

RESEARCHER HANDLING OF INCUBATING ATLANTIC PUFFINS *FRATERCULA ARCTICA* HAS NO EFFECT ON REPRODUCTIVE SUCCESS

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SUMMARY

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Many seabirds are sufficiently sensitive to disturbance, especially during early incubation, that protocols for monitoring breeding success often preclude handling of incubating adults to avoid changing the phenomenon being measured. However, this risk-averse approach can discourage investigation of events that can be detected only in the early part of the breeding season, such as “carry-over” effects from the winter. Wishing to investigate the possibility of physiological carry-over events affecting Atlantic Puffins *Fratercula arctica* on Machias Seal Island, Bay of Fundy, Canada, we first measured the impact on hatching and breeding success of taking blood samples from adults early in the incubation period in 2009–2012, and also compared chick growth rates with those of chicks in burrows where adults were not handled during incubation in 2010–2012. Unexpectedly, we found no significant differences in hatching success, breeding success, or chick growth rates between experimental burrows and controls in any year. We also found that many adults blood-sampled in one year returned to breed in the same burrow in later years, although we have no comparable data from control burrows. We conclude that the influence of disturbance by researchers during early incubation on Atlantic Puffin breeding success is colony-specific, as has been suggested by others. We suggest that researchers assess such impacts in their study system rather than assume effects to be as described elsewhere.

Key words: Atlantic puffin, breeding success, chick growth rate, disturbance, Machias Seal Island

INTRODUCTION

All wildlife research must balance the need for data collection with the need to minimize the impact on the system being studied. Numerous studies have found that anthropogenic disturbance generally has detrimental effects on bird productivity (reviewed in Carney & Sydeman 1999, Carey 2009), but these impacts are highly variable and not always negative (Ibáñez-Álamo *et al.* 2012). The prevailing paradigm among researchers is that any disturbance should be kept to an absolute minimum. However, as conservation questions become more pressing and information about all aspects of the life of birds becomes more necessary, this paradigm severely limits the questions that can be addressed.

At Machias Seal Island (MSI), New Brunswick, Canada, Atlantic Puffins *Fratercula arctica* have been studied extensively since 1995 (Diamond & Devlin 2003, Gaston *et al.* 2009), but disturbance has been minimized during the incubation period because of the species’ reputation of high sensitivity to researcher disturbance during this period (Ashcroft 1979, Rodway *et al.* 1996, Baillie 2001, Harris & Wanless 2011). We have maintained a monitoring regime that involves minimal disturbance (once only during the incubation period with no handling of birds), very similar to that used in other puffin studies. Because of major changes in the island’s seabird community (Gaston *et al.* 2009) and the environment around MSI (Breton & Diamond 2014), questions about the physiological health of the MSI puffins began to arise. The questions could best be answered by collecting blood samples from incubating adults. After handling and blood-sampling adults

during incubation (experimental burrows), we followed the fate of each nest later in the breeding season to detect any effects of our disturbance on hatching (chicks hatched/egg laid) and breeding success (fledgings/egg laid) and on chick growth rates. We compared these measures with those from burrows where adults were not handled during incubation (control burrows). We predicted that the hatching and breeding success and rates of chick growth (mass and wing length) of experimental burrows would be lower than that of control burrows. Since some studies (e.g. Rodway *et al.* 1996) found that early disturbance also reduced return rates of adults in future breeding seasons, we recorded these incidentally, but since adults are not monitored routinely in undisturbed burrows no statistical comparisons could be made.

STUDY AREA AND METHODS

This study was undertaken on MSI (44°30’N, 67°06’W) during the summers of 2009–2012. MSI is a small (9.5 ha), treeless island with a grassy interior and exposed bedrock coastline separated by a boulder berm (Diamond & Devlin 2003). The island lies about 19 km from both the Maine coast and the island of Grand Manan, New Brunswick, at the mouth of the Bay of Fundy.

To test the effect of bleeding adult puffins early in incubation for a larger study of physiological carry-over effects (R.L.H., unpubl. data.), we established experimental burrows during early incubation (mid-May) by selecting burrows in which there was an egg when first checked; consequently, such burrows were short enough that the incubating adult could be extracted by hand. In 2009 we

established 20 new experimental burrows; in 2010 we established 18 new experimental burrows and reused nine from 2009; in 2011 we established eight new experimental burrows and reused 22 from the previous years; and in 2012 we established six new experimental burrows and reused 24. The burrows were initially in only two areas of the island-wide puffin habitat but were distributed more broadly in the last two years.

Control burrows were chosen from previously marked burrows in the colony used for long-term productivity monitoring on the island (Diamond & Devlin 2003), which contained an egg but no adult when checked in early incubation (at the same time as experimental burrows were sampled). These control burrows were spread throughout the island-wide puffin colony in all four years.

We restricted handling and disturbance to burrows where an egg was laid in early to mid-May in order to avoid re-nesting birds, except in 2011 when some ($n = 7$) were handled and bled in early June. Therefore, in 2011 our control burrow sample also included burrows established in early June for comparison's sake.

In 2009 two experimental burrows were dropped because in one no brood patch on the adult was confirmed at the time of sampling, and in the other no egg or chick was ever confirmed in that season. In the remaining 18 burrows, eggs were not explicitly observed at the time of establishment, but all adults had brood patches and the presence of eggs was either confirmed later by direct observation or inferred from the chick's age during burrow checks after hatching. In 2010 two experimental burrows were dropped, one because no egg was confirmed in it and the other because the burrow entrance could not be distinguished later in the season. In the remaining 25 burrows, an egg was confirmed at the time of handling and the fate of each burrow could be determined.

In 2011 one experimental burrow was dropped because it eventually became connected to another active burrow, making it impossible to distinguish which chick belonged to the adult that was handled early in the season. In the 29 remaining experimental burrows, an egg was confirmed in each burrow at the time of adult handling.

In 2012 one experimental burrow was dropped because, after initial handling, the burrow was found to be much longer than the researchers' arms, making the occupants inaccessible. The 29 burrows that were followed all had eggs in them at the time the adult was bled.

We sampled birds in experimental burrows on 13–14 May 2009; 11–13 and 22–25 May 2010; 18–20 and 23–26 May and 2 and 8 June 2011; and 17 and 19 May 2012.

Handling of adult puffins at experimental burrows during incubation began with researchers grubbing (extracting) them from their burrows when they were found incubating an egg (or, if no egg was confirmed, when the adult had an obvious brood patch). Four to six micro-capillary tubes of blood (<400 μ L total volume) were taken from the brachial vein of each adult using a 25-gauge needle. Bleeding was stopped with a cotton ball pressed against the puncture site while measures of body mass, size (wing length, bill depth, culmen length, and head-bill length; Friars & Diamond 2011), and presence of brood patch were recorded. Previously unbanded puffins were banded with a stainless steel US Geological Service band and an incoloy field-readable band (Porzana Ltd.). Previously banded puffins with

unreadable or worn bands had their bands replaced. Most birds were returned to their burrows within 20 min of their initial grubbing, although up to 30 min was needed in a few cases. Researcher activity in any one area of the colony was restricted to 2 h at a time to minimize disturbance to all birds in the area.

In all years, control burrows were checked for chick hatching success ~30 d following the initial discovery of an egg, and if no egg was found they were checked every 3–5 d after that until a chick was found. Following chick hatch, burrows were checked twice during the linear growth phase (10–30 d) and the growth rate of chicks determined; subsequent checks were made every 3–5 d to determine whether chicks fledged. A chick was assumed to have fledged if it disappeared after it reached 35 d old, unless it was later found dead. During chick brooding, any adults that were found in the burrows during checks were removed, banded or identified, measured, and returned to their burrows following handling. Adult encounters became much less common as the brooding period progressed in all years.

Experimental burrows in 2010, 2011 and 2012 were treated in the same way as the control burrows following the initial handling. In these years, the experimental burrows were monitored for hatching success, chick growth and breeding success in the same manner as the control burrows. Adults were also handled following chick hatch in experimental burrows in the same way as the control burrows.

In the 2009 experimental burrows, researchers avoided all activity at the burrows for one to two weeks after initial adult handling; after that, the burrows were carefully checked (remotely, using a flexible video probe) for presence of an adult, egg, or chick at varying intervals until fledging, but no further handling of adults or chicks was done after the initial handling and bleeding during incubation.

Experimental burrows were classified as either “newly handled,” when the puffin that was bled during incubation had not previously been bled, or “previously handled,” when the puffin that was bled during incubation had been bled before. Control burrows were compared with both the smaller subset of experimental burrows that included only newly handled birds, since previously handled birds may become accustomed to the handling and therefore bias the results, as well as to the full complement of experimental burrows that included previously handled birds.

For most comparisons of hatching and breeding success rates between treatment groups in each year, and pooled across all study years, Pearson's chi-squared tests were used. However, in some comparisons between treatment groups (2009 burrow fledging success, 2010 burrow hatching success and 2011 burrow hatching success), two-tailed Fisher's exact test was used because some expected values in the contingency tables were below five.

For comparisons of mass growth rates between treatment groups in 2010 and 2011, *t*-tests were used. For 2012 data, and when all years were pooled, the mass growth rates were compared using Wilcoxon signed-rank tests because the growth rates were not normally distributed. For comparisons of wing chord growth rates between treatment groups in 2011 and 2012, *t*-tests were used; in 2010, and when all years were pooled, the comparisons between treatment groups were done using Wilcoxon signed-rank tests (*W*) due to the non-normality of growth rates. All statistics were run using R statistical software, version 2.15.3.

RESULTS

Hatching and breeding success and growth rates

In all years individually, and when pooled, there were no significant differences in hatching success between control burrows and experimental burrows, whether or not an adult had been bled in a previous year or years (Table 1; $P > 0.05$ in all cases). The same was true for breeding success (Table 2).

Mean mass growth rates (g/d) did not differ significantly between control burrows and either newly bled experimental burrows or the full cohort of experimental burrows (including both previously bled and unbled adults) in any of the years when growth rates were calculated (2010–2012), or when years were pooled (Table 3).

There was no significant difference in average wing chord growth rates (mm/d) of puffin chicks during the linear growth period of growth between control burrows and either the newly bled control burrows or the full experimental cohort in 2010, 2011 or 2012, or when years were pooled (Table 4).

Adult return rates

Our initial study design did not include tracking adult return rates, but when we found adults that had been bled in previous years in the same burrow, we concluded that this phenomenon was worth documenting (Table 5), in view of one other study that found effects of research disturbance on burrow use in subsequent years (Rodway *et al.* 1996). Since we did not routinely handle adults in control burrows, we simply reported on the return rates we found

TABLE 1

Hatching success rates (eggs hatched/eggs laid) of Atlantic Puffin eggs in burrows where no adult was handled during incubation (control) and where an adult was blood-sampled, measured and banded during incubation (experimental)

Year	Value (%)		
	Control	Experimental (excluding repeats) ^a	Experimental (including repeats) ^b
2009	18/20 (90.0)	NA ^c	NA ^c
2010	25/33 (75.6)	14/17 (82.4)	21/25 (84.0)
2011	14/19 (73.7)	10/13 (76.9)	21/29 (72.4)
2012	9/19 (47.4)	9/13 (69.2)	21/29 (72.4)
All ^d	48/71 (67.6)	33/43 (76.7)	63/83 (75.9)

^a Burrows where only newly bled birds were handled during incubation.

^b Include burrows where either previously bled birds or newly bled birds were handled during incubation.

^c Hatch rates were not measured in 2009.

^d Data pooled from 2010 to 2012.

TABLE 2

Breeding success rates (chicks fledged/eggs laid) of Atlantic Puffins in burrows where no adult was handled during incubation (control) and where an adult was blood-sampled, measured and banded during incubation (experimental)

Year	Value (%)		
	Control	Experimental (excluding repeats) ^a	Experimental (including repeats) ^b
2009	13/20 (65.0)	15/18 (83.3)	15/18 (83.3)
2010	20/33 (60.6)	12/17 (70.6)	19/25 (76.0)
2011	11/19 (57.9)	6/13 (46.2)	15/29 (51.8)
2012	8/19 (42.1)	7/13 (53.8)	18/29 (62.1)
All ^c	52/91 (57.1)	40/61 (65.6)	67/101 (66.3)

^a These are the burrows where only newly bled birds were handled during incubation.

^b These include the burrows where either previously bled birds or newly bled birds were handled during incubation.

^c Data pooled from all years.

TABLE 3

Average daily mass growth rates (g/d) of Atlantic Puffin chicks in burrows where no adult was handled during incubation (control) and where an adult was bled, measured and banded during incubation (experimental)

Year	Control chick mass growth rate \pm SD (n)	Experimental (including repeats) ^a		Experimental (excluding repeats) ^b	
		Chick mass growth rate \pm SD (n)	Comparison with control, t or W statistic (P value)	Chick mass growth rate \pm SD (n)	Comparison with control, t or W statistic (P value)
2010	4.38 \pm 2.46 (17)	5.47 \pm 2.81 (21)	-0.253 (0.80)	4.62 \pm 2.83 (14)	-1.276 (0.21)
2011	6.55 \pm 1.71 (11)	4.83 \pm 3.00 (13)	1.754 (0.095)	5.98 \pm 2.26 (5)	0.510 (0.629)
2012	4.83 \pm 5.75 (7) ^c	6.04 \pm 3.03 (15)	31 (0.275)	5.72 \pm 3.66 (8)	8 (0.149)
All ^d	5.15 \pm 3.24 (35) ^c	5.49 \pm 2.93 (48)	768 (0.422)	5.20 \pm 2.96 (27)	464 (0.910)

^a These include the burrows where either previously bled birds or newly bled birds were handled during incubation.

^b These are the burrows where only newly bled birds were handled during incubation.

^c Non-normally distributed.

^d Data pooled from all years.

without being able to make statistical comparisons. Of the puffins that were sampled in 2009, 54.5% were found breeding in the same burrow in one or both of the next two years (2010–2011); of the puffins that were disturbed in 2010, 64.5% were found to have returned and bred in the same burrow within one to three years of disturbance (2011–2013). Of the puffins bled in 2011, 50% were found breeding in the same burrow within two years of the disturbance (2012–2013). Experimental burrows were not searched systematically for banded adults in 2013 because of the abnormally late season and low success in that year, apparently related to unusual oceanographic events and puffin mortality the previous winter (A.W.D. unpubl. data).

Of the 10 birds blood-sampled in 2009 that were not subsequently found breeding in the same burrow, one was confirmed breeding in a nearby burrow, three were seen elsewhere in the colony but not confirmed to be breeding, and six were not seen anywhere in subsequent years (as of August 2013). Only one of the 11 non-returning (in 2011–2013) birds from 2010 was seen elsewhere in the colony. Half (eight of 16) of all non-returning (in 2012 or 2013) birds from 2011 were seen elsewhere within the colony. An additional bird was found breeding in a nearby burrow.

DISCUSSION

Our results illustrate that researcher handling and blood-sampling of adult Atlantic Puffins did not increase reproductive failure at

MSI, although it was conducted during early incubation when the risk of abandonment is expected to be highest (Criscuolo 2001). Of the nests that did fail, we were unable to determine when and why they failed, as we deliberately limited disturbance to a single event during the incubation period. Immediate abandonment by handled puffins would likely show up in lower hatching success, and longer-term stress on the birds due to handling could be revealed by lower chick growth rates, lower breeding success, or the failure to breed in following years; however, none of these effects was observed.

Although Atlantic puffins at other colonies have been considered particularly sensitive to disturbance during incubation (Rodway *et al.* 1996, Harris & Wanless 2011, Harris *et al.* 2012), other researchers (including Rodway *et al.* 1996) and our own results from MSI suggest that disturbance response may vary among colonies. This difference may lie in the type and degree of disturbance; on Skomer Island, Wales, nest failure varied with timing and frequency of burrow visitation before and after chicks hatched (Ashcroft 1979). At Great Island, Newfoundland, researchers found significantly lower breeding success at burrows where they disturbed birds by handling during incubation compared with those that were undisturbed during incubation (Rodway *et al.* 1996).

Undoubtedly, breeding success is not just a function of the amount of disturbance experienced by incubating birds. For instance, in 1992 (Regehr & Rodway 1999) and 1968–1969 (Nettleship 1972) puffin breeding success on Great Island was lower (34% and

TABLE 4
Average daily wing chord growth rates (mm/d) of Atlantic Puffin chicks in burrows where no adult was handled during incubation (control) and where an adult was bled, measured and banded during incubation (experimental)

Year	Control chick wing chord growth rates \pm SD (n)	Experimental (including repeats) ^a		Experimental (excluding repeats) ^b	
		Chick wing growth rates \pm SD (n)	Comparison with control, <i>t</i> or <i>W</i> statistic (<i>p</i> value)	Chick wing growth rates \pm SD (n)	Comparison with control, <i>t</i> or <i>W</i> statistic (<i>p</i> value)
2010	3.08 \pm 0.35 (17)	2.98 \pm 0.74 (21) ^c	177.5 (0.988)	2.82 \pm 0.80 (14) ^c	144.5 (0.321)
2011	3.16 \pm 0.65 (11)	2.87 \pm 0.58 (13)	1.139 (0.268)	2.93 \pm 0.61 (5)	0.689 (0.510)
2012	3.01 \pm 0.78 (7)	3.09 \pm 0.65 (15)	0.411 (0.690)	2.95 \pm 0.65 (8)	0.203 (0.843)
All ^d	3.09 \pm 0.54 (35)	2.98 \pm 0.67 (48) ^c	912.5 (0.621)	2.88 \pm 0.71 (27) ^c	555.5 (0.241)

^a These are the burrows where only newly bled birds were handled during incubation.

^b These include the burrows where either previously bled birds or newly bled birds were handled during incubation.

^c Non-normally distributed.

^d Data pooled from all years.

TABLE 5
Fate of blood-sampled adult Atlantic Puffins in years following bleeding events

Year	n	Returns (cumulative)			Bred elsewhere in colony	Total confirmed	Seen elsewhere in colony	Never seen again
		After 1 year	After 2 years	After 3 years				
2009	22	11	12	12	1	13	3	6 ^a
2010	31	14	19	20	0	20	1 ^b	10 ^c
2011	30	13	14	NA	1	15	8 ^d	7 ^e

Number of burrows dropped in subsequent years due to burrow collapse or grid marker loss during the winter: ^a 3; ^b 1; ^c 4; ^d 1; ^e 4.

21%–37%, respectively) than in most other puffin colonies where researchers use similar burrow monitoring protocols that limit disturbance in early incubation (e.g. in Hornøy, Norway, breeding success as 62%–66% [Barrett *et al.* 1987] and on Skomer Island, Wales, it was 64% [Ashcroft 1979]), including MSI's 18-year mean (62%; A.W. Diamond, unpubl. data), suggesting that other factors at Great Island may also have influenced puffin breeding success. The hatching success in disturbed burrows at Great Island (56%–65%) during those study years (1968–1969, 1992) was also lower than those in the similarly handled colonies (Norway, Wales, and MSI) in all corresponding years except 2012 (47.4%), and than the hatching success in the experimental burrows, where disturbance was much higher, in all years of this study. Low breeding success, regardless of the conservative handling regime, implies an underlying condition or conditions that may have predisposed the Atlantic Puffins at Great Island to abandonment.

Our study was biased towards early-breeding birds, which are likely in better condition than their later-breeding counterparts. The success rates of puffins in this study might therefore not be comparable to rates in other studies in which researchers handled both early- and late-incubating puffins; however, within our study all experimental and control burrows were sampled during the same period of incubation, allowing comparisons within years. In addition to the lack of apparent effects on in-year reproductive success, our disturbance did not appear to have any large effect on return rates of puffins in subsequent years, as return rates were at or above 50% in the first three years of the experiment. As we do not measure rates of return in our regular productivity burrows we have no control data from MSI we can use in comparison. However, others have studied this effect and found varying rates of return to breeding burrows. Harris and Wanless (2011) observed that only ~2% of returning couples changed burrows from one year to the next, whereas Ashcroft (1979) found that 7.8% of birds did not return to their burrow the following year, and Davidson (1994) found 8%–16% of returning pairs switched burrows. Further, “divorce” occurs in 7%–9% of pairings (Ashcroft 1979, Creelman & Storey 1991, Harris & Wanless 2011), which, in addition to normal burrow return-rate variability described above, could account for the rates of return to the same burrow exhibited by our blood-sampled birds.

Disturbance history and ecological conditions may also explain variation in puffin response to researcher activities. Rodway *et al.* (1996) and Baillie (2001) acknowledged that disturbance regimes had different effects on puffin breeding success rates in different colonies. In contrast to other colonies, MSI puffins have experienced researchers' extended activities yearly since 1995, as well as almost daily short-term disturbance by tourists walking through the colony to view birds from blinds, and as a result are habituated to humans (Viblan *et al.* 2012), perhaps decreasing the impact of human presence and disturbance within the colony.

CONCLUSIONS

The prevailing paradigm — that Atlantic Puffins are particularly sensitive to disturbance during incubation — evidently does not apply to the colony on Machias Seal Island. This unexpected discovery opens an opportunity to investigate pre-breeding conditions affecting yearly variation in breeding success. We encourage researchers to continue to exercise caution in all activities that disturb breeding seabirds, but we also suggest designing preliminary studies that test for disturbance effects to

increase our ability to understand why effects specific to species, colonies and disturbances vary so widely. We suggest that carefully designed, disturbance-intensive studies can greatly increase our assessment of the health of the colony, help elucidate the causes and consequences of poor productivity or low survival in seabirds, and enhance management strategies for populations of concern.

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REFERENCES

- ASHCROFT, R.E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. *Ornis Scandinavica* 10: 100–110.
- BAILLIE, S.M. 2001. Atlantic puffin response to changes in capelin abundance in Newfoundland and Labrador: An inter-colony and inter-decade comparison. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- BARRETT, R.T., ANKER-NILSSEN, T., RIKARDBSEN, F., VALDE, K. RØV, N. & VADER, W. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980–1983. *Ornis Scandinavica* 18: 73–83.
- BRETON, A.R. & DIAMOND, A.W. 2014. Annual survival of adult Atlantic Puffins *Fratercula arctica* is positively correlated with Herring *Clupea harengus* availability. *Ibis* 156: 35–47.
- CAREY, M.J. 2009. The effects of investigator disturbance on procellariiform seabirds: A review. *New Zealand Journal of Zoology* 36: 367–377.
- CARNEY, K.M. & SYDEMAN, W.J. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.
- CREELMAN, E. & STOREY, A.E. 1991. Sex differences in reproductive behavior of Atlantic Puffins. *Condor* 93: 390–398.
- CRISCUOLO, F. 2001. Does blood sampling during incubation induce nest desertion in the female Common Eider *Somateria mollissima*. *Marine Ornithology* 29: 47–50.
- DAVIDSON, F. 1994. The ecology of the puffin *Fratercula arctica*. D. Phil. thesis, University of Oxford, Oxford, UK (cited by Harris and Wanless 2011).
- DIAMOND, A.W. & DEVLIN, C.M. 2003. Seabirds as indicators of changes in marine ecosystems: Ecological monitoring on Machias Seal Island. *Environmental Monitoring and Assessment* 88: 153–175.
- FRIARS, K.A. & DIAMOND, A.W. 2011. Predicting the sex of Atlantic Puffins, *Fratercula arctica*, by discriminant analysis. *Waterbirds* 34: 304–311.
- GASTON, A.J., BERTRAM, D.F., BOYNE, A.W., CHARDINE, J.W., DAVOREN, G., DIAMOND, A.W., HEDD, A., MONTEVECCHI, W.A., HIPFNER, J.M., LEMON, M.J.F., MALLORY, M.L., RAIL, J.-F. & ROBERTSON, G.R. 2009. Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. *Environmental Reviews* 17: 267–286.
- HARRIS, M.P., BOGDANOVA, M.I., DAUNT, F. & WANLESS, S. 2012. Using GPS technology to assess feeding areas of Atlantic Puffins *Fratercula arctica*. *Ringing & Migration* 27: 43–49.
- HARRIS, M.P. & WANLESS, S. 2011. The Puffin. London, UK: T & AD Poyser.

- IBÁÑEZ-ÁLAMO, J.D., SANLLORENTE, O. & SOLER, M. 2012. The impact of researcher disturbance on nest predation rates: A meta-analysis. *Ibis* 154: 5–14.
- NETTLESHIP, D.N. 1972. Breeding success of the common puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs* 42: 239.
- REGEHR, H.M. & RODWAY, M.S. 1999. Seabird breeding performance during two years of delayed capelin arrival in the Northwest Atlantic: A multi-species comparison. *Waterbirds* 22: 60–67.
- RODWAY, M.S., MONTEVECCHI, W.A. & CHARDINE, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic Puffins *Fratercula arctica*. *Biological Conservation* 76: 311–319.
- VIBLANC, V.A., SMITH, A.D. GINESTE, B. & GROSCOLAS, R. 2012. Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC Ecology* 12: 10.
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