J. Field Ornithol., 72(1):30–42

EFFECT OF INVESTIGATOR DISTURBANCE ON THE BREEDING SUCCESS OF THE BLACK-LEGGED KITTIWAKE

HANNO SANDVIK
Norwegian Institute for Nature Research (NINA) Polar Environmental Centre N-9296
Tromsø, Norway
and
Department of Biology, University of Tromsø
N-9037 Tromsø, Norway

ROBERT T. BARRETT
Zoology Department
Tromsø University Museum
University of Tromsø
N-9037 Tromsø, Norway

Abstract.—The effect of investigator activity on Black-legged Kittiwakes (*Rissa tridactyla*) was assessed using the disturbance caused by an ongoing intensive study investigating chick growth and adult mass loss. Though the effects were small, investigator disturbance decreased adult nest attendance and increased daily chick loss rates. Whereas overall chick survival until day 18 post-hatch was significantly lower in the high-disturbance plot in the first year of the study, it was substantially higher in the second year. We hypothesize that changes in predator activity as an indirect consequence of disturbance were responsible for this pattern. Herring Gulls (*Larus argentatus*) which nested near the high-disturbance plot and are the main predator of kittiwakes in our study area may have been more susceptible to the effect of disturbance than the kittiwakes themselves. There was otherwise no statistically significant impact of disturbance on chick growth, or on adult kittiwakes extending into the following year. Biases in studies of kittiwakes due to investigator disturbance may thus be negligible when the study is carefully designed. Future studies investigating effects of disturbance on birds should, however, include data concerning potential predators of the focal species and include more than one low-disturbance plot, and should be carried out over two or more years.

EFECTO DEL DISTURBIO CAUSADO POR EL INVESTIGADOR EN EL ÉXITO REPRODUCTIVO DE *RISSA TRIDACTYLA*

Sinopsis.—El efecto de las actividades de un investigador fue determinado utilizando el disturbio causado por éste al estudiar intensivamente el patrón de crecimiento en pichones y la pérdida de masa en adultos de la gaviota *Rissa tridactyla.* Aunque los efectos fueron pequeños, el disturbio causado por el investigador disminuyó la atención al nido por parte de los adultos e incrementó la tasa de pérdida diaria de pichones. Aunque la sobrevivencia global de polluelos hasta los 18 dias de edad fue significativamente menor en el área del disturbio durante el primer año de estudio, fue sustancialmente más alta durante el segundo. Una hipótesis para explicar el fenómeno es que los cambios en las actividades de los depredadores, como consecuencia indirecta del disturbio, fueron responsables de este patrón. La gaviota *Larus argentatus* que anidaba al lado del área del disturbio y quienes son los principales depredadores de *Rissa* pueden haber sido mas suceptibles al efecto del disturbio que la especie objeto del trabajo. De otra manera, no hubo impacto por parte del disturbio.

Colonially breeding seabirds are frequently used in studies of breeding success and breeding behavior. Such studies often result in disturbance that can have clear negative consequences for individual birds or colonies (reviewed by Götmark 1992). However, several studies report that investigator activities had no influence on the study animal or the breeding parameter being measured (e.g., Parsons 1975; Brown and Morris 1994, 1995), and some studies even documented a "positive" effect on the focal species (Götmark and Åhlund 1984; Shields and Parnell 1986; MacIvor et al. 1990). Although disturbance effects might not be a problem for the interpretation of a study when different experimental groups receiving the same disturbance are compared (Götmark 1992), the problem of results not being independent of how they were obtained is not uncommon (Duffy 1979; Lenington 1979; Davis and Balfour 1992). It is especially critical to be able to quantify the impact of investigator disturbance when life-history traits are studied, as investigator-induced changes in chick loss or adult return rates may produce artifacts (cf., Dunnet and Ollason 1978; Gaston et al. 1988). In these cases, disturbance as a possible source of mortality has to be taken into account, and should, ideally, be quantified (e.g., Ollason and Dunnet 1978).

The Black-legged Kittiwake (*Rissa tridactyla*; hereafter referred to as kittiwake) is a seabird that has recently been the subject of several studies, none of which took into consideration the effect the investigators themselves might have had on the birds. To see if this can be justified, we quantified the effect of investigators on the breeding performance of kittiwakes that were subjected to an extensive and intensive study including weighing of chicks and capture of adults. Parameters considered in this context are the nest attendance of adult birds, chick mortality, chick growth, and return rate of adult birds in the following year.

MATERIAL AND METHODS

The study was carried out in 1995 and 1996 on Hornøya in northeastern Norway (70°22′N, 31°10′E) where 21,000 pairs of kittiwakes breed (Furness and Barrett 1985; R. T. Barrett, unpubl. data). Potential predators of kittiwake eggs, chicks, and sometimes adults were Herring Gulls (*Larus argentatus*; 15,000 pairs breeding on Hornøya), Great Black-backed Gulls (*L. marinus*; 200 pairs, Furness and Barrett 1985), and 2–3 pairs of Common Ravens (*Corvus corax*). The study area covered two parts of the cliff on the northern part of the island. The two plots were approximately 100 m apart and out of sight of each other. These two plots were similar in physical parameters such as topography, steepness, height of the cliffs, distance from the sea, and nest density.

Before hatching, all nests containing clutches of two eggs were marked in the two plots. Nests with one or three eggs were not used because this would have introduced clutch size as a possible confounding variable. About 75% of all nests contained two eggs. In the larger plot (89 marked nests), an intensive study of growth patterns in chicks and mass loss in adults very similar to that of Jacobsen et al. (1995) was carried out in both years. This plot will be referred to as the "high-disturbance plot". The disturbance consisted of (1) daily checks of all nests, (2) swapping of chicks within three days after hatching of a nest's second chick (cross-fostering), (3) weighing of chicks twice (9 d and 18 d post-hatch, respectively), and (4) capturing and weighing of individual adult birds twice (2–5 d and 19–23 d post-hatch, respectively).

Records of the hatching progress enabled us to determine the hatching peak of the high-disturbance plot, defined as the median hatching day. In 1995, chicks were weighed and measured two more times (9 and 18 d after this hatching peak). Chicks were weighed to the nearest gram, and their wing lengths (maximum flattened chord) were measured to the nearest millimeter. A body condition index was calculated, using the residuals from the regression between chick body masses and wing lengths (both being log-transformed). Adults were caught using noose-poles. Birds were then individually color-banded. For sexing birds, we measured their head+bill lengths and assumed the larger bird of a pair to be the male (Barrett et al. 1985). Birds of pairs that differed less than 2 mm in head+bill length were not sexed. To carry out this study, the high-disturbance plot was visited and disturbed every day for an average of 5 h each day over a 32 d period during June and July, resulting in a total disturbance of approximately 160 h.

The second (low-disturbance) plot (83 marked nests) was visited twice only during the chick-rearing period for a total of approximately 4 h. The visits took place 9 and 18 d after the hatching peak in the high-disturbance plot. In 1995, all chicks were weighed and measured during these visits; in 1996 they were only counted. After completion of the 1995 study, adult birds in the low-disturbance plot were caught using noose-poles, color-banded and sexed.

In 1995, the nest attendance of the adult birds in both plots was recorded for 13 d starting on 4 July, which was 7 d after the hatching peak. Attendance was defined as the number of adult birds at a nest during twice-daily checks; once in the morning before research activity started, and once in the evening, about 30 min after the end of the research activity in the high-disturbance plot. A total of 42 high-disturbance and 26 low-disturbance nests was observed, but not all were observed during every check. Attendance data were collected from a blind (i.e., without disturbance).

In 1996 and 1997, both plots were searched for returned birds, which could be identified by their unique color band combinations. Only birds that had been sexed were considered in computing the return rate. Clutch sizes laid in 1996 by females that were or were not disturbed in 1995 were recorded.

As a supplemental approach to comparing the high-disturbance with the low-disturbance plot, we calculated the isolated effect of specific kinds of disturbance, viz. swapping of chicks, capture of adult birds, and weighing of chicks in the high-disturbance plot. Instead of using the low-disturbance plot as a comparison, in this analysis we used data collected on the days preceding and following a given disturbance in the comparisons. We did so by calculating the chick loss rate during the 24 h directly after the respective type of disturbance. These were compared with the daily rates of chick loss during the 1–2 d preceding and following the respective

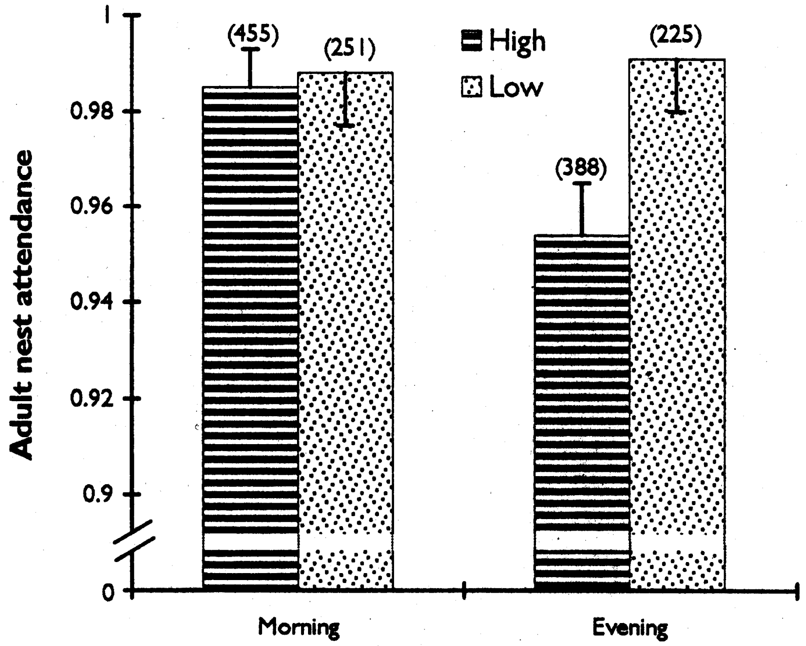

FIGURE 1. Number of adult kittiwakes attending a nest in a high-disturbance and a low-disturbance plot during twice daily snap-shot observations in 1995 (number of nest-observations in brackets). Morning observations were conducted before research activity in the high-disturbance plot started, evening observations after its completion.

day of disturbance. The method follows Mayfield's proposal (1961, 1975) to use nest-days as a measurement of nest exposure. Our chick loss rate was computed as the number of chicks lost per day, weighed by the number of nests that contained at least one chick prior to the respective day.

Unless otherwise stated, tests are logistic regressions (PROC CATMOD, PROC GENMOD, and PROC LOGISTIC, using maximum likelihood estimates, SAS Institute 1996). All *P*-values are two-tailed. Measures are expressed as means ±1 standard error (SE).

RESULTS

The mean number of adults attending each nest was lower in the high-disturbance plot (0.970 ± 0.007, $n = 843$) than in the low-disturbance plot (0.989 ± 0.008, $n = 476$; $\chi^2 = 4.08$, $P = 0.044$; Fig. 1). Although there was no difference in the overall attendance between the morning and evening observations ($\chi^2 = 1.90$, $P = 0.169$), the effect of disturbance was more pronounced in the evening (Fig. 1), though not significantly so (disturbance × time interaction, $\chi^2 = 2.83$, $P = 0.093$; all statistics from three-way logistic regression). Separate analyses of both plots showed that adult nest attendance was higher during the morning observations than during the evening observations in the high-disturbance area ($\chi^2_{1,841} = 5.58$, $P = 0.019$), but not in the low-disturbance area ($\chi^2_{1,474} = 0.04$, $P = 0.840$; Fig. 1).

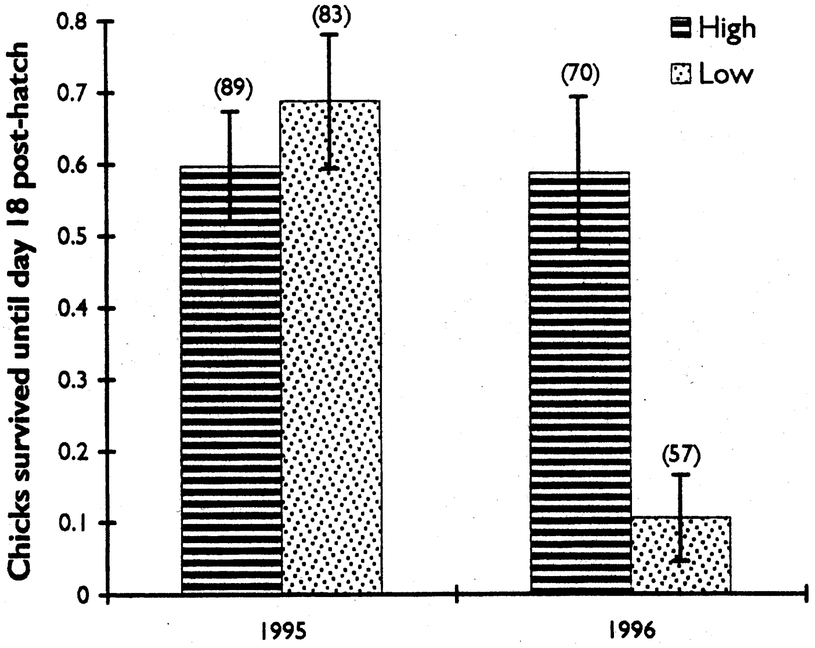

FIGURE 2. Number of kittiwake chicks per nest surviving to day 18 after the hatching peak (see text) during two years of the study, in high-disturbance and low-disturbance plots, respectively (number of nests in brackets).

The hatching peaks were on 27 June 1995 (27.1 ± 0.3 d, $n = 131$) and on 1 July 1996 (1.0 ± 0.4 d, $n = 107$), respectively. The number of chicks surviving to day 18 after the hatching peak was lower in the high-disturbance plot than in the low-disturbance plot in 1995 ($\chi^2_{1,176} = 6.52$, $P = 0.039$), but higher in 1996 ($\chi^2_{1,125} = 9.66$, $P = 0.008$), as was also illustrated by the disturbance × year interaction (three-way logistic regression with two main effects, viz. disturbance and year, and their interaction using data from both years: all $\chi^2_{1,324} > 10.2$, all $P < 0.002$); i.e., the relation between chick production and treatment differed significantly between years (Figure 2).

Nine and 18 d after the hatching peak, neither body masses, wing lengths, nor body condition indices differed between high-disturbance and low-disturbance chicks (Table 1). Chicks in the low-disturbance plot tended to gain slightly more mass between days 9 and 18, relative to their early body mass, but this tendency was not significant (Table 1).

The re-sighting rate of adult kittiwakes in the year after disturbance did not differ between high-disturbance and low-disturbance plots (Fig. 3). Males disturbed in 1995 showed an insignificant tendency in the expected direction ($\chi^2_{1,65} = 2.76$, $P = 0.098$; Fig. 3). Nor was there any difference between the clutch sizes laid by birds highly disturbed the previous year (1.92 ± 0.09, $n = 25$) and those laid by low-disturbance birds (1.97 ± 0.06, $n = 32$; $\chi^2 = 0.62$, $P = 0.430$).

The daily rate of chick loss was higher than expected by chance alone

TABLE 1. Kittiwake chick body mass and body condition in high- and low-disturbance plots. Chick body mass and wing length were measured 9 d (early) and 18 d (late) after the hatching peak (see text) in 1995. Body condition was defined as 1000 times the residuals from the regression between log-transformed body mass and wing length. Values give means ± 1 SE (number of nests in brackets). Tests performed were *t*-tests.

Parameter		Low-disturbance chicks	High-disturbance chicks	t	P
Body mass (g)	early	133.6 ± 9.2 (44)	146.0 ± 8.1 (51)	1.02	0.312
	late	269.0 ± 12.1 (36)	279.3 ± 10.8 (41)	0.64	0.524
Wing length (mm)	early	44.8 ± 2.9 (44)	48.8 ± 3.1 (51)	0.97	0.335
	late	107.7 ± 5.5 (36)	114.8 ± 5.7 (41)	0.91	0.365
Body condition	early	−45.82 ± 25.72 (44)	−3.76 ± 19.38 (51)	1.33	0.188
	late	3.45 ± 20.26 (36)	−0.77 ± 16.17 (41)	−0.16	0.870
Mass gain	absolute (g)	134.9 ± 5.3 (34)	131.2 ± 5.7 (40)	−0.48	0.634
	relative (%)	119.5 ± 11.3 (34)	101.8 ± 8.3 (40)	−1.29	0.200

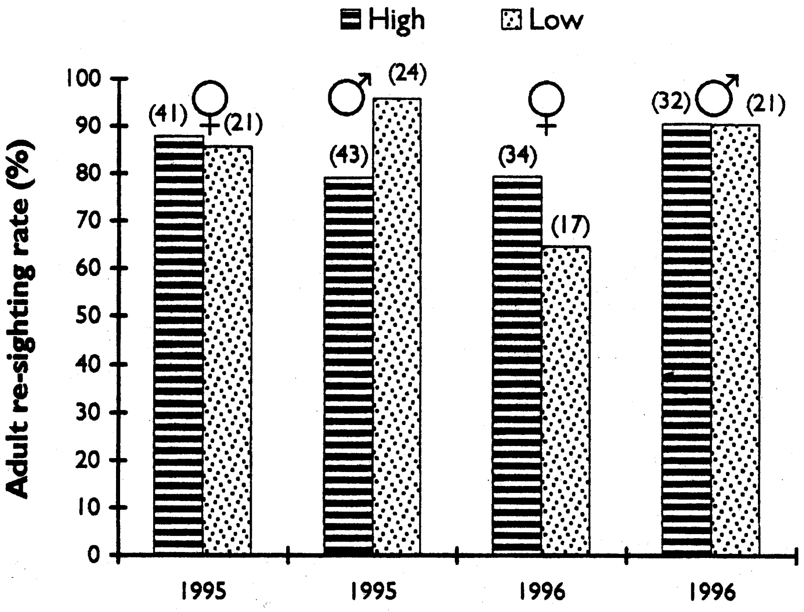

FIGURE 3. Proportion of adult kittiwakes re-sighted in the year following high and low levels of disturbance. Only birds that could be sexed are considered.

after the capture of adults (2–5 d post-hatch), and in 1995 also after the swapping of chicks (1–3 d post-hatch; Table 2). Weighing of chicks at 9 d post-hatch had no effect on the daily rates of chick loss, nor did swapping of chicks in 1996 (Table 2).

DISCUSSION

We examined the effect of investigation-caused disturbance on the breeding performance of kittiwakes. This was done by comparing a high-disturbance plot with a low-disturbance plot. One problem with carrying out studies such as this one is that it would be optimal to randomize chicks, assigning them with the same probability to high-disturbance and low-disturbance nests within the same plot. This is, however, impractical in colonial seabirds, as disturbance of one nest cannot be restricted to that nest only, but will spread through the colony to the neighboring nests. As a result, two distinct parts of the colony have to be used. This leads to the problem that other factors may confound the results (cf., Pierotti 1982; Burger et al. 1995). In our case, we assumed a similar distribution of hatching dates in both plots without being able to test this assumption. However, the fact that the wing lengths of chicks, an indicator of chick age (Barrett and Runde 1980), on given days did not differ between the plots (Table 1), corroborated our assumption. Other approaches would be either to use several low-disturbance plots, rather than a single one and/or to use absence and presence of a certain type of disturbance on different days as a means of quantifying the impact of disturbance. Though such comparisons cannot measure the cumulative

TABLE 2. Number of kittiwake chicks dying per nest per day during the first 24 h after a specified kind of disturbance, compared to the preceding and subsequent 24 h or 48 h (amount of nest exposure in brackets, i.e., number of nest-days). Tests performed were logistic regressions, using chick losses (none/one/two) per nest-day as dependent and the absence vs. presence of a given kind of disturbance prior to the given day as independent variables.

		Daily chick loss (%)			
Kind of disturbance	Year[a]	Before, and more than 1 d after, treatment	Within 24 h after treatment	χ^2	P
Swapping of chicks[b]	1995	5 (132)	29 (42)	9.52	0.009
Swapping of chicks[b]	1996	19 (95)	19 (32)	1.43	0.489
Capture of parents[c]	1995 + 96	4 (165)	12 (162)	4.72	0.030
Weighing of chicks[d]	1995 + 96	8 (118)	7 (61)	0.06	0.805

[a] When differences between years were insignificant, data for both years of the study were combined.

[b] Calculated for the first 4 d after hatching of a nest's second chick. Swapping took place within the first 3 d of this period.

[c] Calculated for the first 6 d after hatching of a nest's second chick. Capture of adults took place between the second and fifth day after hatching of a nest's second chick.

[d] Calculated for the ninth until eleventh days after hatching of a nest's second chick. Weighing took place at day 9 post-hatch.

effect of disturbance over periods of several days, they have the advantage of being accomplishable without the need of a control plot (see Table 2).

Furthermore, effects of investigator disturbance can vary significantly between years (Fig. 2, Table 2). This is in accordance with the hypothesis that the readiness of long-lived birds to desert their nests should vary between years in relation to environmental factors (Erikstad et al. 1998). There may therefore be a need for not only more than one low-disturbance plot but also for more than one year of study before one can conclude whether or not a species is susceptible to disturbance.

Adult nest attendance.—Adult nest attendance was decreased by disturbance. Disturbance may have caused absence from nests either directly or indirectly through increased stress. The latter may lead to an increase in the daily energy expenditure in adults or chicks or both (Hubert and Hüppop 1993; Gabrielsen and Smith 1995; Hüppop 1995), thus increasing food requirements and thereby parental workloads. It is, however, difficult to distinguish between such indirect effects and the absence caused directly by the birds being flushed off their nests by investigators. Nevertheless, our results provide evidence for the importance of the direct effect, in that nest attendance at the high-disturbance plot was lower in the evening, after a day of disturbance, than in the morning. There was no such difference at the low-disturbance plot (Fig. 1).

Nestling survival.—We also found a lower chick survival among high-disturbance birds in 1995 (Fig. 2). Lower fledging success as a response to investigator disturbance has been reported for other seabirds (Kadlec and Drury 1968; Gillett et al. 1975; Ollason and Dunnet 1978; Fetterolf 1983; Safina and Burger 1983; Mousseau 1984; Piatt et al. 1990; Rodway et al. 1996). In the second year of our study (1996), the trend was, however, reversed. Chicks in the low-disturbance nests had a survival probability until day 18 post-hatch that was only 18% of that of the high-disturbance chicks. Robert and Ralph (1975) also found that the survival of Western Gull (*L. occidentalis*) chicks was inversely proportional to the degree of disturbance. Their explanation of habituation is, however, not compatible with our data for 1995. The pattern observed by us in 1996 can, therefore, not be explained in terms of disturbance of kittiwakes. The most parsimonious explanation is that a factor totally unrelated to the disturbance caused these differences. This interpretation cannot be excluded because the birds could not be randomized. However, we believe these unexpected results may be explained by the effects of disturbance on one of the kittiwakes' principal predators, the Herring Gull. Herring Gulls breed all over the island, including the slopes below the cliff faces on which this study was carried out and to which investigators withdrew to weigh, measure, band, and observe the kittiwakes. In other words, any disturbance of the kittiwakes also involved regular, and probably greater disturbance of the gulls nesting nearby. Disturbance has been shown to cause Herring Gulls (N. van Swelm, pers. comm.) and other birds (Conover and Miller 1978; Knight and Fitzner 1985) to move to another breeding site in a year following disturbance. It is thus possible that after the first year with high levels of disturbance, the gulls, which are more susceptible to disturbance than kittiwakes (cf., Gabrielsen and Mehlum 1989; Götmark 1992; Kania 1992; Wanless 1992), may have moved to other, less disturbed areas of the colony in the second year of the study. In these areas, the predation pressure on kittiwakes might consequently have increased. As the low-disturbance plot was quite close to the high-disturbance plot, some of the moving gulls may have settled there in 1996. Other examples of the predator of the focal species being more susceptible to disturbance than the focal species itself have been reported by Götmark and Åhlund (1984), Shields and Parnell (1986), and MacIvor et al. (1990).

It is not appropriate to use this ad hoc explanation for testing our data which were collected on the basis of a different working hypothesis (Popper 1959), especially because no counts of Herring Gulls were made. However, it leads to a clear recommendation: studies of disturbance in colonially breeding birds should also take into account and quantify the presence of any predators near the prime target species.

Chick growth and body condition.—In addition to chick survival, chick quality is another factor determining breeding success. In alcid and other larid species, it has been found that high-disturbance chicks grow more slowly and/or reach a lower fledging mass (Cairns 1980; Harris and Wanless 1984; Pierce and Simons 1986; Hatchwell 1989). Our results on chick body mass gain have the same tendency, but are not significant (Table 1).

Adult re-sighting rates.—Males from low-disturbance nests had a 17%

higher probability of being observed in the following year than males from high-disturbance nests in the first year of the study (Fig. 3). However, this tendency was not statistically significant, nor were the observations from the second year or from females in the expected direction. It is important to remember, however, that statistical insignificance of a given effect does not necessarily mean it is biologically insignificant (cf., Shrader-Frechette and McCoy 1992). The trend in male survival would have been statistically significant using a one-tailed probability, which could have been defended in this case. A lower fraction of observed birds in the high-disturbance group is strong evidence for a fitness cost of disturbance. This conclusion holds, independent of whether the birds not observed died, were intermittent breeders, had early breeding failures, or moved to another (part of the) colony (cf., Fairweather and Coulson 1995). Similar effects of disturbance are known from the Fulmar (*Fulmarus glacialis*; Dunnet and Ollason 1978; Ollason and Dunnet 1978).

As regards breeding success in the year following disturbance, it has been demonstrated by Rodway et al. (1996) that the respective differences between high-disturbance and low-disturbance plots persisted in the following year in the Atlantic Puffin (*Fratercula arctica*). This effect could have been brought about by lower return rates of high-disturbance adults, rather than by decreased breeding performance. We were able to distinguish between these two causes, but could not find the latter effect in the kittiwake, using clutch sizes laid as an indicator of investment into breeding following a year with disturbance.

Chick loss after disturbance.—The design of the study that was responsible for the disturbance in the high-disturbance plot aimed to minimize disturbance. However, the comparison of the daily rate of chick loss between days with and without a certain type of disturbance (Table 2) shows that even these routines could not exclude disturbance as a cause of chick loss. Chick loss occurred more often than would be expected by chance after the early capture of adults, and, in one year, after swapping of chicks. We were unable to distinguish directly different causes of chick loss because we only checked nests once a day. Mostly, dead chicks were simply missing, rather than lying in the nest. It was therefore impossible to reconstruct whether chick loss was due to predation, or whether the chick died of other reasons and was subsequently removed by siblings, parents, or predators.

However, one reason for chick loss during this period is that kittiwakes are not fully homeothermic until an age of 6–8 d (Barrett 1978). The early capture of adults took place at a chick age of 2–5 d (i.e., well within the period when chicks are dependent upon their parents for maintaining their temperature). It is possible that the reason for the increase in chick loss after capture of adults and after swapping (1–3 d post-hatch) was due to hypothermia because the adults returned too late to their nests. It seems that while the disturbance mainly affects the adult birds, the chicks are affected only indirectly. This is in agreement with observations from Harris and Wanless (1984) and Ollason and Dunnet (1980).

Conclusions.—The extent of the disturbance effect, if at all negative, was relatively low. Taking into consideration the uncommonly high disturbance levels in our study, this means that biases in results of previous—and future—studies of the kittiwake may be regarded as negligible. On the other hand, research activity in our study was kept to the minimum possible necessary to carry out our work. The fact that we could, nevertheless, demonstrate negative, if weak, effects of disturbance, emphasizes the importance of carefully designing studies to reduce disturbance (Rodgers and Burger 1981; Götmark 1992).

ACKNOWLEDGMENTS

We thank Laila Dalhaug and Magne Asheim for help during the field work, and C. Ray Chandler, Kjell Einar Erikstad, Per Fauchald, Geir W. Gabrielsen, Sveinn Are Hanssen, Michael P. Harris, Ralph D. Morris, and Torkild Tveraa for comments on the manuscript. The project was financed by the Governor of Finnmark and Tromsø University Museum. H. S. received a scholarship from the Friedrich-Ebert-Stiftung.

LITERATURE CITED

BARRETT, R. T. 1978. Adult body temperature and the development of endothermy in the Kittiwake (*Rissa tridactyla*). Astarte 11:113–116.

———, AND O. J. RUNDE. 1980. Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. Ornis Scand. 11:228–235.

———, R. FIELER, T. ANKER-NILSSEN, AND F. RIKARDSEN. 1985. Measurements and weight changes of Norwegian adult Puffins *Fratercula arctica* and Kittiwakes *Rissa tridactyla* during the breeding season. Ringing Migr. 6:102–112.

BROWN, K. M., AND R. D. MORRIS. 1994. The influence of investigator disturbance on the breeding success of Ring-billed Gulls (*Larus delawarensis*). Colonial Waterbirds 17:7–17.

———, AND ———. 1995. Investigator disturbance, chick movement, and aggressive behavior in Ring-billed Gulls. Wilson Bull. 107:140–152.

BURGER, J., I. C. T. NISBET, J. M. ZINGO, J. A. SPENDELOW, C. SAFINA, AND M. GOCHFELD. 1995. Colony differences in response to trapping in Roseate Terns. Condor 97:263–266.

CAIRNS, D. 1980. Nesting density, habitat structure and human disturbance as factors in Black Guillemot reproduction. Wilson Bull. 92:352–361.

CONOVER, M. R., AND D. E. MILLER. 1978. Reaction of Ring-billed Gulls to predators and human disturbances at their breeding colonies. Proc. Colonial Waterbird Group 1978: 41–47.

DAVIS, H., AND D. BALFOUR, EDS. 1992. The inevitable bond: examining scientist–animal interactions. Cambridge University Press, Cambridge, U.K.

DUFFY, D. C. 1979. Human disturbance and breeding birds. Auk 96:815–816.

DUNNET, G. M., AND J. C. OLLASON. 1978. The estimation of survival rate in the fulmar, *Fulmarus glacialis*. J. Anim. Ecol. 47:507–520.

ERIKSTAD, K. E., P. FAUCHALD, T. TVERAA, AND H. STEEN. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79:1781–1788.

FAIRWEATHER, J. A., AND J. C. COULSON. 1995. The influence of forced site change on the dispersal and breeding of the Black-legged Kittiwake *Rissa tridactyla*. Colonial Waterbirds 18:30–40.

FETTEROLF, P. M. 1983. Effects of investigator activity on Ring-billed Gull behavior and reproductive performance. Wilson Bull. 95:23–41.

FURNESS, R. W., AND R. T. BARRETT. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16:305–313.

GABRIELSEN, G. W., AND F. MEHLUM. 1989. Kittiwake activity monitored by telemetry. Proc. Int. Symp. Biotelem. 10:421–429.

———, AND E. N. SMITH. 1995. Physiological responses of wildlife to disturbance. Pp. 95–

106 *in* R. L. Knight and K. J. Gutzwiller, eds. Wildlife and recreationists: coexistence through management and research. Island, Washington D.C.

GASTON, A. J., I. L. JONES, AND D. G. NOBLE. 1988. Monitoring Ancient Murrelet breeding populations. Colonial Waterbirds 11:58–66.

GILLETT, W. H., J. L. HAYWARD JR., AND J. F. STOUT. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492–495.

GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithol. 9:63–104.

———, AND M. ÅHLUND. 1984. Do field observers attract nest predators and influence nesting success of common eiders? J. Wildl. Manage. 48:381–387.

HARRIS, M. P., AND S. WANLESS. 1984. The effects of disturbance on survival, age and weight of young Guillemots *Uria aalge.* Seabird 7:42–46.

HATCHWELL, B. J. 1989. The effects of disturbance on the growth of young Common Guillemots *Uria aalge.* Seabird 12:35–39.

HUBERT, B., AND O. HÜPPOP. 1993. The influence of excitement on heart rate and oxygen consumption of kittiwakes (*Rissa tridactyla*). Proc. Int. Congr. Appl. Ethol. Berl.: 541–543.

HÜPPOP, O. 1995. Störungsbewertung anhand physiologischer Parameter [Engl. abstr.]. Ornithol. Beob. 92:257–268.

JACOBSEN, K.-O., K. E. ERIKSTAD, AND B.-E. SÆTHER. 1995. An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla.* Ecology 76:1636–1642.

KADLEC, J. A., AND W. H. DRURY. 1968. Structure of the New England Herring Gull population. Ecology 49:644–676.

KANIA, W. 1992. Safety of catching adult European birds at the nest. Ringers' opinions. Ring 14:5–50.

KNIGHT, R. L., AND R. E. FITZNER. 1985. Human disturbance and nest site placement in Black-billed Magpies. J. Field Ornithol. 56:153–157.

LENINGTON, S. 1979. Predators and Blackbirds: the "uncertainty principle" in field biology. Auk 96:190–192.

MACIVOR, L. H., S. M. MELVIN, AND C. R. GRIFFIN. 1990. Effects of research activity on piping plover nest predation. J. Wildl. Manage. 54:443–447.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MOUSSEAU, P. 1984. A comparison of two methods to assess the breeding success of Ring-billed Gulls. J. Field Ornithol. 55:151–159.

OLLASON, J. C., AND G. M. DUNNET. 1978. Age, experience and other factors affecting the breeding success of the fulmar, *Fulmarus glacialis,* in Orkney. J. Anim. Ecol. 47:961–976.

———, AND ———. 1980. Nest failures in the Fulmar: the effect of observers. J. Field Ornithol. 51:39–54.

PARSONS, J. 1975. Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44:553–573.

PIATT, J. F., B. D. ROBERTS, W. W. LIDSTER, J. L. WELLS, AND S. A. HATCH. 1990. Effects of human disturbance on breeding Least and Crested Auklets at St Lawrence Island, Alaska. Auk 107:342–350.

PIERCE, D. J., AND T. R. SIMONS. 1986. The influence of human disturbance on Tufted Puffin breeding success. Auk 103:214–216.

PIEROTTI, R. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63:854–868.

POPPER, K. R. 1959. The logic of scientific discovery. Hutchinson, London.

ROBERT, H. C., AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. Condor 77:495–499.

RODGERS, J. A., JR., AND J. BURGER. 1981. Concluding remarks: symposium on human disturbance and colonial waterbirds. Colonial Waterbirds 4:69–70.

RODWAY, M. S., W. A. MONTEVECCHI, AND J. W. CHARDINE. 1996. Effects of investigator disturbance on breeding success of Atlantic puffins *Fratercula arctica.* Biol. Conserv. 76: 311–319.

SAFINA, C., AND J. BURGER. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. Condor 85:164–171.

SAS INSTITUTE. 1996. The SAS system for Windows: release 6.12. SAS Institute, Cary, North Carolina.

SHIELDS, M. A., AND J. F. PARNELL. 1986. Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. Auk 103:531–539.

SHRADER-FRECHETTE, K. S., AND E. D. MCCOY. 1992. Statistics, costs and rationality in ecological inference. Trends Ecol. Evol. 7:96–99.

WANLESS, S. 1992. Effects of tail-mounted devices on the attendance behavior of Kittiwakes during chick rearing. J. Field Ornithol. 63:169–176.

Received 25 May 1999; accepted 28 January 2000.