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Diving Depths of Northern Gannets: Acoustic Observations of *Sula Bassana* from an Autonomous Underwater Vehicle

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ABSTRACT.—The Autonomous Underwater Vehicle (AUV) *Autosub-1* made observations of the sea surface with an upward-looking echosounder during fish surveys in the vicinity of Shetland and Orkney (North Sea) in July 1999. Echograms from the AUV contained vertical traces extending downwards from the sea surface that were caused by diving seabirds. Visual observations provided evidence that those seabirds were Northern Gannets *Sula bassana*. Analysis of trace extent suggests a mean dive depth of 19.7 m ($n = 19$, $SD = 7.5$). Data on gannet diving depths are sparse, but this value is somewhat deeper than that accepted for the related Cape Gannet (*Morus capensis*, mean 5.9 m) which has been used in foraging models for the Northern Gannet. These observations have implications for our understanding of the foraging capabilities of gannets, and the interactions of gannets with commercially targeted fish species.

One of the factors that limits availability of prey to seabirds at sea is the depth to which the birds can dive. Conversely, differing diving capabilities amongst taxonomically distinct groups of seabirds can result in the effective partitioning of commonly targeted resources. In the Southern Ocean, for example, penguins, prions, and albatrosses are all able to exploit Antarctic krill (*Euphausia superba*) in overlapping geographical areas by targeting them at different depths in the water column (Croxall et al. 1997). Knowledge of birds' diving capabilities is essential for understanding foraging strategies of individual species, for modeling food-web interactions in ecosystems containing multiple predatory species, and for identifying areas of potential competition between seabird diet and commercial fisheries.

The Northern Gannet (*Sula bassana*) is a plunge diver and its large size (it is the largest pelagic seabird in the North Atlantic) makes its foraging efforts spectacular and conspicuous. In the North Sea, the diet of the Northern Gannet includes herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and sandeels

(*Ammodytes* spp.) (see Wanless 1984, Martin 1989), and they are also able to exploit discard from fishing vessels (Furness et al. 1992). Although their diet is well described, until very recently little was known of the depth range over which Northern Gannets are able to catch prey.

Data on foraging location and diving depths of predators at sea, including seabirds, have been obtained from a variety of mechanical and electronic telemetering devices attached directly to the animals under study (e.g. Burger and Wilson 1988, Wanless et al. 1997, Hull 1999, Waugh et al. 1999). Although satellite tags have been deployed on Northern Gannets breeding on the coast of the North Sea to investigate their foraging range (Hamer et al. 2000), there are no published data on the diving depths of gannets from that area, an area that is of major importance for the species as a whole. In summer 1999, Garthe et al. (2000) deployed time–depth recorders on Northern Gannets breeding off Canada's Atlantic coast. At the same time that their study was underway, we made independent observations of Northern Gannets diving in the North Sea. Our observations were obtained by an Autonomous Underwater Vehicle (AUV) engaged in a fishery survey around the islands of Shetland and Orkney (Fernandes and Brierley 1999). Our data indicate that Northern Gannets have diving capabilities in excess of those previously acknowledged, and suggest that the effective vertical foraging range of the species should be reconsidered.

Methods.—In July 1999, the AUV *Autosub-1* was deployed from the Fisheries Research Vessel *Scotia* during an acoustic survey for herring in the northern North Sea (Fernandes et al. 2000). *Autosub-1* is a 6.8 × 0.9 m, torpedo-shaped unmanned submersible vehicle: it is battery-powered and can conduct preprogrammed underwater missions at speeds of up to 3 knots, to depths of 500 m with a duration of over 24 h. During our study the AUV was deployed on missions that were on average 8 h long. For the vast majority of that time, the AUV was unattended, tens of kilometers away from *Scotia*, purposefully surveying transects geographically distinct from those that the ship was sampling.

For this study, *Autosub-1* was equipped with a Simrad EK500 scientific echosounder operating 38 and 120 kHz transducers generating conical 7° sampling

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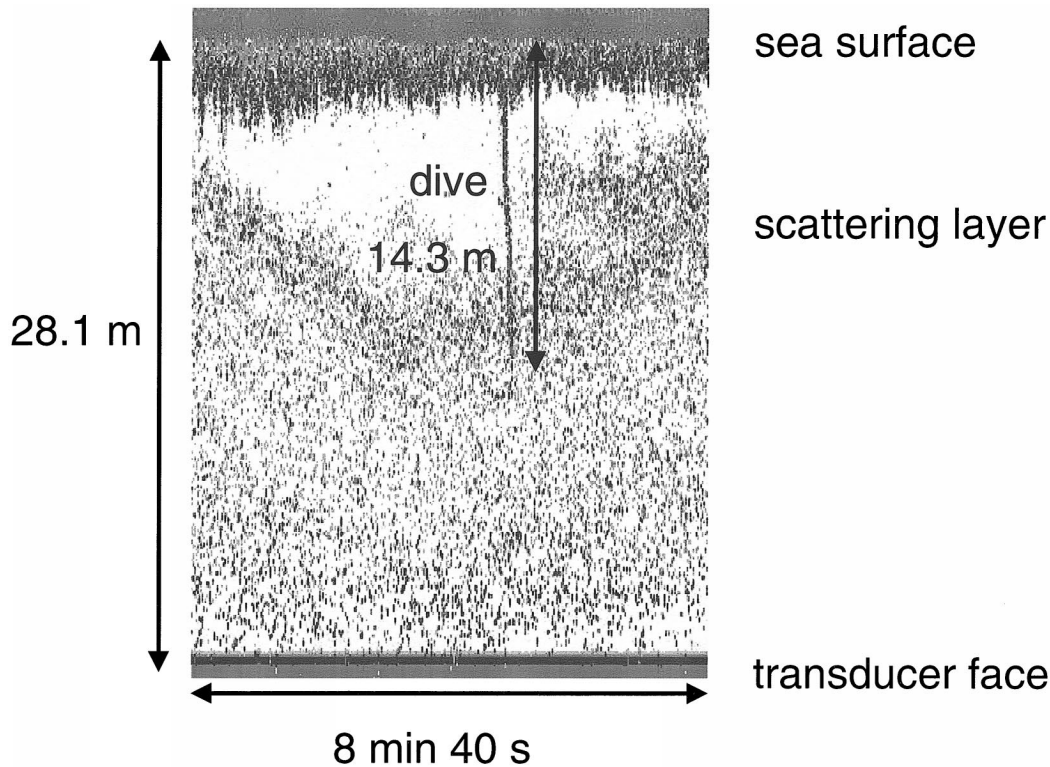


FIG. 1. Example echogram from the upward-facing 120 kHz transducer, showing the sea surface, a Northern Gannet dive trace, and an acoustic scattering layer composed possibly of the prey upon which the gannet was diving. At a nominal survey speed of 1.2 ms^{-1} (from left to right), 8 min 40 s equates to a distance of 624 m. See text for further explanation.

beams. Acoustic samples (pings) were collected every 1 s during each deployment and data were logged over an ethernet to a local personal computer using SonarData Echolog EK software. Echograms were downloaded at the end of each mission and viewed using the SonarData Echoview software package.

The echosounder transducers on *Autosub-1* could be arranged to be both downward looking, both upward looking, or one up and one down. The AUV was deployed on 12 missions with an upward looking transducer. The principal objective of the upward looking transducer was to obtain information on near-surface schools of herring *Clupea harengus* (Fernandes and Brierley 1999). On those deployments, the AUV was programmed to cruise at depths of either 20, 30, or 50 m, or to remain at a fixed depth above the seabed (effectively undulating between 35 and 50 m depth), and the sea surface was always "visible" acoustically.

Typically, an *Autosub-1* mission would begin with the vehicle "pottering" at the surface while waiting to obtain a GPS fix for navigation. During that time,

gannets were often attracted to the vehicle (it is bright yellow and equipped with strobe lights to aid relocation and recovery). Once a GPS fix had been obtained, the vehicle would be instructed by radio to dive and begin its mission. On many occasions when the AUV dive took place, gannets that had been circling above and in the vicinity of the vehicle dived at it. Some of those dives were visible clearly on the echograms and could be attributed directly to gannets: the insulating layer of air trapped amongst the birds' feathers makes the birds strong acoustic reflectors, and the bubble train trailing behind the diving birds leaves a conspicuous streak on the echogram (Fig. 1). Dives of exactly the same appearance were also evident in echograms recorded when the AUV was unattended; it is data from those dives that are considered in this paper. Dive depths were evaluated from the echograms as the difference between the range from *Autosub-1* to the sea surface and the closest approach of the dive trace to *Autosub-1* (see Fig. 1).

Results.—Nine of the 12 *Autosub-1* missions when one or more echosounder transducers were facing

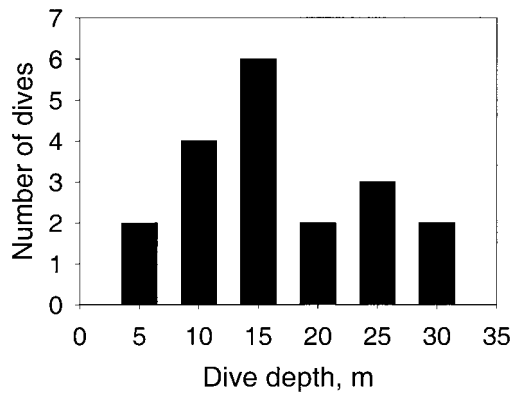


FIG. 2. Histogram of Northern Gannet dive depths ($n = 19$).

upwards towards the sea surface obtained good data (along a total survey track of over 330 km) and, during those, 19 gannet-like dive traces were evident on echograms recorded during the time the AUV was unattended. Those 19 dive traces were indistinguishable from those traces that coincided with the AUV dives, which we knew were caused by gannets: binocular observations made from the FRV *Scotia* (range < 200 m) of the diving AUV detected Fulmars (*Fulmarus glacialis*), but no auks (Alcidae), and so we are confident that the dives apparent on the echograms are due to gannets. The unattended missions were conducted mostly off shore, in areas where auks are known to be less prevalent and, furthermore, the dives we observed (Fig. 1) were of quite different appearance to dives by Common Murres (*Uria aalge*) observed in the Clyde Sea with a multibeam 3-dimensional sonar (P. G. Fernandes unpubl. data). We did not include gannet dives recorded by the AUV at the start of its missions in our analysis because those bird dives were, without doubt, triggered by the AUV dive and cannot therefore be considered as natural—their inclusion may have biased our conclusions.

Weather conditions deteriorated somewhat during the course of two missions, causing the sea surface to become increasingly disturbed. Air bubbles mixed downwards by wave action (Thorpe 1992) then partially obscured dive traces and, because we are less confident in our ability to distinguish dives at those times, we have not included data from those sections of cruise track.

The mean gannet dive depth from the 19 observations was 19.7 m (SD = 7.5, range 8.0 to 34.0 m). A histogram of dive depths is shown in Figure 2: the distribution did not differ significantly from normal (Anderson-Darling test, $P = 0.135$).

To investigate the possibility that the birds were diving on the AUV itself, we compared dive depth

with AUV depth. The scatter of dive depths was quite large, but the relationship between dive depth and AUV depth was highly significant (ANOVA, $F = 16.45$, $df = 17$, $P = 0.001$).

Discussion.—There are few published observations of diving depths of gannet species, and we are aware of only one such data set for the Northern Gannet (Garthe et al. 2000), which was collected at the same time (but in a different location using a different technique) as the data reported here. The observations we report here are thus valuable both because they enhance understanding of the foraging capabilities of this species generally and, more specifically, provide the first data on foraging depths for Northern Gannets in the North Sea.

Observations by Adams and Walter (1993) on the Cape Gannets (*Morus capensis*) suggest that it can achieve a maximum dive depth of 12.6 m (mean 5.9 m, SD = 4.0 m). Garthe et al. (2000) reported a deeper maximum dive depth of 22 m for the Northern Gannet (mean 5.2 m, SD not reported). The Cape Gannet is a slightly smaller bird than the Northern Gannet and that between-species difference in previously reported maximum dive depths is in line with expectations that maximum dive depth is size dependent (see Burger 1991). Our observations suggest that Northern Gannets in fact have the potential to dive deeper still (mean 19.7 m, SD = 7.5 m).

Adams and Walter (1993) considered that it would only be possible for Cape Gannets to achieve their maximum observed dive depths by active swimming. During the course of the present fishery survey, Northern Gannets were often observed diving on the cod end of the trawl net during recovery, and were also seen swimming down to retrieve sinking, dead herring that had been discarded from the trawl deck. Those birds are clearly capable swimmers (see Nelson 1978). Garthe et al. (2000) report that the deeper gannet dives they recorded involved bent-winged underwater flight. Prince et al. (1994) have similarly suggested that some albatross species must regularly swim underwater to achieve recorded depths.

In addition to suggesting a new maximum diving capability for Northern Gannets, our observations differ from those of Garthe et al. (2000) in another key respect: they reported that the distribution of dive depths was Poisson-like, whereas the distribution of dive depths we observed did not differ significantly from normality. We believe that there are two possible explanations for this difference. Firstly, it is probable that the depths of prey species being sought by gannets in the North Sea (herring, mackerel, and sand eels) and the northeast Atlantic (predominantly capelin [*Mallotus villosus*]) differ. Secondly, we suggest that the loggers attached externally to the gannets studied by Garthe et al. (2000) may have either underestimated achieved

dive depths due to sampling limitations, or may have hampered the birds such that they were unable to reach their full potential depth. Garthe et al. (2000) suggest strongly that their recording devices had no negative effect on the birds. Concerns remain, however, that external recording devices may hamper performance by increasing drag (cf. Culik and Wilson 1991), and sampling-rate limitations of depth recorders may lead to a distorted representation of diving behavior (Wilson et al. 1995), a problem that may be particularly acute in animals that undertake dives where the time at maximum depth is short and where the rate of depth change is rapid. Direct observations of dives could overcome those potential limitations, and we suggest that our observations from the AUV are particularly valuable because they are of birds that were not encumbered by instruments. The use of time–depth recorders did however enable Garthe et al. (2000) to gather information on dive profiles, enabling them to distinguish between U and V shaped dives. Limitations inherent with our sampling technique do not enable those type of differences to be distinguished. The echo sounder transducers we were operating had 7° beam angles. At a range of 50 m, they provided a circular sampling window 6.1 m in diameter, but that window decreased in size as range from the AUV decreased (diameter = $2 \times \tan 3.5^\circ \times \text{range}$), being 1.2 m at 10 m range (Fig. 3). Only dives that passed directly down the center of the echosounder beam would be observed in full and, unless the descent and ascent components of the dive were spatially very close, it is unlikely that bubble trails from both would be detected. The AUV traveled typically at a speed of 1.2 m s⁻¹ and, at a range of 50 m, would have been able to observe a fixed point in the water column above for only a little over 5 s. Another implication of the conical acoustic sampling window is that the deeper a dive was the more likely it was to pass out of the sampling beam (see Fig. 3): our reported dive depths are therefore likely to be conservative estimates. The acoustic records do however reveal something of the prey field upon which the gannets were diving. Figure 2, for example, shows a scattering layer that deviates around the maximum depth of the gannet dive. The deviation may be due to prey actively attempting to avoid the diving gannet. Different sampling techniques clearly reveal different aspects of foraging behaviour, and our data and those collected at the same time, albeit in a different location, by Garthe et al. (2000) should be viewed together to provide the most comprehensive information so far available on diving behavior of Northern Gannets.

It is possible that the AUV itself was the cue for the gannet dives observed here. If that is so, then how often gannets would naturally dive to the depths we have recorded is questionable. We believe though that gannet dive-depths and AUV operating depths appeared to be related significantly because the con-

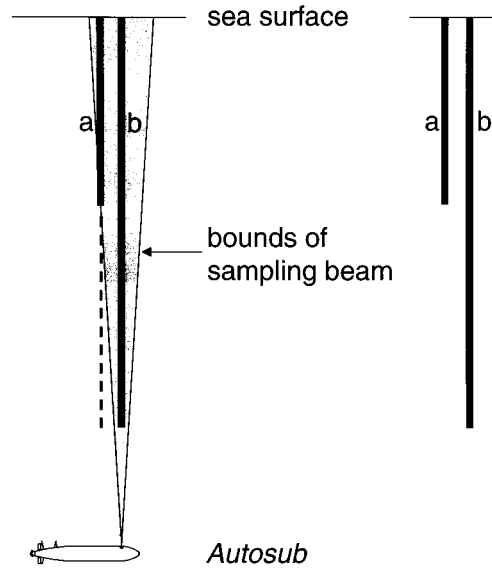


FIG. 3. Schematic representation of the acoustic sampling window above the AUV (left) showing the echogram traces (right) of two dives that descended to the same depth either partially (a) or entirely (b) within the 7° echo sounder beam (shaded). The deeper part of dive (a) is undetected (dashed line) because it passes outside the beam. The figure is to scale with the AUV at 33 m; the echo sounder beam diameter at the sea surface is 4 m.

ical shape of our sampling window made it more likely that deep gannet dives would be detected when the AUV was deeper. Whether naturally cued or not, however, the fact that gannets were recorded diving to depths >25 m at least demonstrates a potential to do so for natural foraging. Other species of sea birds have been recorded at considerable depths, depths that are often much beyond those generally believed to be possible (Harrison 1996). Light-mantled Sooty Albatross (*Phoebastria palpebrata*), for example, have been recorded diving to 12.4 m (Prince et al. 1994) and Sooty Shearwaters (*Puffinus griseus*) have reached depths of 65.4 m (Weimerskirch and Sagar 1996).

The potential for Northern Gannets to dive in excess of 25 m enables them to exploit considerably more than "the upper few meters" of the water column in the North Sea (Garthe et al. 1999) previously thought possible. Previous fishery surveys around Shetland have concluded that herring are only found near the surface in the northern reaches of the fishery survey area (E. J. Simmonds pers. comm.). Interestingly, that is close to a large breeding colony of gannets at Hermaness at the extreme north of Shetland. Mackerel and sandeels—another important food for gannets—are more pelagic in

distribution. Although herring are otherwise predominantly associated with the bottom during daylight, they do form midwater schools (Fernandes et al. 2000), and the extended diving range of gannets reported here may make these fish accessible further afield. The possibility that gannets are exploiting herring over a wide geographic area (see Hamer et al. 2000 for data on foraging ranges of Northern Gannets in the North Sea) has implications for the effects of fishing activities on gannets. Although Northern Gannet populations are presently on the increase (del Hoyo et al. 1992, Murray and Wanless 1997), and North Sea herring stocks do not appear to be in decline, the potential for future conflict between fisheries and gannets remains.

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Factors Affecting Reed Warbler Risk of Brood Parasitism by the Common Cuckoo

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ABSTRACT.—In this study we conducted a multiple logistic regression analysis of factors hypothesized to influence the risk of Reed Warbler (*Acrocephalus scirpaceus*) brood parasitism by the Common Cuckoo (*Cuculus canorus*) on study sites in the south-eastern part of the Czech Republic. We collected data from Common Cuckoo nesting sites surrounding two fishponds. Our logistic regression models were based on the dichotomous dependent variable, parasitism of the Reed Warbler nest, and seven independent variables. Our first model used all data available across sites and years and resulted in a final model in which the only significant contributor was the independent variable “cuckoo view,” the view of host nests from the cuckoo’s vantage point in a tree. A second model was developed using data limited to sites and years with the largest sample sizes and expected to yield the most reliable results. That model resulted in three significant contributors: site, cuckoo view, and neighborhood view. In both data sets, the odds of nest parasitism were shown to increase as the view of the host nest became more direct. However, a direct view of the focal nest raised the risk of parasitism to a much greater degree than did a direct view of the neighborhood of nests. Our results provide support for a nest-exposure hypothesis of brood parasitism risk. Although our models have identified nest exposure to be the best predictor of nest parasitism in this system, work remains to unravel the potentially complex relationship among Common Cuckoos, habitat structure, and Reed Warbler hosts.

In recent decades, scientists have focused particular attention on the process by which avian brood parasites search for host nests. In fact, as early as the 1920s, the ornithologist E. Chance (1922, 1940) described female Common Cuckoos (*Cuculus canorus*) using visual vantage points in trees to observe their host’s nest building activity. From such vantage points, the cuckoo would later fly secretively down to the host nest and, usually within seconds, lay its egg. Subsequently published observations by Gärtner (1981, 1982) and Wyllie (1981) have supported Chance’s original observations. Despite the fact that watching the activity of the hosts is frequently referred to as the only nest-finding cue employed by the cuckoo, systematic studies of its nest-searching behavior are more or less lacking (Øien 2000). Recently, Alvarez (1993), Øien et al. (1996), and Moskát and Honza (2000) have observed that hosts breeding close to trees suffered a higher risk of being parasitized by cuckoos than those breeding farther away from trees. That higher risk is hypothesized to occur because it is easier for cuckoos to spot host-nesting activity when the nests are built near trees. Furthermore, Øien et al. (1996) and Moskát and Honza (2000) recorded the degree of concealment of host nests (referred to as “cuckoo view”) and found a strong, negative relationship between the degree of nest concealment and risk of parasitism.

Clotfelter (1998) recently reviewed the literature on the nest searching behavior of the North American generalist brood parasite, the Brown-headed Cowbird (*Molothrus ater*), and suggested four different hypotheses that might explain how this parasite searches for and localizes nests. He found little sup-

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TABLE 1. Total number of Reed Warbler nests found at Mlynsky South and North and Hlohovecky North in 1993 and 1994, number of nests used in the models, number and percentage of nests parasitized by Common Cuckoos, and lengths of study sites.

Study site and year	Total no. of nests	No. nests used in model	No. and % nests parasitized	Study site length (m)	Mean distance between nests
Mlynsky S 1993	49	36	11 (30.6)	1102	22
Mlynsky S 1994	77	64	15 (23.4)	1684	22
Mlynsky N 1994	120	89	16 (18.0)	1490	12
Hlohovecky N 1993	45	32	4 (12.5)	1695	38
Hlohovecky N 1994	74	45	6 (13.3)	1635	22
Total	365	266	52 (19.5)	7606	21

port for the "nest-exposure hypothesis," which assumes that visually conspicuous nests are at a higher risk of parasitism. Neither could he find any support for the "nesting-cue hypothesis," which predicts that hosts that are more aggressive towards adult parasites suffer a higher risk of parasitism. However, he found good support for the "perch-proximity hypothesis," which predicts nests close to trees to suffer a higher risk of being parasitized, and the "host-activity hypothesis," which predicts that active hosts attract brood parasites (for further references, see Clotfelter 1998). Recent studies by Larison et al. (1998) and Burhans and Thompson (1998) have similarly showed effects of habitat and microhabitat variation on risks of parasitism by Brown-headed Cowbirds among North American hosts (but see also Averill-Murray et al. 1999, Chace and Cruz 1999, and Spautz 1999).

Clotfelter's (1998) approach can easily be applied to cuckoos. Øien et al. (1996) found support for both the nest-exposure hypothesis and the perch-proximity hypothesis. They found that nests of Reed Warblers (*Acrocephalus scirpaceus*) located close to trees, with little concealment, suffered a higher risk of being parasitized by cuckoos than concealed nests located farther from trees. Furthermore, in an experimental setting, Øien (2000) has found that well-exposed Reed Warbler nests, into which eggs are artificially placed, may suffer parasitism by cuckoos even though the nests are not actively visited by the host.

Methods.—The study was conducted in the Breclav district in the southeastern part of the Czech Republic. In that area, Reed Warblers are one of the most important hosts of cuckoos. The study area is situated near the village Lednice (47°40'N 16°34'E), ~40 km south of Brno, and 70 km north of Vienna, Austria. Most Reed Warbler nests were found in reed beds (*Phragmites australis*), with a smaller number in reedmace stands (*Typha angustifolia*) (Honza et al. 1998). We collected data from nesting sites surrounding two fishponds—Mlynsky (107 ha) and Hlohovecky (104 ha). The ponds and reed beds are surrounded by arable land, but are separated from it by a strip of mature parkland and forest. Cuckoos use

trees within that forested strip for perching. Descriptions of the study area are also given by Hudec (1975), Moksnes et al. (1993), Øien et al. (1996) and Honza et al. (1998). The fieldwork related to this paper was carried out during the periods 1 June to 20 July 1993, and 15 May to 10 July 1994. Øien et al. (1996) reported on a portion of the data used in this study; however, here we expand the analysis using multiple logistic regression methods to explore the influence of a set of independent variables on nest parasitism.

We located Reed Warbler nests by systematically searching reed beds and reedmace vegetation surrounding the fishponds. We numbered each nest and marked its position with a small plastic tag on the outer edge of the reed bed towards the open water. Further, we recorded the number of eggs in each nest and, when we found nests during incubation, we floated the eggs to determine how long they had been incubated (Hays and Lecroy 1971). By that method and by direct observations, we were able to estimate laying dates for most clutches. To record clutch size, estimate breeding success of each nest, and assess nest parasitism by Common Cuckoos, all nests were checked at least two to three times and up to seven times a week. Most Reed Warblers accepted the cuckoo egg; however, rejected cuckoo eggs were easily found because egg rejection was most often accomplished by desertion of the nest. There was no difference between acceptor and rejecter nests with regard to nest-site characteristics (*F* test, *P* = 0.764).

We divided the Mlynsky and Hlohovecky ponds each into two observational units: the northern and southern banks. In both ponds, an area at each short end (east and west) was either inaccessible or had a very low density of reeds and, hence, few Reed Warbler nests.

The Mlynsky South reed-bed habitat was relatively narrow (2–6 m) and close to potential perch trees. The reed bed in that site was more or less continuous, only occasionally broken by 30–50 m stretches of open water. Nest density was medium, whereas rate of parasitism was higher than at other sites (Table 1). Mlynsky North, on the other hand, consisted of an unbroken reed bed. The reed bed was here quite

wide (up to 50 m), with most nests situated farther away from trees—well concealed from the cuckoo. Nest density was particularly high, while the rate of parasitism was moderate relative to other sites (Table 1).

The reed beds at Hlohovecky North were much more heterogeneous than the Mlynsky sites. The Hlohovecky North reed bed was discontinuous, having long sections totally lacking reeds. Some portions, on the other hand, consisted of 30–40 m of narrow reed strips, with one or two Reed Warbler nests. Other areas were similar to Mlynsky North, with broad reed belts with poor cuckoo view. Very few of those areas were of sufficient extent for a cuckoo female to simultaneously monitor several nests. Because of low host density and low rate of parasitism, the Hlohovecky South area was not surveyed in this study.

We used multiple logistic regression techniques to model the relationship between the dichotomous dependent variable, parasitism of the Reed Warbler nest (0 = not parasitized, 1 = parasitized), and seven independent variables, described below. The logistic regression model is defined as: Probability (event) = $e_z / (1 + e_z)$, where $z = B_0 + B_1X_1 + B_2X_2 + \dots + B_nX_n$; where B_0 through B_n are coefficients estimated from the data, X_1 to X_n are the independent variables, and e is the base of the natural logarithms, ~ 2.718 (Hosmer and Lemeshow 1989). All modeling was conducted using SPSS 6.1 for Macintosh (Norusis 1995). Only nests that were found to be active during the season for which data on all seven independent variables were available, and for which the parasitism status was known, were included in the analyses (see Table 1).

The following seven independent variables, believed to be important on the basis of previous studies of that population, were used in the analysis. (1) *Distance to tree* was measured as the horizontal distance (nearest meter) between each nest and the nearest tree branch where it was possible for a cuckoo to sit watching the nest. (2) *Cuckoo view* is the degree of concealment of the nest as measured from nest looking toward the branches of the nearest tree. Categorized as follows as in Øien et al. (1996): *No Nest View* (= 0), nest very well concealed. *Indirect Nest View* (= 1), nest less well concealed, however, cuckoo could only discover the nest by watching the activity patterns of the nesting birds. *Direct Nest View* (= 2), cuckoo had an unimpeded view of the nest. (3) *Neighborhood view* was measured as median degree of concealment within a radius of 40 m of focal nest based on the nest-view parameters given above. Limited to two categories: *No Nest View* to *Indirect Nest View* = 0, and *Direct Nest View* = 1, because very few neighborhoods resulted in no nest view. (4) *Number of neighbors* was measured as number of nests within a radius of 40 m of the focal nest, independent of whether those neighboring nests were simultaneous-

TABLE 2. Final logistic regression model for Reed Warbler nests parasitized by Common Cuckoos at Mlynsky South and North and Hlohovecky North in 1993 and 1994. Variables are listed in the order entered into the final model.

Variable	Wald χ^2	df	P	Odds ratio
Site	1.52	1	0.22	0.78
Year	0.06	1	0.81	1.11
Cuckoo view—none	13.44	2	0.001	
Indirect	7.95	1	0.005	11.24
Direct	12.81	1	0.000	27.19
Neighborhood view	3.63	1	0.06	2.38
Distance to tree	0.46	1	0.50	1.01
Number of neighbors	0.05	1	0.83	1.02
Number active neighbors	0.57	1	0.45	1.13
Constant	19.90	1	0.000	

ly active or not. (5) *Number of neighbors simultaneously active in breeding* represents those nests breeding within a radius of 40 m of focal nest and where egg laying occurred during the same, synchronous time period as in focal nest, that is, focal nest laying date plus four days. This assumes that a neighborhood with several simultaneously active nests is more attractive to cuckoos than one with fewer simultaneously active nests. (6) *Site* is Mlynsky North, Mlynsky South, or Hlohovecky North. (7) *Year* is 1993 or 1994.

Results.—Sufficient data (>40 nests located) were obtained for initial consideration in the modeling analyses from the southern bank of Mlynsky pond in 1993 and 1994 and from the northern bank of Mlynsky in 1994. We obtained sufficient data from Hlohovecky pond from the northern bank only in both 1993 and 1994. Over the two year period (1993–1994), we investigated 365 nests, 72.9% of which we used in our models, 52 (19.5%) of which were parasitized (Table 1).

We first used all available data, combined from each location and year, to build a logistic regression model in which the independent variables listed above were entered into the model in three phases. In the first phase, site and year were forced into the model. In the model resulting from that step, site was significant (Wald $\chi^2 = 4.68$, $P = 0.03$).

In the second phase, the variables cuckoo view, neighborhood view, and distance to nest were forced into the model, in addition to those entered in the first phase. In the resulting model, whereas site was no longer found significant ($P = 0.16$), cuckoo view was a significant contributor to the model (reference level: Wald $\chi^2 = 13.15$, $P = 0.001$).

In the third phase, the remaining variables, number of neighbors and number of active neighbors were also entered. The final model then contained all seven independent variables (Table 2). With all variables included in the model, cuckoo view remained

TABLE 3. Final logistic regression model for Reed Warbler nests parasitized by Common Cuckoos at Mlynsky South and North in 1994. Variables are listed in the order entered into the final model.

Variable	Wald χ^2	df	P	Odds ratio
Site	6.88	1	0.01	6.09
Cuckoo view—none	12.05	2	0.002	
Indirect	8.43	1	0.004	13.38
Direct	12.03	1	0.000	32.70
Neighborhood view	7.33	1	0.007	7.67
Distance to tree	0.12	1	0.73	0.99
Number of neighbors	0.95	1	0.33	1.18
Number active neighbors	0.36	1	0.55	0.89
Constant	21.01	1	0.000	

significant (Wald $\chi^2 = 13.44$, $P = 0.001$) and neighborhood view was marginally significant (Wald $\chi^2 = 3.63$, $P = 0.06$). No other variables were significant contributors to the model. The goodness-of-fit of the model, as measured by a decreasing $-2 \log$ likelihood parameter step ($-2 \log$ likelihood = 257.61, 212.37, and 210.35, respectively) increased at each. In an additional step, the interaction of the two significant variables, cuckoo view and neighborhood view, was added. The interaction did not produce a significant effect (Wald $\chi^2 = 0.54$, $P = 0.46$) and therefore the model shown in Table 2 does not reflect that additional phase of modeling.

We then produced a second model using only the data from Mlynsky South 1994 and Mlynsky North 1994. We chose those data sets because they had the largest sample sizes and would be likely to produce the most reliable results in the modeling process. The Mlynsky 1994 model (Table 3) was developed in the same way as the combined model described above. At the first phase, site was the only variable entered into the model and it did not prove to be significant (Wald $\chi^2 = 0.68$, $P = 0.41$). Second, cuckoo view, neighborhood view, and distance to nest were added to site in the model. At this point in the modeling process, three variables—site, cuckoo view, and neighborhood view—were significant (Wald $\chi^2 = 7.75$, $P = 0.01$; Wald $\chi^2 = 11.75$, $P = 0.003$; and Wald $\chi^2 = 6.98$, $P = 0.01$ respectively). In a third step, number of neighbors and number of active neighbors were added, resulting in a model in which site, cuckoo view, and neighborhood view remained significant (Table 3). The $-2 \log$ likelihood parameter declined at each step ($-2 \log$ likelihood = 153.54, 108.26, and 107.27 respectively). Adding in the interaction of the significant variables, cuckoo view and neighborhood view, did not produce a significant interaction (Wald $\chi^2 = 1.90$, $P = 0.17$) and therefore the model shown in Table 3 does not reflect that final phase of modeling.

In both datasets, the odds of nest parasitism, as expressed by the odds ratios (Tables 2 and 3), were

shown to increase as the view became more direct. However, a direct view of the focal nest raised the risk of parasitism to a much greater degree than a direct view of the neighborhood of nests.

Discussion.—Øien et al. (1996), reporting on Common Cuckoo parasitism of Reed Warblers in a data set representing a minor overlap with the data used in our current analysis, found that the distance from nests to trees had a significant influence on the risk of being parasitized, independent of the cuckoo view. Their analytical technique was a two-way analysis of variance. Our models, using logistic regression analyses, did not show distance to tree to be a predictor of Reed Warbler parasitism. Although our results do not exclude distance to tree as an important factor in determining parasitism, that variable, arguably the most direct measure of the perch-proximity hypothesis, did not improve our models significantly beyond that accomplished by the variables cuckoo view and neighborhood view. Neighborhood view was not assessed by Øien et al. (1996).

Though we do not have direct measures of host-activity behavior, we used number of neighbors and number of active neighbors as proxy measures of that activity. The variables, number of neighbors and number of active neighbors, did not prove important to either of our models and, therefore, we found no support for Clotfelter's host-activity hypothesis in the Common Cuckoo and Reed Warbler parasite-host system.

When all sites were included in our model, cuckoo view was the only explanatory variable for risk of parasitism of Reed Warbler nests by Common Cuckoos. Site, cuckoo view, and neighborhood view were predictors of nest parasitism in the restricted model of Mlynsky 1994. Our results, therefore, provide support for Clotfelter's (1998) nest-exposure hypothesis.

Given the apparent significance of the cuckoo's view of nests, differences between sites in available cuckoo perching positions are expected to influence risk of parasitism and site differences did prove significant within the more limited Mlynsky 1994 model. Yearly changes in reed-vegetation density and reed-bed width would also influence potential risk through influencing nest exposure. Reed Warblers, therefore, may be expected to be phenotypically plastic in choice of nest site, as they are in their response to more direct parasitism pressure (Øien et al. 1996, 1999).

Though represented in our study as a single variable, cuckoo view, nest exposure is actually a composite of vegetative factors and a range of responses of both the parasite and the host species to given conditions. Whereas our models have identified nest exposure as the best predictor of nest parasitism in this system, work remains to unravel the potentially complex relationship among Common Cuckoos, habitat structure, and Reed Warbler hosts. Habitat structure, mediating between parasite and host, is

increasingly influenced by human actions (e.g. manipulation of wetlands, introduced species, removal of large trees) in this and other parasite–host systems. Whether rapid, human-induced environmental change favors one player over another remains to be determined. Mapping seasonal and yearly distribution of perching trees, reed-bed vegetation, and Reed Warbler nests would provide a starting point for spatially explicit modeling of that dynamic relationship.

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