

STUDIES ON PATROLLING FLIGHTS AND ‘CANCELLED LANDINGS’ BY THE NORTHERN FULMAR (*FULMARUS GLACIALIS*) ON LUNDY

by

ARE VÆRØYVIK*, SUNYEONG LEE, EUAN BIELBY AND SHAYAN SHOAEE,

Biological Sciences, University of Exeter, Perry Rd, Exeter EX4 4QG

**corresponding author, email: Værøyvik, Are are.vik@online.no*

ABSTRACT

Northern Fulmars arrive on land around January to prepare for the breeding season. Energy conservation is important during this time, but they perform seemingly purposeless “patrolling flights”. We observed patrolling flights of the fulmars along Gannet’s Rock, Lundy Island, for six days during the pre-laying period, and noticed a novel behaviour, “cancelled landings”, performed during the flights. We explored the possibility that these flights, and the cancelled landings, play a role in mate-seeking. We propose that the flights represent an energetically costly ‘honest signal’ leading to courtship, and that performing cancelled landings represent approaching a potential mate. Results showed that longer flight durations predicted landing in a different location compared to the take-off location. However, this effect was mediated by the effect of performing cancelled landings. Furthermore, longer flights were not predictive of landing next to a conspecific, or of performing courtship behaviours. Cancelled landings were predictive of landing next to a conspecific, but not of performing courtship behaviours. This almost unstudied behaviour of patrolling flights may help give insight into the breeding status of fulmar populations, although longer studies are needed to confirm the basis of the behaviour.

Key words: *Northern Fulmar, patrolling flights, breeding, courtship, mate-seeking*

INTRODUCTION

Most seabirds spend their lives predominantly at sea, but must come to land to breed (Ballance, 2007). Such birds spend their winters alone and conjoin at their breeding sites to find mates and produce offspring (Hunter, 1999). The Northern Fulmar (*Fulmarus glacialis*) belongs to this category, nesting and breeding on cliff shelves and ledges in the Northern Atlantic, Northern Pacific, and High Arctic (Hatch & Nettleship, 1998). As a monogamous species, Northern Fulmars generally retain their mate- and nest-site across breeding seasons (Carrick & Dunnet, 1954, Ollason & Dunnet, 1978, Warham, 1964). However, extra-pair copulations can occur, although rarely (Hunter *et al.*, 1992), and can be initiated by both males and females (Hatch, 1987).

During the breeding season, Northern Fulmars occasionally depart from the cliffside to embark on foraging journeys that can span hundreds of kilometres (Dunnet & Ollason, 1982, Edwards *et al.*, 2013). They have specialised adaptations for minimising the energy costs of such flights, such as lower basal metabolic rates compared to other seabirds (Bryant & Furness, 1995). They also predominantly employ gliding flight when on foraging journeys (Alerstam *et al.*, 1993), giving them lower at-sea metabolic rates than seabirds that rely on other flying techniques such as flapping flight or pursuit diving (Birt-Friesen *et al.*, 1989), especially during windy conditions (Furness & Bryant, 1996). Such energy conserving measures are especially relevant prior to egg-laying, when Northern Fulmars require substantial endogenous reserves to support on-land activities such as nest maintenance, and pair-bonding and courtship behaviours (Mallory & Forbes, 2008).

Interestingly, Halle (1979) describes a breeding-season behaviour of the Northern Fulmar that seemingly spends energy for no obvious purpose. Termed by him as “patrolling flights” they occur within a restricted space along the cliffside, and consist of riding the wind back and forth, side-to-side, using the turbulence of the updraft. They require great dexterity and rely on frequent adjustments of the wings and tail to respond appropriately to the winds.

Surprisingly, there seems to be no other research, or even mention of this behaviour in the literature. Halle (1979) suggests patrolling flights to be a pure pastime. Birds may at



Plate 1: Fulmar in flight near a Lundy cliff © Richard Campey.



Plate 2: Fulmar pair at a nest site on Lundy © Richard Campey.

times perform behaviours “for fun” (Emery & Clayton, 2015) but given the importance of conserving energy reserves during the pre-laying period, it seems likely that these repetitive behaviours have an adaptive significance beyond mere leisure.

We studied fulmars nesting on Gannet’s Rock on Lundy Island in 2024 between April 27th and May 3rd, before their egg-laying period (Fisher, 1966) to investigate their patrolling flights. During preliminary observations, we made similar observations as those described by Halle (1979), where individuals would regularly perform seemingly purposeless flights outside and around the nest-sites on the cliff shelves before landing and taking off again shortly after. Unlike Halle’s (1979) descriptions, we mainly observed figure-of-eight-like flight patterns in front of the cliff shelves, often sailing over the various nest-sites at the intersection of the figure-of-eight shape. Additionally, we noticed that they frequently appeared to attempt landing at a certain spot occupied by one or more conspecifics, slowing down and extending their legs, but then cancelling at the last second and continuing their figure-of-eight-like flights. In some cases, where multiple cancelled landings were performed at the same site during a single flight, the behaviour seemed almost ritualistic.

Given the limited pre-existing information about this behaviour, many equally justifiable hypotheses could be explored. For instance, it could be posited that it serves some form of social function, or that it is a way for immature birds to practice their flying. It may be that the patrolling flights are linked to their breeding activities. Since the pre-laying period is characterised by mating and breeding behaviours (Mallory & Forbes, 2008), it seems plausible that these flights serve some purpose in mate-finding. We suggest that the flights themselves could represent an energetically costly honest signal (Zahavi, 1975). Fulmar chick survival is highly dependent on male parental investment (Hatch, 1987), so patrolling flights may serve as a signal of their adeptness at performing flights as an indicator of future foraging success, similarly to how some female passerines use male

song rate to assess their ability to feed their chicks (e.g., Hofstad *et al.*, 2002, Welling *et al.*, 1997). Based on the consistent observations of cancelled landings at occupied nest-sites, we propose that this behaviour may represent approaching a potential mate. Relying on the assumption that Northern Fulmars are mate- and nest-site faithful (Carrick & Dunnet, 1954, Ollason & Dunnet, 1978, Warham, 1964), and that extra-pair copulations are rare (Hunter *et al.*, 1992), we considered the act of landing in a different location than the take-off location to represent being unpaired and seeking to find a mate. We also recorded the act of landing next to a conspecific and performing any of the three courtship behaviours (bill-fencing, bill-opening, and head-swinging) as further indicators of mate-seeking.

METHODS

We investigated the potential significance of two aspects of patrolling flights by fulmars: (1) flight duration, (2) the performance of cancelled landings.

Subjects

The study was on the fulmar population nesting on Gannet's Rock on Lundy Island. Daily counts suggested there were approximately 30 individuals during the time of the study. Individuals were not identified or sexed. The observations were made a few weeks before the population was expected to lay eggs.

Procedure

Individual fulmars were observed over six days through focal follows performed by four observers. Initially, the four observers split up into two groups, in which one observer performed the focal follows, using no equipment during flight, and 8x magnification binoculars when the individual was landed, while communicating their observations to the other observer, who recorded the data. Data were recorded using the "Timestamped Field Data" app from Neukadye on an iPad. This allowed for touch-based recording of flight durations and the different variables. However, from day 4-6, three observers performed both jobs of observing and logging data, as this was made possible through the acquisition of another device with the "Timestamped Field Data" app. Here, the three observers used binoculars to perform the focal follows, while the fourth observer assisted with observing behaviours performed while landed.

A focal follow was initiated by the take-off of an individual, after which one of the observers exclaimed that they were following this individual. A focal follow was concluded: (1) after the individual had performed three flights, to promote capturing a wider range of the population, (2) when it had remained landed for five minutes, to promote the acquisition of data from more flights, (3) or when it went out of sight, or was suspected to be mixed up with another individual (in this case the recordings from the current flight were discarded). To promote reliability, we defined the behavioural variables prior to the observations, and practiced recording these variables in concordance with our definitions on day 1. We attempted to avoid pseudo replication by clearly communicating which experimenter observed which individual, and by tracing the observed individual with a pointed finger while in flight. However, given the limited number of individuals each one was likely recorded more than once. All variables recorded are defined and described in Table 1.

Table 1: Descriptions of the variables used in the present study.

Variable	Description
Flight duration Continuous, independent variable	Duration of individual flights, starting from take-off until landing. Measured in seconds.
Landing location Binary, dependent variable	Whether the focal individual landed in the same location as it took off from, or a different location, as judged by the observer's vision and memory. Recorded as "different location" (0) or "same location" (1).
Landing context Binary, dependent variable	Whether the focal individual landed next to a conspecific, or alone. The individual was considered to have landed next to a conspecific if it was perceived by the observer to be less than two "fulmar lengths" (a fulmar's length as seen from the side) away from the nearest conspecific, and alone if two or more fulmar lengths away from the nearest conspecific. Recorded as not alone (0) or alone (1).
Cancelled landing Binary, independent variable	When an individual initiated landing by breaking and extending its legs, sometimes lightly touching the surface with its feet, but cancelled the landing last second and continued flying. Only occurred at occupied nest-sites. Recorded as did not (0) or did (1) perform one or more cancelled landings during a flight.
Courtship behaviours Binary, dependent variable	Whether an individual performed a courtship behaviour following a patrolling flight. Recorded as did not (0) or did (1) perform either of the three following courtship behaviours: Bill-fencing: individual rubbed bills with another individual up and down both sides alternately (described in Luders, 1977). Bill-opening: individual performed forwards neck-extension with its bill wide open (described in Nelson and Baird, 2001). Head-swinging: individual performed side-to-side, or up-and-down head movements with its bill closed. (described in Luders, 1977).

Statistical Analysis

Data was analysed using the programming language “R” in RStudio. Logistic regression analyses assessed relationships between predictor variables flight duration and performing cancelled landings and outcome variables landing location, landing context, and courtship behaviours. The predictors were divided into separate models due to collinearity. The model assessing the relationship between performing cancelled landings and landing location violated assumptions of logistic regression. This relationship was instead assessed using a Fisher’s exact test, and the direction of the relationship was inferred graphically. A *post-hoc logistic regression mediation analysis using Baron and Kenny’s (1986) four-step method* was conducted to assess whether the effect of flight duration on landing location was mediated by the performance of cancelled landings. Figure 1 was produced with the “ggplot2” package in RStudio; Figures 2 and 3 were produced in Excel; Figure 4 was produced in Word.

RESULTS

Longer flight durations predicted landing location but not landing context or performing courtship behaviours. The output from the logistic regression models is presented in Table 2. The relationship between flight duration and landing location is illustrated in Figure 1.

Figure 1: Illustration showing the difference in flight duration (measured in seconds) between flights concluded by landing in the same and different location compared to the take-off location.

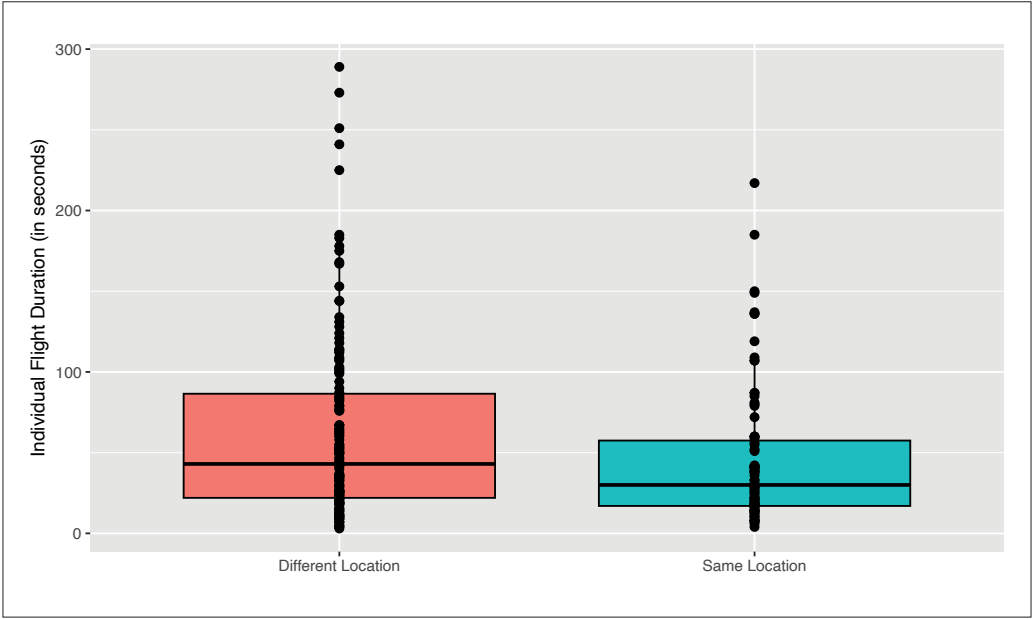


Table 2: Effects of flight duration on the different outcome variables. The model for the effect of flight duration on landing location fits significantly better than the null model ($X^2_1 = 5.68, p = 0.017$).

Flight Duration	b ± s.e.	Wald Z	df	p	OR	95% CI
Land Location	-0.007 ± 0.003	-2.242	1	0.025	0.99	0.987-0.999
Land Context	0.004 ± 0.003	1.100	1	0.271		
Courtship	0.001 ± 0.003	0.314	1	0.754		

Did performing cancelled landings predict landing location, landing context, or performing courtship behaviours?

As derived from the logistic regression models, performing cancelled landings predicted landing context (relationship illustrated in Figure 2), but not performing courtship behaviours. The output from the logistic regression models is shown in Table 3. As derived from the Fisher's exact test, performing cancelled landings was significantly associated with landing location ($p = 0.002$, relationship illustrated in Figure 3). Descriptive statistics of all variables are presented in Table 4.

Table 3: Effects of performance of cancelled landings on the different outcome variables. The model for the effect of performance of cancelled landings on landing context fits significantly better than the null model ($X^2_{21} = 4.64, p = 0.031$).

Cancelled Landing	b ± s.e.	Wald Z	df	p	OR	95% CI
Land Context	0.628 ± 0.293	2.143	1	0.032	1.87	1.058-3.343
Courtship	0.250 ± 0.292	0.856	1	0.392		

Figure 2: Illustration showing that flights with cancelled landings were more often concluded by landing alone, and flights without cancelled landings were more often concluded with landing next to a conspecific.

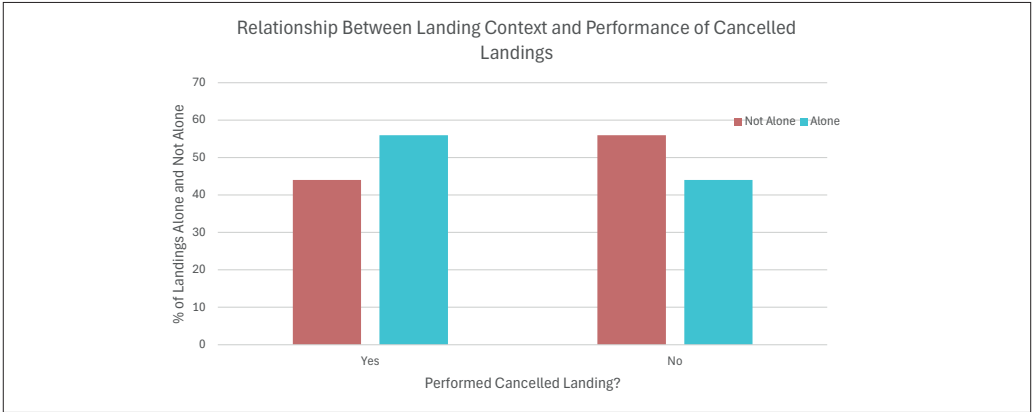


Figure 3: Illustration showing that the difference between landing in the same and different location compared to the take-off location was much larger in flights that featured cancelled landings. Flights were concluded with landing in a different location more frequently after having performed a cancelled landing.

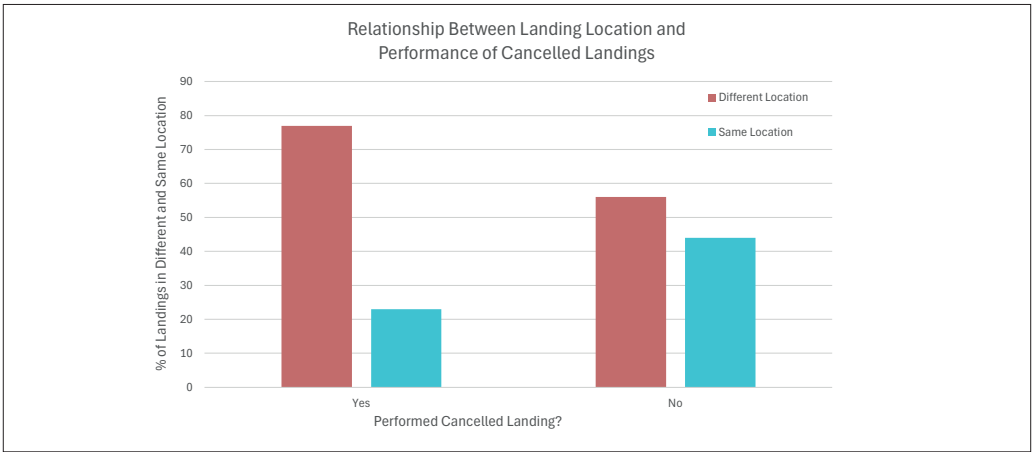


Table 4: Descriptive statistics of all variables.

Variable	n	Min	Max	Mean	SD
Flight Duration	229	3	289	56.03	53.33
Land Location	229	0	1	0.38	0.49
Land Context	229	0	1	0.48	0.50
Cancelled landing	206	0	1	0.36	0.48
Courtship	206	0	1	0.53	0.50

Was the effect of flight duration on landing location mediated by the performance of cancelled landings?

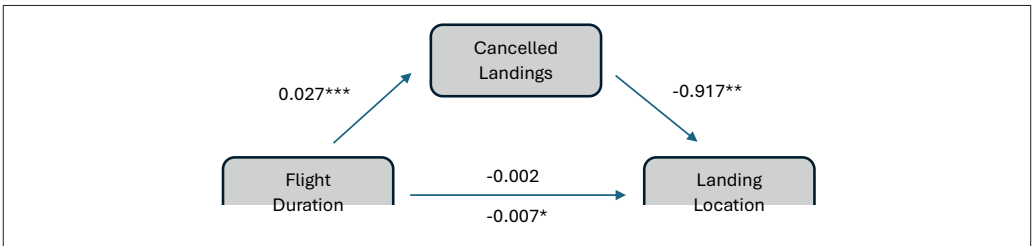
Step 1: Flight duration was significantly correlated with landing location ($b \pm s.e. = -0.007 \pm 0.003$, Wald $Z = -2.242$, $df = 1$, $p = 0.025$).

Step 2: Flight duration was significantly correlated with the performance of cancelled landings ($b \pm s.e. = 0.027 \pm 0.004$, Wald $Z = 6.103$, $df = 1$, $p = <0.001$). The model was inevitably affected by multicollinearity as the two predictors were significantly correlated, and there was evidence of non-linearity in the logit ($b \pm s.e. = -0.025 \pm 0.009$, Wald $Z = -2.702$, $df = 2$, $p = 0.007$).

Step 3: The performance of cancelled landings was significantly correlated with landing location ($b \pm s.e. = -0.917 \pm 0.374$, Wald $Z = -2.449$, $df = 2$, $p = 0.014$).

Step 4: The performance of cancelled landings mediated the relationship between flight duration and landing location ($b \pm s.e. = -0.002 \pm 0.004$, Wald $Z = -0.433$, $df = 2$, $p = 0.665$). The Sobel test (Sobel, 1982) for the indirect effect of cancelled landings was significant ($z = 2.25$, $p = 0.025$).

Figure 4: Directed Acyclic Graph (DAG) showing that the performance of cancelled landings mediated the relationship between individual flight duration and landing location.



DISCUSSION

We found that longer flight durations were predictive of landing in a different location compared to the take-off location, but not of landing next to a conspecific, or of performing courtship behaviours. Performing cancelled landings was predictive of landing in a different location compared to the take-off location, and of landing alone, but not of performing courtship behaviours. These results only partly confirm our initial hypotheses. In the following paragraphs, we provide possible interpretations of these findings.

Our hypothesis that longer flights predicted landing in a different location compared to the take-off location was confirmed. However, since longer flights did not predict landing next to a conspecific, or performing courtship behaviours, it seems unlikely that they are related to mate-seeking. Therefore, our suggestion that patrolling flights represent an energetically costly honest signal of future foraging success is likely to be incorrect. However, it remains interesting as to why longer flights predicted landing in a different location. It is possible that instead of mate-seeking, patrolling flights serve the purpose of scouting the cliffside for potential nest-sites, and that landing in a different location represents finding a suitable nest-site. Finding ideal nest-sites is likely to be important for fulmars as it promotes successful egg-hatching (Mallory & Forbes, 2011). Thus, individuals that land in a different location may simply have had more time to scout the cliffside for a suitable nest-site. However, this interpretation is problematic because it leaves the purpose of shorter flights unexplained.

Why should an individual stop their patrolling flight if they have not found what they are looking for? It is possible that shorter flights are simply thwarted by other factors, such as energy levels, or from being too energetically costly due to lack of wind or updraft. Indeed, wind facilitates less costly flight in the Northern Fulmar (Furness & Bryant, 1996).

Alternatively, these flights may serve a different purpose altogether. Logically, longer flights would allow more time to perform cancelled landings. Therefore, we suspected that the significant effect of flight duration on landing location may have been mediated by the effect of performing cancelled landings. To assess this possibility, we conducted a logistic regression mediation analysis using Baron and Kenny's (1986) four-step method, which showed that this was the case. This means that performing cancelled landings was the better predictor of landing in a different location than the take-off location, and that the significant effect of flight duration likely was explained by the effect of performing cancelled landings.

Since fulmars mate for life, and extra-pair copulations are rare, mate-seeking behaviours should also be rare. Although we did not identify individuals, cancelled landings appeared to be a widespread behaviour performed by most members of the colony. If cancelled landings indeed are a common behaviour, this may point to an explanation other than mate-seeking. However, given our finding that performing cancelled landings predicted landing in a different location compared to the take-off location, and landing alone, we will explore the possibility that it does play a role in mate-seeking. Since cancelled landings only occurred over occupied nest-sites, we postulated that individuals performing cancelled landings were "asking" the nest-host for approval to join. Our finding that performing cancelled landings more often led to landing alone, and that not performing cancelled landings more often led to landing next to a conspecific (see Fig 2), provides support for this explanation. It is possible that cancelled landings signify rejection by the host, while landings without cancellation signify approval. However, although significant, the difference between these groups was small. As with landing duration, performing cancelled landings did not predict performing courtship behaviours. It is possible that our selection of courtship behaviours is unsuitable for use as indicators of courtship or mate-seeking. Bill-fencing is suggested to be predominantly performed when females approach lone males (Hatch, 1987), so it is possible that it serves a specific purpose rather than

being a general courtship behaviour. Behaviours often considered indicative of courtship in fulmars are also reported to be involved in hostile interactions, such as site-defence (Luders, 1977, Nelson & Baird, 2001).

Landing in a different location than the take-off location may not be indicative of being unpaired, as we have assumed in the present study. Our recommendation for future studies of Northern Fulmar patrolling flights is to identify each individual of the focal population, and determine their paired status (see Hatch, 1987). Identity- and paired status-data can be compared to establish which individuals are more likely to perform cancelled landings, land in a different location than the take-off location, or perform patrolling flights at all. Identifying individuals may be particularly useful since fulmars have a delayed sexual maturity compared to some other seabirds, with an average age of 9.2 years at first breeding (Ollason & Dunnet, 1978), meaning that there can be many non-breeders present on the cliff (Hatch & Nettleship, 1998). Future studies may also record pre-flight context, such as whether an individual was alone or in a pair before taking off, to better understand whether the flights may be related to mate-seeking or something else. Studies with greater time-budgets could also investigate whether patrolling flights persist after chick hatching. If fulmars continue their patrolling flights after hatching, then this behaviour may be unrelated to mate-seeking. Such studies could also assess associations between aspects of patrolling flights and subsequent success or failure in mate-finding and reproduction. This could be especially useful for uncovering whether cancelled landings indeed represent rejection by the nest-host, and whether landings without cancellations represent approval.

CONCLUSIONS

We have produced exploratory data on the almost unstudied behaviour of the Northern Fulmar patrolling flights. We found a relationship between longer flight durations and landing location which was mediated by performing cancelled landings, and a relationship between performing cancelled landings and landing context. But there was no relationship between flight duration and courtship behaviours, nor between performing cancelled landings and courtship behaviours.

The potential links between performing cancelled landings and mate-seeking require further investigation. Future studies could be longer, enabling identification of the individuals of the focal population and their paired status, to investigate whether some are more likely to participate in the different aspects of patrolling flights, and assess whether there are associations between such aspects of patrolling flights and subsequent success or failure in mate-finding and breeding.

It must also be recognized that there are other potentially valid hypotheses that could also explain the observed behaviour. These could include (a) that the birds undertaking the ‘cancelled landings’ are immature birds of pre-breeding age that are ‘practicing’ breeding behaviour, rather than actively looking for mates; or (b) that the ‘cancelled landings’ play a social function that has nothing to do with mate selection. In addition, the longevity of fulmars and the stability of their pairings means it was not possible to say what proportion of the birds at the Gannet Rock site already had a mate and would not be seeking a breeding partner.

If these flights are indeed linked to breeding behaviours, identifying their role could provide information about individuals' breeding status. For instance, identifying which individuals are actively seeking mates or successfully forming pairs. Such information can be useful in quantifying changes in proportion of successful breeders as an indicator of colony health (Mallory & Forbes, 2013).

We have included an ethogram featuring noteworthy behaviours from our observations (see Appendix), as this is not available in the existing literature. This includes the three behaviours we used in our study to indicate courtship, as well as other behaviours we noticed, and behaviours described in books and research papers. This ethogram could be applied in future Northern Fulmar research.

ACKNOWLEDGEMENTS

We thank our supervisors Dr. Lisa Leaver, Dr. Andrew Higginson, and Ingerid Helgestad for their professional guidance and feedback throughout the project. We also thank the reviewers for their constructive criticisms, which we have tried to address. We also thank the University of Exeter for providing us with the necessary equipment to conduct our study.

REFERENCES

- Alerstam, T., Gudmundsson, G. A., & Larsson, B. (1993). Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 340(1291), 55-67. <https://doi.org/10.1098/rstb.1993.0048>
- Ballance, L. T. (2007). Understanding seabirds at sea: why and how? *Marine Ornithology*, 35, 127-135. https://digitalcommons.usf.edu/marine_ornithology/vol35/iss2/7
- Baron, R. M., & Kenny, D. A. (1986). The moderator–mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *Journal of personality and social psychology*, 51(6), 1173. <https://doi.org/10.1037/0022-3514.51.6.1173>
- Birt-Friesen, V. L., Montevecchi, W. A., Cairns, D. K., & Macko, S. A. (1989). Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology*, 70(2), 357-367. <https://doi.org/10.2307/1937540>
- Bryant, D. M., & Furness, R. W. (1995). Basal metabolic rates of North Atlantic seabirds. *Ibis*, 137(2), 219–226. <https://doi.org/10.1111/j.1474-919x.1995.tb03242.x>
- Carrick, R., & Dunnet, G. M. (1954). Breeding of the Fulmar *Fulmarus glacialis*. *Ibis*, 96(3), 356-370. <https://doi.org/10.1111/j.1474-919x.1954.tb02329.x>
- Dunnet, G. M., & Ollason, J. C. (1982). The feeding dispersal of fulmars *Fulmarus glacialis* in the breeding season. *Ibis*, 124(3), 359-361. <https://doi.org/10.1111/j.1474-919x.1982.tb03785.x>
- Edwards, E. W., Quinn, L. R., Wakefield, E. D., Miller, P. I., & Thompson, P. M. (2013). Tracking a northern fulmar from a Scottish nesting site to the Charlie-Gibbs Fracture Zone: Evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites. *Deep Sea Research Part II: Topical Studies in Oceanography*, 98, 438-444. <https://doi.org/10.1016/j.dsr2.2013.04.011>

- Emery, N. J., & Clayton, N. S. (2015). Do birds have the capacity for fun?. *Current Biology*, 25(1), R16-R20. <https://doi.org/10.1016/j.cub.2014.09.020>
- Fisher, J. (1966). The Fulmar population of Britain and Ireland, 1959. *Bird Study*, 13(1), 5–76. <https://doi.org/10.1080/00063656609476107>
- Furness, R. W., & Bryant, D. M. (1996). Effect of Wind on Field Metabolic Rates of Breeding Northern Fulmars. *Ecology*, 77(4), 1181–1188. <https://doi.org/10.2307/2265587>
- Halle, L. J. (1979). The Flight of Seabirds. *The Virginia Quarterly Review*, 55(1), 22-40. <https://www.jstor.org/stable/26436364>
- Hatch, S. A. (1987). Copulation and mate guarding in the northern fulmar. *The Auk*, 104(3), 450-461. <https://doi.org/10.2307/4087544>
- Hatch, S. A., & Nettleship, D. N. (1998). Northern fulmar (*Fulmarus glacialis*). In Poole, A., & Gill, F. (Eds.), *The birds of North America*, No. 361 (pp. 1-32). The Birds of North America, Inc., Philadelphia, PA. <https://doi.org/10.2173/tbna.361.p>
- Hofstad, E., Espmark, Y., Moksnes, A., Haugan, T., & Ingebrigtsen, M. (2002). The relationship between song performance and male quality in snow buntings (*Plectrophenax nivalis*). *Canadian Journal of Zoology*, 80(3), 524-531. <https://doi.org/10.1139/z02-033>
- Hunter, F. M. (1999). On the function of pre-laying breeding site attendance in the northern fulmar *Fulmarus glacialis*. *Atlantic seabirds*, 1(1), 3-16. <https://natuurtijdschriften.nl/pub/546063/ASB1999001001002.pdf>
- Hunter, F. M., Burke, T., & Watts, S. E. (1992). Frequent copulation as a method of paternity assurance in the northern fulmar. *Animal Behaviour*, 44(1), 149–156. [https://doi.org/10.1016/S0003-3472\(05\)80764-X](https://doi.org/10.1016/S0003-3472(05)80764-X)
- Luders, D. J. (1977). Behaviour of Antarctic petrels and Antarctic fulmars before laying. *Emu*, 77(4), 208-214. <https://doi.org/10.1071/MU9770208>
- Mallory, M. L., & Forbes, M. R. (2008). Costly pre-laying behaviours and physiological expenditures by northern fulmars in the High Arctic. *Écoscience*, 15(4), 545-554. <https://doi.org/10.2980/15-4-3187>
- Mallory, M. L., & Forbes, M. R. (2011). Nest shelter predicts nesting success but not nesting phenology or parental behaviors in high arctic Northern Fulmars *Fulmarus glacialis*. *Journal of Ornithology*, 152, 119-126. <https://doi.org/10.1007/s10336-010-0556-2>
- Mallory, M. L., & Forbes, M. R. (2013). Behavioural and energetic constraints of reproduction: Distinguishing breeding from non-breeding northern fulmars at their colony. *Écoscience*, 20(1), 48-54. <https://doi.org/10.2980/20-1-3552>
- Microsoft Corporation. (2018). *Microsoft Excel*. Retrieved from <https://office.microsoft.com/excel>
- Microsoft Corporation. (2018). *Microsoft Word*. Retrieved from <https://office.microsoft.com/word>
- Nelson, J. B., & Baird, P. H. (2001). Seabird communication and displays. In Schreiber, E. A., & Burger, J. (Eds.), *Biology of marine birds* (pp. 307-358). CRC Press: Boca Raton, FL. <https://doi.org/10.1201/9781420036305>
- Neukadye, LLC. (2023). *Timestamped Field Notes* (Version 4.9) [Mobile app]. Apple Store. <https://apps.apple.com/us/app/timestamped-field-notes/id521505393>
- Ollason, J. C., & Dunnet, G. M. (1978). Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. *The Journal of Animal Ecology*, 961-976. <https://doi.org/10.2307/3681>

Posit team (2024). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL <http://www.posit.co/>.

Sobel, M. E. (1982). Asymptotic confidence intervals for indirect effects in structural equation models. *Sociological Methodology*, Vol. 13, 290-312. <https://doi.org/10.2307/270723>

Warham, J. (1964). Breeding behaviour in the Procellariiformes. In Carrick, R., Holdgate, M. & Prevost, J. (Eds.), *Biologique Antarctique* (pp. 389-394). Paris, Hermann.

Welling, P. P., Ryttonen, S. O., Koivula, K. T., & Orell, M. I. (1997). Song rate correlates with paternal care and survival in willow tits: Advertisement of male quality?. *Behaviour*, 134(11-12), 891-904. <https://doi.org/10.1163/156853997x00214>

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, <https://ggplot2.tidyverse.org>.

Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of theoretical Biology*, 53(1), 205-214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)

Appendix: Ethogram featuring noteworthy behaviours of the Northern Fulmar noted during the study on Lundy

Behaviour		Description
State	Resting	Individual sits with its wings folded and its breast resting on its feet. In paired birds, resting positions can vary and include face-to-face, half-face, side-by-side, or head-to-tail orientations.
State	Flying	Aerial locomotion
Event	Cancelled landing	Individual initiates landing by braking and extending legs, but cancels last second, sometimes lightly tapping the surface with their feet, and continues flying.
Event	Bill-fencing	Two individuals rub their bills together along both sides alternately.
Event	Nest-clearing	Individual removes materials from its nest by digging with their feet.
Event	Bill-opening	Individual performs forwards neck- extension with widely open bill.
Event	Head-swing	Individual moves its head from side to side. This movement is generally accompanied by raising its head and/or opening its bill.
Event	Head-tossing	Individual repeatedly throws its head back, usually accompanied by calling.
Event	Oil-ejection	Individual ejects stomach oil from its mouth, usually preceded by high-pitched sounds.
Event	Bowing	Individual moves its head up and down.
Event	Mating	The male mounts the female, often stroking her bill or nibbling the nape of her neck.
Event	Preening	Individual grooms its feathers using the bill.
Event	Allopreening	Individual nibbles head, cheeks, neck, throat or flanks of its partner.