunity to

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