THE EFFECT OF RADIO TRANSMITTERS ON THE BEHAVIOR OF COMMON MURRES AND RAZORBILLS DURING CHICK REARING¹

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Abstract. We compared site attendance, length and number of absences from the colony, and prey delivered to the young of control Common Murres (*Uria aalge*) and others which carried radio transmitters that had either an external or internal aerial during chick rearing. Birds with the internal aerial behaved similarly to control birds. However, birds with the external aerial spent less time in the colony, were absent for long continuous periods, and often returned without a fish for the chick. This did not reduce fledging success because their mates compensated by increasing the food brought in. Fewer observations were made on Razorbills (*Alca torda*) with external aerial transmitters, but they indicated no profound effect on behavior.

Key words: Common Murre; Razorbill; attendance behavior; prey delivery; device-related disturbance.

INTRODUCTION

Biologists have seldom observed the foraging of seabirds directly. The need for such data is becoming increasingly important with the growing concern over the conflict between expanding human fisheries and seabird numbers (e.g., Furness 1984). Information on how far a bird forages from the colony during the breeding season has usually been inferred from the time it was away from the breeding site before it returned to feed its chick (Pearson 1968) or from the distribution of birds at sea (e.g., Nettleship and Gaston 1978, Schneider and Hunt 1982, Blake et al. 1984, Tasker et al. 1987). Radiotelemetry provides a more direct approach. Although this technique has been widely used with terrestrial birds (e.g., Lance 1978, Kenwood 1980, Marquiss and Newton 1982), only recently has the development of light, waterproof, powerful transmitters stimulated studies in a wide range of seabirds (e.g., Harrison and Stoneburner 1981: Trivelpiece et al. 1986: Anderson and Ricklefs 1987; Wanless et al., in press).

Telemetry has allowed workers to collect data which were previously unobtainable, but the results are of value only if it can be established that radio-tagged animals behave normally. The fact that such data can often be collected only by using telemetry makes this validation almost impossible, because comparable information is hard to collect from control animals. However, this does not absolve the basic need of any research project to ensure that the technique gives unbiased results (Lance and Watson 1977). Where the effects of radio transmitters on their bearers have been critically evaluated, the response has varied from no detectable effect to a marked reduction in reproductive performance. Furthermore, it has varied not only between species but also within a species according to age, sex, the time of attachment in relation to the breeding cycle, the weight of the transmitter, and its method of attachment (e.g., Boag 1972, Ball et al. 1975, Lance and Watson 1977, Leuze 1980. Sibly and McCleery 1980, Smith 1980, Clark et al. 1987). Early in our study we found that Common Murres (Uria aalge) sometimes deserted after being fitted with radios during incubation, but that minimizing handling time during the attachment of the radio reduced the likelihood of desertion (Wanless et al. 1985). Since then we have attempted to minimize adverse effects by (a) using transmitters mainly during the chickrearing period, (b) minimizing handling time, and (c) minimizing transmitter weight. In this paper we present data on the attendance behavior,

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length of fishing trips and prey delivery of Common Murres carrying two types of transmitter, and make comparisons with untagged control birds. Our aim was to indicate when results obtained by current radiotelemetry techniques should be treated with caution. We also report on some less complete data from Razorbills (*Alca* torda).

METHODS

STUDY AREA, BIRDS AND RADIOS

The study was carried out on the Isle of May National Nature Reserve, Firth of Forth, Scotland in 1984 to 1987. Information on attendance and foraging behavior was obtained from 12 radio-tagged Common Murres (five males, six females, one sex unknown) and three radio-tagged Razorbills (one male, two females). In both the Common Murre and the Razorbill the male parent takes the chick to sea when it leaves the breeding site (Harris and Birkhead 1985). Therefore we assumed that a bird which remained on the site after its chick had fledged was a female, and a bird which left with the chick was a male.

Two Common Murre pairs breeding on the same ledge as the birds carrying external aerial transmitters in 1986 were designated as controls. The members of these pairs were individually recognizable; in one the male was the bridled morph and in the other, both individuals were uniquely color-banded. One control female (A) was later radio-tagged so that the pair's behavior before and after could be compared. Data were also collected on the mates of the other two birds with external aerials. In 1987, 18 and five individually identifiable Common Murres and Razorbills, respectively, were used as controls.

Two types of transmitters were used, both operating on the 173 MHz telemetry band and attached to the bird by glueing the device in the center of the back. The first type, used only on Common Murres, had an internal tuned loop transmitting aerial; the total weight of these devices, waterproofed and potted in fiberglass resin, was 6 to 8 g or ca. 0.7% of the mean weight of a breeding Common Murre at the colony (full details in Wanless et al. 1985). The second type, used on both Common Murres and Razorbills, had a thin external aerial 20 to 25 cm long. Its potted weight was 7.0 to 8.3 g, or 1.1 to 1.2% and 0.6 to 0.8% of the weight of Razorbill and Common Murre, respectively (see Wanless et al., in press). For Common Murres two internal aerial transmitters were used each year 1984 to 1986 and three external aerial transmitters were used in 1986 and 1987. All three Razorbills were followed in 1987. Sample sizes in each year and for each sex were too small to examine differences at these levels and therefore data were pooled for all analyses except those comparing prey delivery.

Radio signals were detected using a two-element quad antenna or a five- or 12-element vertically polarized yagi antenna connected to an AVM or RX-81 receiver. Signals were either monitored directly by an observer or, when a tracking session was not in progress, automatically by connecting the receiver to a chart recorder.

SITE ATTENDANCE AND LENGTHS OF ABSENCES

Both receiving methods recorded the time a radio-tagged bird spent on the breeding site and the lengths of absences. In 1986, observations on control birds were made during three 4- to 5hr observation periods spread throughout the hours of daylight. If a bird left or returned between watches it was assumed to have left or returned midway through the unmonitored period. In 1987, information from checks every 2 hr from 17:00 GMT on 20 June to 21:00 on 22 June was used to calculate the proportion of time each Common Murre and Razorbill was present on the site. Attendance behavior at night was obtained by checking the sites at last and first light (22:00 and 02:00 respectively). Birds do not arrive or depart during the hours of darkness (pers. observ.), therefore, a bird was either present or absent for these 4 hr. Data from the Razorbills were also used to estimate the length of each absence.

FORAGING FREQUENCY AND PREY DELIVERY

We compared the number of foraging trips made each day by birds in the various categories. The data were not strictly comparable, since visual observations on the controls and mates of some of the Common Murres with external aerials were not continuous, which resulted in the values obtained for these categories being minima. Absences of less than 10 min were excluded since visual and telemetry observations showed that birds were usually preening and washing on the

	% time on site (hr followed)							
	1	2	3	4	5	6	, x	
Internals	59 (37)	58 (269)	72 (227)	60 (353)	56 (194)	58 (211)	61	
Externals	54 (309)	51ª (240)	48 (175)	47 (208)	43 (9)	35 (177)	46	
Mates of externals	69 (286)	79⁵ (183)	83 (136)	-	-	_	77	
Controls	65 (168)	63 (165)	76ª (68)	71 ^ь (65)	-		69 [.]	

TABLE 1. Proportions of time spent at the breeding site by Common Murres carrying internal and external aerial transmitters (six of each), three mates of birds with external aerials, and four control birds. Data for the mates are presented directly below their partners; for the controls the first and second observations refer to one pair, and the third and fourth to another pair.

b The same pair before and after a transmitter was attached to the female.

^c An additional 18 breeding adults were checked every 2 hr 17:00 20 June to 21:00 22 June 1987. The mean proportion of time a bird was observed on its site was 62% (SE = 4%). The overall proportion of time for the two control groups combined was 65% (SE = 2%).

sea close to the colony rather than on foraging trips during such absences. No detailed observations were made of Razorbill controls but a rough comparison was obtained from the twohourly checks described above.

Records were kept of the number of arrivals with and without fish made by Common Murres and Razorbills with external aerial transmitters, the mates of some of these birds, and untagged birds elsewhere in the colony.

RESULTS

PROPORTION OF TIME SPENT ON THE SITE

Twenty-two control Common Murres spent, on average, 65% (SE = 2%) of their time on the site (Table 1). Bearing an internal aerial transmitter had no detectable effect on a bird's attendance (Mann-Whitney U = 38, P > 0.05). However, birds with an external aerial spent less time on the site than controls (Mann-Whitney U = 6, P < 0.001). The Common Murre chick is normally guarded continuously by one or the other of the pair. Therefore, the reduction in the proportion of time spent on the site by birds bearing external aerials might have led either to the mates of these birds increasing the proportion of time spent on the site or the chick being left unattended. In fact the former occurred and mates spent more time on the site than controls (Mann-Whitney U = 9, P < 0.05). Similarly female A spent 76% of the time at the site before the transmitter was attached but only 51% afterwards, and the mate increased the proportion of time from 71% to 79%. Thus, in contrast to control pairs in which site attendance was apparently shared more or less equally (differences of 2% and 5% respectively in the two pairs), there was a marked inequality in pairs where one member was carrying an external aerial transmitter, the differences being 15%, 28%, and 35% respectively.

There was no significant difference (Mann-Whitney U = 4, P > 0.05) in the proportion of time spent at the site by five control Razorbills

TABLE 2. Length of absence (min) from the site for Common Murres carrying internal or external aerial transmitters, mates of the latter and controls (n as in Table 1).

	With tra	ansmitter		Without transmitter		
			Pair	Control 86		
	Internal aerial	External aerial	Mate			
No. of absences	196	88	113			
Length of absence (m	nin)					
Mean \pm SE	141 ± 5	428 ± 40	95 ± 12	155 ± 17		
Minimum	6	12	6	6		
Maximum	955	1,818	689	667		

 $(\bar{x} = 57\%)$ and three carrying external aerial transmitters ($\bar{x} = 66\%$).

LENGTH OF ABSENCE

Absences from the site ranged from a few minutes to many hours (Table 2) but there were broad differences in the frequency distributions between the categories ($\chi^2 = 103$, df = 6. P < 0.001) (Fig. 1): birds with external aerials tended to be away for long periods more often than either control hirds or hirds with internal aerials and mates of birds with external aerials tended to have shorter absences

Lengths of absence for Razorbills carrying external aerial transmitters ($\bar{x} = 280 \text{ min}$) did not differ from those of control birds ($\bar{x} = 240 \text{ min}$, Mann-Whitney U = 424, P > 0.05).

NUMBER OF DAILY ABSENCES

On average, control Common Murres were away for a minimum of 2.5 occasions day⁻¹ (SE = 0.2) (Table 3). Values for the controls were not different from the number of daily absences of birds with internal aerial transmitters (Mann-Whitney U = 6, P > 0.05) but were significantly higher than values for birds with external aerials (Mann-Whitney U = 0, P < 0.005). The mates of birds in the latter category compensated for the change in their partner's behavior and had the highest number of absences day⁻¹, although the value was not significantly different from the control group.

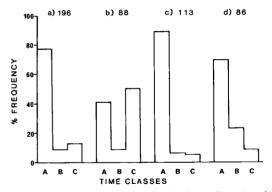


FIGURE 1. Frequency (%) distributions of lengths of absence (min) for Common Murres with (a) internal aerial transmitters, (b) external aerial transmitters. (c) mates of (b), and (d) controls. Absences are grouped $0-200 \min (A)$, $201-400 \min (B)$ and $401 + \min (C)$. Figures above each histogram are the sample sizes.

The number of absences day⁻¹ for five control Razorbills ($\bar{x} = 1.9$) did not differ from those for three birds with transmitters ($\bar{x} = 1.4$, Mann-Whitney U = 5, P > 0.05).

Between 1984-1987. Common Murre and Razorbill chicks on the Isle of May were fed 3.6-4.0 and 2.6-2.9 times day⁻¹, respectively (Harris and Wanless 1986, 1988, unpubl. data). These frequencies agree well with the values in Table 3, assuming that Common Murres with internal aerial transmitters, control birds, and Razorbills with external aerial transmitters were taking an

TABLE 3. Number of absences day-1 for six Common Murres carrying internal and for five carrying external aerial transmitters, three mates of externals, four controls, and three Razorbills carrying external aerial transmitters. Values for mates and controls are minimal because observations on such birds were not continuous. Details for controls and mates are as in Table 1.

	Mean no. absences day ⁻¹ \pm SE (days followed)							
	1	2	3	4	5	6	Mean	
Common Murres								
Internals	2.0 ± 0.2 (13)	4.0 (1)	1.4 ± 0.8 (13)	1.8 + 0.3 (9)	2.2 ± 0.2 (8)	2.3 ± 0.3 (9)	2.3	
Externals	1.7 ± 0.2^{a} (10)	2.1 ± 0.3 (8)	1.4 ± 0.2 (14)	1.2 ± 0.2 (8)	1.6 ± 0.3 (8)	_	1.6	
Mates of externals	3.0 ± 0.4 ^ь (11)	3.6 ± 0.5 (8)	3.3 ± 0.3 (15)	-	_	_	3.3	
Controls	2.4 ± 0.2^{a} (5)	2.2 ± 0.8 ^b (5)	3.1 ± 0.4 (9)	2.4 ± 0.4 (9)	-	_	2.5	
Razorbills								
Externals	2.0 ± 0.7 (9)	1.1 ± 0.2 (15)	1.2 ± 0.6 (12)	-	-	-	1.4	

** The same pair before and after a transmitter was attached to *. Values for the radio-tagged Razorbills did not differ from those of five controls (Mann-Whitney U = 5, ns).

	Radio-tagged pairs						Control pairs				
	1		2			3		1		2	
	ð	Ça	ి	Ŷ	8°	Çab	đ	ş	₿ ^b	Şр	
Arrival with fish	16	2	0	37	24	6	11	11	1	10	
Arrival without fish	11	13	12	9	10	7	10	7	3	3	
Total	27	15	12	46	34	13	21	18	4	13	
% with fish	59	13	0	80	71	46	52	61	25	77	

TABLE 4. Prey delivery by three pairs of Common Murres when one member was carrying an external aerial transmitter, and two control pairs in 1986.

* Individuals carrying transmitters.

^b Same pair, before and after a transmitter was attached to the female.

approximately equal share in chick provisioning with their mate.

PREY DELIVERY

No detailed observations were made of how often Common Murres with internal aerial transmitters fed their chicks but they were seen to bring back some fish.

Males of the two control pairs in 1986 carried fish on 48% of 25 returns to the young and females brought in fish on 68% of 31 returns (Table 4). Females tend to bring in slightly more fish than their mates (Wanless and Harris 1986) but in the present case the difference, though in the expected direction, was not significant ($\chi^2 = 2.2$, df = 1, P > 0.05). Birds carrying transmitters had lower proportions of arrivals with fish; indeed one radio-tagged male was never seen with a fish (radio-tagged vs. control males $\chi^2 = 8.5$, df = 1, P < 0.01) and two females (one of which had a high proportion of arrivals with fish prior to attachment) had a lower foraging success than control females ($\chi^2 = 9.6$, df = 1, P < 0.01).

TABLE 5. Prey delivery by two radio-tagged Common Murres and three Razorbills compared with 18 and five control birds in 1987.

		Arr	ivals		% arriv-
	Sex	With fish	With- out fish	Total	als with fish
Common Murre	ç	1	4	5	20
Common Murre	Ŷ	6	2	8	75
Total		7	6	13	54
Controls		148	45	193	77
Razorbill	ę	10	2	12	83
Razorbill	ç	5	5	10	50
Razorbill	ð	1	4	5	20
Total		16	11	27	59
Controls		6	4	10	60

Mates of birds with transmitters had high success rates so that there was no difference either in the overall foraging success of the radio-tagged and control pairs ($\chi^2 = 5.4$, df = 4, P > 0.05) or in the provisioning rate of the pair where observations were made before and after the transmitter was attached ($\chi^2 = 0.01$, df = 1, P > 0.05).

In 1987 a radio-tagged female brought in a fish on only one of five observed arrivals whereas a second female brought in fish on six out of eight arrivals (Table 5). Thus for the two birds combined, 54% of arrivals were with fish; this was lower than the 77% of 193 arrivals of controls, but the difference was not statistically significant ($\chi^2 = 3.4$, df = 1, P > 0.05).

The proportions of arrivals with fish for three Razorbills with external aerial transmitters varied considerably from 20–83% (Table 5). Overall the proportion of occasions when fish were brought back by control and radio-tagged individuals did not differ ($\chi^2 = 0$, df = 1, P > 0.05).

DISCUSSION

Accurate data on activity budgets are essential to seabird energetics models (e.g., Furness 1978, Gaston 1985). Such data may be obtained using either electronic activity recorders (e.g., Prince and Francis 1984, Cairns et al. 1987) or radiotelemetry as in this study. However our results from Common Murres carrying external aerial transmitters would have been biassed as these birds spent less time in the colony, were absent for long continuous periods, and had a reduced prey delivery. In contrast, results from Razorbills with external aerials and Common Murres with internal aerials were similar to those of controls and thus apparently provided reliable estimates of activity budgets. However, our acceptance of these data rests on the assumption that differences which were not shown to be statistically significant (P < 0.05) were therefore not biolog-

ically significant. In many cases the sample sizes for the controls were very small which would tend to reduce the likelihood of differences being significant. If our comparison had been less detailed some of the adverse effects could easily have been overlooked since the differences were of degree rather than absolute, e.g., none of the birds deserted, they continued to brood, go off on feeding trips, bring in some fish for the young, and, except for one Common Murre chick which fell onto a lower ledge (where it was reared successfully by another pair), all the chicks left the site successfully. This high fledging success was due, at least in part, to the untagged mate increasing its contribution to the breeding effort by spending more time on the site guarding the chick and using its off-duty time to make short, frequent, and generally successful feeding trips. Parental behavior in alcids appears to be flexible. Under experimental conditions adults respond to increased demands of the chicks by bringing in more food (e.g., Lloyd 1977, Harris 1983) and in this study mates of birds with external aerials were able to compensate for reduced prey delivery by their partners. In general, male and female Common Murres make equal contributions to incubation and chick rearing except that females may bring in slightly more fish (Wanless and Harris 1986). Burger (1987) found that Herring Gull (Larus argentatus) pairs with a more equitable distribution of parental effort fledged significantly more young than those in which the division of labor was unequal, and there is some evidence of a similar effect in the Common Murre. Successful pairs have a significantly more equitable distribution of time spent incubating and more equal aggression rates (E. Stuart, unpubl. data). Thus the unequal distribution of parental effort we recorded in radio-tagged pairs might ultimately be expected to lead to reduced breeding success.

Although Common Murres with external aerial transmitters brought back fewer fish for the chick they showed no obvious signs of loss of condition and were apparently able to feed themselves. Two Razorbills were recaught 14–16 days after their transmitters were attached; one had lost 50 g (8% of its body weight at the time of attachment) whilst the other had gained 62 g (10%). These changes could have been due to different amounts of food being present in the stomach; however, digestion is rapid in alcids (Partridge 1986) so this explanation is unlikely. More data are needed to demonstrate any consistent effect of the device on body weight.

Estimates of the costs of transporting the transmitters, calculated from formulae in Caccamise and Hedin (1985), suggest that they caused a proportionate reduction in surplus power of 1.4% and 2.5% for normal Common Murres and Razorbills respectively, and 2.3% and 3.8% if birds were carrying an average load of fish (9 g for Common Murres, 7 g for Razorbills; Harris and Wanless 1986, 1988). Transmitter weight per se seems unlikely to have been the reason for the device-related disturbance in Common Murres as the external aerials were generally lighter than the internals. Also both our transmitter types were considerably lighter than the 25-g timers (2.5% of body weight) fitted to Common Murres by Cairns et al. (1987), which apparently had no ill effects on incubation or chick rearing. However, these authors did not compare the behavior of experimental and control birds in detail but just noted that all their study birds were "incubating or rearing chicks in apparently normal fashion during the observation period." Wilson et al. (1986) concluded that the attachment of recording devices may adversely disturb the foraging behavior and reproductive energetics of marine animals and considered that the crucial factor was the streamlining of the package rather than its mass. This may have been the case in our study, since when an alcid is diving and the plumage is sleeked close to the body a transmitter attached in the middle of the back will alter the flow of water over the body. Carrying an external aerial would increase the drag on a bird underwater which could explain why Common Murres with external aerials were affected whilst those with internal aerials were not. However, the reason(s) why we did not detect differences in Razorbills carrying external aerials is obscure. Future studies should emphasize more the streamlining and positioning of transmitters, perhaps following the method of Cairns et al. (1987) of attaching devices to the leg or tail.

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LITERATURE CITED

- ANDERSON, D. J., AND R. E. RICKLEFS, 1987. Radiotracking Masked and Blue-footed boobies (*Sula* spp.) in the Galapagos Islands. Natl. Geogr. 3:152– 163.
- BALL, I. J., D. S. GILMER, L. M. COWARDIN, AND J. H. RIECHMANN. 1975. Survival of wood duck and mallard broods in north-central Minnesota. J. Wildl. Manage. 39:776–780.
- BLAKE, B. F., M. L. TASKER, P. HOPE JONES, T. J. DIXON, R. MITCHELL, AND D. R. LANGSLOW. 1984. Seabird distribution in the North Sea. Nature Conservancy Council, Huntingdon, United Kingdom.
- BOAG, D. A. 1972. Effect of radio packages on behaviour of captive red grouse. J. Wildl. Manage. 36:511-518.
- BURGER, J. 1987. Selection for equitability in some aspects of reproductive investment in Herring Gulls Larus argentatus. Ornis Scand. 18:17–23.
- CACCAMISE, D. F., AND R. S. HEDIN. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bull. 97:306–318.
- CAIRNS, D. K., K. A. BREDIN, AND W. A. MONTE-VECCHI. 1987. Activity budgets and foraging ranges of breeding Common Murres. Auk 104: 218-224.
- CLARK, N. A., T. A. VARLEY, J. EVANS, AND G. A. WRIGHT. 1987. Breeding success of Mallard Anas platyrhynchos at Loch Leven National Nature Reserve. Bird Study 34:129–134.
- FURNESS, R. W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47:39–53.
- FURNESS, R. W. 1984. Modelling relationships among fisheries, seabirds and marine mammals, p. 162– 169. In D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service, Ottawa.
- GASTON, A. J. 1985. Energy invested in reproduction by Thick-billed Murres (Uria lomvia). Auk 102: 447–458.
- HARRIS, M. P. 1983. Parent-young communication in the Puffin Fratercula arctica. Ibis 125:56-73.
- HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae, p. 155–204. *In D.* N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, London.
- HARRIS, M. P., AND S. WANLESS. 1986. The food of young Razorbills on the Isle of May and a comparison with that of young Guillemots and Puffins. Ornis Scand. 17:41–46.
- HARRIS, M. P., AND S. WANLESS. 1988. The breeding biology of Guillemots Uria aalge on the Isle of May over a six year period. Ibis 130:172–192.
- HARRISON, C. S., AND D. L. STONEBURNER. 1981. Radiotelemetry of the Brown Noddy in Hawaii. J. Wildl. Manage. 45:1021–1025.
- KENWOOD, R. E. 1980. Radio monitoring birds of prey, p. 97-104. In C. J. Amlaner, Jr. and D. W. MacDonald [eds.], A handbook of biotelemetry and radio tracking. Pergamon Press, Oxford.

LANCE, A. N. 1978. Survival and recruitment success

of individual young cock Red Grouse *Lagopus l. scoticus* tracked by radio-telemetry. Ibis 120:369–378.

- LANCE, A. N., AND A. WATSON. 1977. Further tests of radio-marking on red grouse. J. Wildl. Manage. 41:579-582.
- LEUZE, C.C.K. 1980. The application of radio tracking and its effect on the behavioural ecology of the Water Vole Avricola terrestris (Lacepede), p. 361– 366. In C. J. Amlaner, Jr. and D. W. MacDonald [eds.], A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.
- LLOYD, C. S. 1977. The ability of the Razorbill Alca torda to raise an additional chick to fledging. Ornis Scand. 8:155–159.
- MARQUISS, M., AND I. NEWTON. 1982. A radio tracking study of the ranging behaviour and dispersion of European Sparrowhawks *Accipiter nisus*. J. Anim. Ecol. 51:111–133.
- NETTLESHIP, D. N., AND A. J. GASTON. 1978. Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories, in August and September 1976. Occasional Papers 39. Canadian Wildlife Service, Ottawa.
- PARTRIDGE, K. E. 1986. The feasibility of using X-rays to monitor digestion in the Guillemot Uria aalge. Seabird 9:52–54.
- PEARSON, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521–552.
- PRINCE, P. A., AND M. D. FRANCIS. 1984. Activity budgets of foraging Gray-headed Albatrosses. Condor 86:297–300.
- SCHNEIDER, D., AND G. L. HUNT. 1982. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska, p. 86-95. In D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service, Ottawa.
- SIBLY, R. M., AND R. H. McCLEERY. 1980. Continuous observations of individual herring gulls during the incubation season using radio tags; and evaluation of the technique and a cost-benefit analysis of transmitter power, p. 345–352. In C. J. Amlaner, Jr. and D. W. MacDonald [eds.], A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.
- SMITH, H. R. 1980. Growth, reproduction and survival in *Peromyscus leucopus* carring intraperitoneally implanted transmitters, p. 367-374. *In C. J. Amlaner, Jr. and D. W. MacDonald [eds.], A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.*
- TASKER, M. L., A. WEBB, A. J. HALL, M. W. PIEN-KOWSKI, AND D. R. LANGSLOW. 1987. Seabirds in the North Sea. Nature Conservancy Council, Peterborough, United Kingdom.
- TRIVELPIECE, W. Z., J. L. BENGTSON, S. G. TRIVELPIECE, AND N. J. VOLKMAN. 1986. Foraging behavior of Gentoo and Chinstrap penguins as determined by new radiotelemetry methods. Auk 103:777– 781.

- WANLESS, S., AND M. P. HARRIS. 1986. Time spent at the colony by male and female Guillemots Uria aalge and Razorbills Alca torda. Bird Study 33: 168-176.
- WANLESS, S., M. P. HARRIS, AND J. A. MORRIS. 1985. Radio-monitoring as a method for estimating time budgets of Guillemots Uria aalge. Bird Study 32: 170-175.
- WANLESS, S., J. A. MORRIS, AND M. P. HARRIS. In press. Diving behaviour of guillemot Uria aalge, puffin Fratercula arctica and razorbill Alca torda as shown by radio-telemetry. J. Zool. Lond.
- WILSON, R. P., W. S. GRANT, AND D. C. DUFFY. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology 67:1091–1093.

